

THE MOVEMENT PATTERNS OF FREE-RANGING ANIMALS

NEW THEORY AND METHODS OF STUDY ILLUSTRATED BY COMPARISONS OF THE  
ROUTES OF TRAVEL ASSOCIATED WITH RESIDENCY, TRANSIENCY AND EXPERIMEN-  
TAL DISPLACEMENT IN A POPULATION OF EASTERN BOX TURTLES (TERRAPENE C.  
CAROLINA)

by

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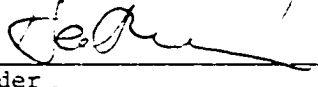
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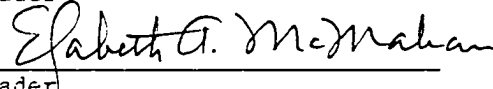
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**STEPHEN P. HALL.** The movement patterns of free-ranging animals: new theory and methods of study illustrated by a comparison of the routes of travel associated with residency, transiency, and experimental displacement in a population of eastern box turtles (Terrapene c. carolina) (Under the direction of R. **HAVEN WILEY.**)

Continuous tracking methods, including radio-telemetry and spool-trailer techniques, provide data that can be used to understand how movements are organized in time as well as in space. Their potential has been hindered, however, by a lack of analytical methods to handle long sequences of movement. Without such methods, previous studies of home-range, search, and orientation have not achieved an integrated view of movements.

In this study, I present a general model for the control of animals' movements that combines the stochastic properties of random and correlated walks with the organismal properties of decision and orientation. The pattern of movements generated by this model consists of hierarchically nested walks, each of which represents a different level of the organism's control over its movements.

To compare this model with actual movements, I derive two new equations that predict the characteristics of oriented sequences of movement, specifically sequences governed by compass orientation. The first equation relates the distribution of the azimuths of a series of straight-line displacements to the distribution of the turns between them. The second relates mean squared distance of travel to the number of displacements. These equations permit, with some approximations, analysis of routes determined purely by remote tracking, when

little or no information is available on the contexts of the movements.

The movement patterns of box turtles provide a rigorous test of both theory and methods, displaying a complex mixture of spatial constraints, extended orientation, and search for varied goals. This complexity is further increased by an apparent wide range of individual differences.

Analysis of their routes reveals that a nested hierarchy of control is indeed present. Stochastic elements are involved as well as deterministic ones, sequential rules as well as positional ones, and taxes as well as kineses. The diversity among individuals, however, is only superficial. The movements of residents within their home ranges are structurally similar to those of transients and of animals experimentally displaced to unfamiliar areas. A simple behavioral model based on vector-navigation can account in a simple way for most, if not all, variations in the movement patterns of box turtles.

## TABLE OF CONTENTS

Acknowledgments .....	vii
I. Introduction .....	1
A. Divisions in the study of animal movements .....	2
B. Trailcraft in modern times .....	9
C. The home range paradigm .....	11
D. The search paradigm .....	22
E. The orientation paradigm .....	36
F. Stochastic walk models .....	46
G. The box turtle as a subject for movement studies .....	62
H. Thesis and hypotheses .....	80
II. Methods, Materials, Study Site, and Population .....	85
A. Trailing .....	86
B. Surveying .....	92
C. Traverse adjustments and cartography .....	96
D. Description of the study site .....	103
E. Description of the subjects .....	108
III. Volitional Walks .....	118
A. The reality underlying an organismal walk .....	119
B. The intrinsic movement tendencies of an organism .....	123
C. Directional dominance and orientational fields .....	126
D. Course deflections as stochastic and behavioral events ..	144
E. Hierarchies of route control .....	162
IV. Mathematical Analysis of Vector Sequences .....	169
A. Transformation of an observed series of steps into a pure sequence of deflections .....	172
B. The basic features of a menotactic walk .....	182
C. The nature of the turn angles in a menotactic walk .....	191
D. The mean squared distances of travel in a menotactic walk .....	202
V. Application of Menotactic Walk Analysis to Telemetric Data ..	224
A. The limitations of movement data collected by telemetric methods .....	225
B. The properties of steps in an artificial partition .....	227
C. Single sequence tests for artificially determined walks ..	238
D. Mean squared distance analysis of artificially determined walks .....	256



VI. Results .....	264
A. Analysis of the 25 foot partition .....	265
B. Analysis of higher level partitions .....	338
VII. Discussion .....	398
A. Evidence for the discrete, hierarchical nature of box turtle routes of travel .....	399
B. Hypotheses concerning the orientational structure of the routes .....	411
C. Hypotheses for the search functions of the routes .....	443
D. Hypotheses concerning the route structure of home range .	452
E. Conclusions: the prospects for a unified study of animal movements .....	469
Literature Cited .....	483
Appendix I. Symbols .....	506

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Helmut Mueller, founder of the behavior group at UNC, also encouraged me by example to maintain continuity with the entire tradition of ethology, not just the truncated version that extends back to 1975, the date of publication of Wilson's Sociobiology. I credit him (and Hinde's Animal Behavior, which Helmut required us all to read) with inspiring the synthetic approach I have attempted, as well as the critical eye I used in evaluating the standard methods of movement study. Any scandalous remarks made in this dissertation, however, are entirely my own, though also in keeping with Helmut's example.

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## **CHAPTER I. INTRODUCTION**

### **A REVIEW AND EVALUATION OF THE STUDY OF ANIMAL MOVEMENTS**

## **LA Divisions in the Study of Animal Movements**

A common thread runs through the studies of home range, search, and orientation. All three disciplines of movement study look for signs of patterning in the routes animals travel through their environment. Their basic assumption is that organismal motility is always under some sort of control, that animals never wander haphazardly but show faithfulness to certain areas, efficiency in their search for hidden resources, or guidance by even the most rarified of spatial cues. All three have the same goals: to discover the rules that govern individual movement decisions and to find the adaptiveness of the overall patterns of movement that result from those decisions.

Despite their underlying similarity of interests, the three branches of movement study have taken widely divergent paths, viewing movement patterns in as radically different ways as did the blind men of Hindustan in describing the various tactile aspects of an elephant. Students of home range, pondering the seemingly solid external surfaces of large-scale movement patterns, have been impressed by spatial permanence and sheer areal extent. Their methods have focused primarily on measuring the girth of the patterns or on mapping all the seemingly fixed bumps and dips of their exterior. Students of search, being caught up in the snaky end of the subject, have emphasized the opposite, the spatial unpredictability of movement patterns and the utility of sequential flexibility in probing for hidden resources. Their methods deal mainly with the dynamic twists and turns of move-

ment sequences and with patterns that can be virtually random with respect to space. Students of orientation, stuck on the projectile-like processes of movement patterns, have also been concerned with dynamic properties, but have found them to be much more rigid and deterministic than those investigated by students of search. Their methods treat routes of travel as simple ballistic trajectories guided towards definite targets by exactly specifiable forces.

The movements of free-ranging animals, of course, encompass all these aspects. During the appetitive phase of movements, the animal can indeed employ the sort of kineses usually associated with search but it may utilize taxes at the same time. Tactic control over searching movements can serve to make the routes either more linear than they would be otherwise or, conversely, more convoluted, as in true area-restricted search. In switching to the consummatory, pursuit phase of movements, the animal will likewise be expected to employ taxes, but the existence of stochastic, deflectional features of the environment or course errors made by the animal itself may prevent its following an ideal, smooth trajectory. Instead there might be kinesis-like effects imposed on the movements. In either phase, memories for places can additionally play a major role. These can serve over the short run simply to make the search path more efficient through more exact avoidance of areas previously traversed, or they may take part in a dead-reckoning form of navigation towards definite but not directly perceived targets. Over the longer run, such memories built up as part of the processes of search and orientation are often incorporated to form the basis for a home range. Since search and orientation are both dynamic processes, the foundations of

home range will thus be constantly shifting. Conversely, home ranges exist to make more routine and thus predictable the processes of search and orientation.

The control of movements can therefore take on a diversity of forms even within the course of a single day's travels; it is sometimes beyond the ability of any one of the three disciplines to account for even a fragment of a route. Clearly a more comprehensive viewpoint is required, a way of standing back from the "elephant" and seeing it as a whole. In addition to discovering how all the various aspects of movement patterns are connected, such a viewpoint would reveal that the whole is not simply the sum of its separate parts but is instead a dynamic, integrated system.

The need for a wider perspective is especially apparent when the movements of free-ranging animals are considered, where the routes of travel and the behavioral and environmental contexts through which they lead are more of the organism's choosing than of the investigator's. If the object of such a study is to see how an animal gives order to its daily life through structuring its overall pattern of movements, then it is neither desirable nor usually feasible to subject the organism to the rigorous experimental controls of orientation studies or to select the context of the movements as is done in both studies of search and home range. What would be desirable is to follow the animal wherever its movements take it, on or off its home range, from searching movements to pursuit, and through one form of taxis to another.

The decision to undertake an integrated investigation of movement patterns was one forced on me by the nature of my subjects. Although I originally set out to map all the specific contexts, both behavioral and environmental, through which box turtles travel, I soon found this to be nearly impossible. For one thing, the turtles were highly reluctant subjects, being always well aware of my presence and quite content to sit and wait for the annoyance to depart. A greater obstacle, however, was the sheer complexity of their movements and the tremendous range of both the individual and group variability they displayed. These were not the simple animals they appeared to be (or if they are, then the complexity of the free-ranging movements of even simple animals has not been sufficiently appreciated). The amount of contextual information needed to account for the differences within even the largest scale patterns, let alone all the twists and turns of the daily paths, seemed simply out of reach.

At the same time, both the quality and quantity of route data I was able to collect using the standard spool-trailer technique of box turtle studies (described in Chapter II) was amazing. This was information that not only shows the fine spatial structure of the movements but was also continuous through spans of weeks, months, or even years. Without any contextual information whatsoever, the patterns evident within the bare routes of travel appeared to contain a wealth of information on all three aspects of movements: stability, efficiency, and directedness. Moreover, they show these features to be quite inextricably interwoven; any one section of a route appears to show the action of all three simultaneously.

In attempting to make full use of this information, I had to look for methods elsewhere than in the traditional areas of study, for reasons that will be discussed in detail in this chapter. Not only were there no analyses applicable to all three areas but those employed by each discipline dealt with only fragments of a route. What I needed was a means of dealing with route data as such, with continuous series of both sequentially and spatially organized movements.

As described in Section I.F, I found a partial answer in the study of stochastic walks. The classic models of the random and correlated walk have proved highly successful in predicting the features of routes associated with the Brownian movements of both molecules and cells. Waser (1976) also demonstrated their value as null models in looking for evidence of spatial constraints on the movements of higher organisms. Their main limitation, however, is that they model essentially non-oriented behavior, where patterns of movements are determined by blind impacts rather than by an organism's orientational decisions.

The second part of the solution came from Mittlestaedt's theory of orientation as a control process (Mittlestaedt, 1964a, b), discussed in Section I.E. By combining the stochastic walk models' notion of discrete "steps" as representing random deflections with the idea of an orientational sollwert acting to bring the animal back on course following a deflection, I developed a theoretical walk model that does do justice to an animal's ability to choose its own routes of travel.

Furthermore, these ideas concerning the structure of oriented movements lead to a larger theory of routes as representing nested hierarchies of walks, each level within which defined by discrete



switches between orientational targets. Here, finally, seemed a theory both complex and flexible enough to embrace all aspects of an animal's movement patterning. As will be discussed in Chapter III, oriented walks taken by themselves serve to show the interrelationship between kineses and taxes while the hierarchical structure of the routes shows the accommodation that is possible between the spatial constraints of home range and the sequential rules involved in search and orientation.

This theory became workable, though, only after the discovery of two equations, presented in Chapter IV, that predict the behavior of long sequences of oriented steps. The first describes the relationship between the directional components of the deflections in a series and the angular differences between them. Where the form of orientation is menotaxis (compass orientation) this equation predicts features of the sample of turn angles between steps based on knowledge of the sample of step azimuths. It thus examines a very common form of movement by using the relationship between the standard variables of the studies of search and orientation, respectively. The second equation examines the behavior of the mean squared sums of the step deflections, and considers both their distance and directional components. Where the form of orientation is menotaxis again, this equation predicts the mean squared distance of travel over a number of steps based on knowledge of the sample of the step components. It thus allows a direct comparison to be made between a widespread form of orientation and a commonly hypothesized form of search, the correlated walk. Furthermore, by looking at distances traveled over a number of steps it permits the detection of spatial constraints,

bringing in the subject matter of home range. The two equations taken together provide not only a way to handle long sequences of movements but also present applications to all three areas of movement study, either separately or combined into an integrated investigation.

As powerful as these equations and underlying theory seem to be, they are still not free of all the limitations of earlier methods of movement analysis. If anything, they actually require more contextual information than ever before, information necessary to define the deflections, targets, steps, and walks.

Even so, I show in Chapter V that approximate methods based on this theory can still go a long way in the investigation of telemetrically acquired data. If nothing else they serve to indicate the critical points where contextual information must be sought and thus economize the effort needed to collect it. More important, even these approximate applications can be used to investigate movement patterns in an integrated way, addressing questions from all three traditional branches of movement study. This approach also allows the asking of completely novel questions, ones that arise most naturally from considering the sort of abundant, detailed, and continuous data now being collected on an impressive variety of species moving through a wide range of circumstances.

## **I.B. Trailcraft in Modern Times**

The need for comprehensive methods for dealing with route data is especially apparent when one reviews the literature on the movement studies that have been done over the past twenty-five years. While methods of keeping track of an animal have improved greatly during that period, methods for interpreting the data they produce have not kept pace.

Prior to 1960, field investigations in all three areas of movement study were typically restricted to working with mere glimpses of their subjects obtained only from time to time. Movement data consequently took the form of a scatter of observation points. If the individual could be kept in view long enough, vanishing bearings or turn-angles could sometimes also be obtained. Studies such as Stickle's (1950) or Murie's (1936) that collected data on continuous movements or trackways stand out against this background but were clearly limited as to the species and circumstances to which their methods could be applied.

After 1960, all this changed. Not only did interest increase concerning the details of animals's routes of travel, as indicated by the studies of Kaufmann (1962), Schaller (1963) and Hall (1963), but new technology greatly widened the scope and opportunities for these kinds of studies. Radar ( Lack and Varley, 1945; Sutter, 1956; Harper, 1957), sonar (Trefethen, 1956; Johnson, 1960), radio-isotope tagging (Godfrey, 1954), aircraft tracking (Griffin and Hock, 1949; Hitchcock, 1952; Michener and Walcott, 1967), and particularly radio-telemetry (for an overview of the early work see the symposia edited by Slater, 1963; 1965) made it possible to track nearly any kind of

organism from mice to whales, bats to homing pigeons, and water-snakes to sharks. Including the organisms studied by more conventional observation, especially primates (Jay, 1965; Mason, 1968; Altman and Altman, 1970) and hymenoptera (Manning, 1956; Pyke, 1978a; Heinrich, 1976), literally hundreds of species now have human (or robot) trackers in relentless pursuit.

In sharp contrast to the quality and quantity of the route data being collected in all these studies are the limitations of the methods by which they are interpreted. Whereas the data are now often obtained as a continuous series of movement vectors, ever more closely approximating the subjects's routes of travel, they are still analyzed as if they were obtained only as mere glimpses of movement: as isolated points, separated vectors, or disassociated collections of two-step fragments of a route. The paradigms of all three disciplines of movement study still belong fundamentally to the pre-1960 era. They only incompletely utilize the abundance of movement information now available.

### **L.C. The Home Range Paradigm**

The study of the association between animals and their individual ranges has developed around the opportunities and limitations of making repeated observations of a subject's location. Studies of avian territoriality have depended on the site-specificity of conspicuous behavior, such as singing, visual display, or fighting, to outline the area held by the individual. Studies of mammalian home range have evolved predominately around the method of live-capture, mark and recapture. In both cases (and in their derivative forms in the study of other groups), large samples of locational data can be acquired but it is frequently not known (nor cared) how the animal moves between sightings or recaptures.

Both paradigms justify this basic limitation by making certain stringent assumptions about the animal's pattern of movements.

(1) The home range encompasses the area where all normal, daily activities are carried out; territory is the defended subset of that region. In the performance of these normal behaviors, a routine pattern of movements is followed (Burt, 1943; Brown, 1962). Specifically, the animal displays a definite tendency to repeat the same route decisions each time it visits a particular site or region within its range.

(2) This routine of movements results in stable range boundaries (Kaufman, 1962; Tanaka, 1963), or, more typically, in a stationary distribution of the probabilities for visiting various points within an only stochastically defined area (Hayne, 1949; Dice and Clark, 1953; Harrison, 1958).

(3) The spatial pattern of visits, the utilization distribution, can be treated as atemporal and non-sequential (Van Winkle, 1975). This follows if movement decisions are believed to depend only on position, not on the prior sequence of movements (Dunn and Gipson, 1977; Macdonald, et. al., 1980). Consequently, observations of an animal at various points within its range can be treated as independent random variables (Hayne, 1949; Dice and Clark, 1953; Calhoun and Casby, 1958; Harrison, 1958; Jennrich and Turner, 1969; Mazurkiewicz, 1969; Koepfle, et. al., 1975; Anderson, 1981; Don and Rennols, 1983). So can the vectors connecting any pair of observation points (Davis, 1953; Brant, 1962; Koepfle, et. al., 1977; Ford and Krumme, 1979).

So strongly have these assumptions been held that even where detailed information is now available on animals's routes of travel, they still determine the form of data analysis. As viewed according to the traditional paradigm of home range studies, the new tracking technologies have their main value only in being more reliable and less disruptive to the animal's normal behavior than earlier methods. The data they produce are treated simply as a more intensive sample of locational "fixes", and it is still the distribution of visits to points in space (Tester and Siniff, 1965; Inglis, et. al., 1979; Banks, et. al., 1975; Macdonald, et. al., 1980), or to sample quadrats (Siniff, 1966; Adams and Davis, 1967; Schneider, et. al., 1971; Voight and Tinline, 1980) that is of primary interest, not the way the points are connected sequentially.

The use of route data in these studies, however, is ironic. The obvious connectedness of the fixes clearly violates the assumption of

independent random sampling that is basic to most analyses of the utilization distribution. The data are hopelessly auto-correlated; even a series of purely random movements will generate a non-random spatial distribution of points.

The few attempts to remedy this problem do so only by disregarding the mounting evidence for the sequential patterning of routes (as found, for example, by Siniff and Jessen, 1969). Dunn and Gipson's (1977) method of analysis, the only one that explicitly accommodates serial-correlation among positional fixes, not only requires that the animal makes its route decisions on the basis of position alone, but that these decisions display a bivariate-normal tendency. In this model, as in the similar ones of Holgate (1971) and Yang (1979), the animal is therefore not allowed to orient its movements over as many as three successive fixes or to show any non-uniform distribution of deflections between fixes. Neither can it use its range in a patchy manner nor in any other way that results in an asymmetric or multimodal utilization distribution.

Although these restrictions are clearly not met by any real animal, for a few species, at least, they may appear to apply if a large enough interval of time separates the fixes. The recommendation of Schoener (1981) and Swihart and Slade (1985a, b) is to use a statistical procedure to first determine the interval where successive fixes no longer show sequential correlation and to use only points separated by that amount of time in estimating the home range by whatever method. Even though Dunn and Gipson's procedure is more accommodating of serial correlation, it too can be applied only if data are collected in the form of independent "bursts" of fixes, trail

fragments separated far enough apart in time to be treated as unconnected.

All this is allowable so long as the basic assumptions of the home range paradigm are still accepted. By disregarding inconvenient detail (or by choosing not to collect it) the situation remains similar to the state that existed prior to the 1960s, when data were still collected by live-trapping or other occasional observation. But throwing great quantities of good data overboard is still not enough to save the situation. Even in the relatively undetailed descriptions obtained in the traditional manner through sightings taken far apart in time and space, there can also be unmistakable signs of sequential patterning. The routes taken through particular parts of the range often display the influence of prior experience with the resources found there (Manning, 1956; Gill and Wolfe, 1977; Kamil, 1978), or with more neutral stimuli such as landmarks or other familiar objects (Shillitoe, 1963). Decisions about which areas to visit may further depend on a daily or seasonal plan of range-use rotation (Martinsen, 1968; Hamilton and Watt, 1970). These reversable or cyclic shifts in range usage can further grade into permanent alterations of size, shape, of location of the overall home range. Such changes also depend upon experience, reflecting either the maturation of the individual or a change in its status or changes within the population or habitat (Stickel, 1946, 1960; Layne, 1954; Calhoun and Webb, 1953; Brown, 1969).

Even at the highest spatial or temporal scale of measurement, sequential rules of movement can thus be as evident as positional rules. Whether or not the data are obtained as continuous routes or



as isolated glimpses, serial correlation among the fixes is an inescapable problem. The simple sequential act of moving from place to place thus creates a dilemma at the very core of the paradigms of home range and territory.

For some researchers, such as Stickel and Warbach (1960) and Ambrose (1969), the problem of higher-order sequentiality meant that home range had to be sampled as intensively and briefly as possible. Movement patterns observed over longer periods of time could not be safely termed a home range since they might actually be composites of several consecutively held ranges. This solution to the problem, however, only intensifies the effects of shorter-term sequential patterns as the price of minimizing those of the longer-term. Furthermore, this solution will also miss any stable, cyclic patterns that the longer-term shifts in range usage may themselves obey (Martinsen, 1968). Despite these evident problems, the tendency to define a home-range using the smallest number of fixes possible has become well entrenched.

For others, such as Brant (1962), the very concept of home range was too protean to be held onto. If one-way shifts in range could not be safely distinguished from reversable or cyclic usage patterns within a greater home range, then the very notion of "routine" movements was in doubt. How could "occasional sallies" outside the home-range be distinguished from the "normal" sampling excursions that precede shifts in patch usage? Brant's recommendation was to give up such distinctions and to use the distances between successive sightings as an index simply of "vagility".

Most researchers of home range, however, have found agnosticism such as Brant's too extreme. Whether or not the operations used to plot home range accurately reflect the "true" home range of the animal, the spatial information they provide is too important to be ignored (Hayne, 1949; Yerger, 1953). Both the animal's current position and its past history of movements will determine, to a large extent, where it will turn up next. Simple indices of vagility, in contrast, are not nearly as informative.

More reasonable are the views of Martinsen (1968), Maza, et. al. (1973), and O'Farrel (1978). They advocated the discarding of the old assumptions of static movement patterns and positionally determined routines but not the concept of home range itself. They looked at an animal's pattern of movement as being as dynamic as any other aspect of behavior, reflecting continuous internal as well as external changes in circumstance. Their definition of "routine" replaces the notion of spatial fixity with one of regularly occurring processes. Routine movements are those normal, everyday or seasonal changes in location that accompany predictable cycles in behavior or environment, or that result from the regular acquisition of new information. The last view also coincides with those of other researchers that exploration and reconnaissance are of routine occurrence, not just limited to occasional excursions out from an already familiar area (Shillitoe, 1963; Sheppe, 1966; Brant and Kavenau, 1964, 1965; and Metzgar, 1973).

While the studies mentioned were relatively advanced in discarding the static view of home range, they still retained the old point-distribution or areal forms of analysis. But those methods are, in fact, no longer appropriate even in providing crude "snapshots" of

home range. Of what value are even instantaneous pictures of essentially protean phenomena? They still depend too much upon the assumption of independent random sampling of spatial behavior, even though their viewpoint implicitly denies this possibility. As a means of analyzing continuous route data, any sort of strictly spatial analysis simply does not do justice to the available information.

Methods that consider the connectedness of the fixes are clearly called for in dynamic models of ranging behavior. The situation is analogous to the investigation of other dynamic behavioral processes where sequential methods are in common use (e.g., Slater, 1973; Cane, 1978). Several studies have, in fact, shown the potential for applying standard sequential analyses to the study of home range.

One avenue has been to apply directly to movement data the methods of contingency table analysis that are common in most investigations of behavioral sequences. Connolly (1979), for instance, found a significantly non-random association between the time of day and the visits to particular quadrats by gray squirrels. Although his methods did not deal with route data as such, his result strongly implied a time-table of range usage and, consequently, a fairly static itinerary of daily routes of travel. Taking a quite different approach, Getty (1981) examined the transition probabilities for movements between quadrats by chipmunks. This method, although more explicit in dealing with movement sequences, failed to find a non-random pattern even though sequential patterns were plainly evident. Getty's explanation of this discrepancy was that a higher-order pattern of space usage (radial foraging) obscured any non-random tendencies at the finer scale of measurement he was examining.

A more general problem in applying these sort of quasi-spatial methods of analysis is that they still presume some degree of fixity in the spatial organization of movements; a significant result is obtained only where the animal has a tendency to repeat a given route decision each time it visits a particular point (or quadrat) in space. Movement patterns that are more strongly determined by sequential rather than spatial rules cannot be distinguished from a purely random process using these approaches. Unfortunately, it is just that sort of pattern that can be expected under a dynamic model of home range.

A much more generally useful approach to route analysis was presented by Siniff and Jessen (1969). In possession of the great volume of detailed movement data being collected at the automated radio-tracking facility at Cedar Creek, they were able to view routes as a series of straight line trajectories rather than as a collection of disjointed fixes. Their perspective was consequently as much sequential in nature as spatial. Their basic data were the distances traveled between successive, equitemporal fixes and the relative angles formed between the pairs of adjacent route segments. For the purposes of analysis, it was completely irrelevant whether or not the subject had ever before passed through a given point (or quadrat). This appeared to be, therefore, an approach with sufficient flexibility to do justice to a new, equally flexible model of home range.

Indeed, their main interest was to model the processes underlying the home range phenomenon. Rather than just theorize about the route decisions that would result in a particular utilization distribution (as was done, for example, by Dunn and Gipson, Holgate, and Yang), they did the reverse: having observed some of the stochastic compo-

nents of route behavior, they then constructed a computer model from these pieces and examined just how realistically the generated movement patterns matched the observed. Their approach was thus very similar to Holling's well-known modelling of predation (Holling, 1965). Using these methods, highly complex hypotheses about behavior can be investigated. For example, Montgomery (1974), using the Siniff and Jessen model as his starting point, studied the effects on pair-bonding in red foxes of various manipulations of hypothetical modes of communication.

Unlike the old models of home range, these process models are subject to far fewer constraints on their assumptions. The problem of serially-correlated data, for instance, is no longer a major hurdle. In fact, one of Siniff and Jessen's basic findings was that route decisions actually are dependent, at least passively, on immediately prior decisions; the heading of any particular route segment was found to be strongly related to that of the one preceding it in the series. Routes of travel were observed that were not solely governed by their position within the home range. Where this finding would have ruled out the use of Dunn and Gipson's method, the relationship between segments was easily accommodated by a component model of ranging behavior.

This approach, however, is not without liabilities. No matter how elaborate the model may be, the question always arises as to whether all the necessary components have been included or whether all the possible interactions between them have been considered. In Siniff and Jessen's pioneering effort, only a very few components were, in fact, included and absolutely no interactions. Step lengths

and the angles between them were treated as both independent of one another and independent among themselves. The choice of step length was simply assumed to have no effect on either the next turning angle or the length of the next step. The same was true with regard to the choice of turning angle. Their model, therefore, did not allow for any form of active orientation, which would involve interactions at least among the angles, if not among the step lengths. Furthermore, except for the boundary constraints also built into the model, no positional determinants of route behavior were considered.

The question for this, as well as for any other component model, is how well does it predict phenomena beyond those that are constructed into it? If there is, in fact, any major flaw in Siniff and Jessen's study, it lies in the method they used in testing their model's validity. While their relatively simple model might actually apply to certain types of home range, their use of the old methods of point-distributional analysis to test its fit to observed data was inappropriate, if not entirely misleading. Not only is there the clearly defined problem of serial correlation among their data, but there is the more important question of whether any purely spatial analysis of movement pattern is sensitive enough to distinguish among different sequential processes. Could there not, in fact, be several widely different sequential models that could generate similar spatial patterns?

This problem is not a trivial one, since it affects the entire concept of a dynamic home range. The fundamental problem for any home range study is the demonstration of spatial constraints on movements. It is not enough simply to show that the animal does not move

at random through a particular region of space. It must be demonstrated that no purely sequential pattern of movements is responsible for the animal's remaining within that area. For a dynamic version of home range, where some drifting of the range is expected over time, spatial constraints might not occur consistently at any particular site or region. Furthermore, over some large scale of measurement, the drifting of range can itself become representative of a purely sequential process. The most general problem for home range studies to solve, therefore, is to determine the largest scale of movements over which some sort of spatial constraints operate. Only after this scale has been found is it reasonable to ask further whether the range constitutes a "home" area or more simply a transiently occupied resource patch.

Because of the possible stochastic nature of the spatial constraints, validation of a model for home-range processes requires a basis for comparison other than that provided by an atemporal, spatial pattern of points. Although the paradigms of search and orientation do provide methods that are freer of these particular problems, I will show that they too have not yet evolved beyond the expectation that samples of movements come in essentially fragmentary packages.

### **I.D. The Search Paradigm**

One major component of the routine activities that define a home range is searching behavior, which comprises all the activities that bring the animal into initial contact with its resources. While the theory of home range gives some general consideration to these activities, the study of search has been carried out mainly in different contexts. Moreover, in several ways the paradigm of search studies is founded upon a nearly opposite set of assumptions from that of home-range.

(1) Whereas the existence of a home range usually infers a basic familiarity by the organism with the location of important environmental features, the definition of search implies a function for movements in the absence of remembered positional information. Whether the animal is searching for food or other resources, mates, new living space, the way home from an excursion, or simply general information about its environment, no perceptual cues are presumed available that would allow a strictly searching animal to steer directly towards its goals.

(2) Whereas the known space of a home range is assumed to have a definite, fixed structure, the space in which search is conceptualized to occur is indeterminate in configuration. Single goals, such as a misplaced home or a vacancy in the social fabric, are treated as if they were located at some random direction and distance from the organism. Multiple goals, such as food items or mates, are treated as though they were randomly distributed in space or occurring in randomly distributed patches. Furthermore, since the goal items themselves may be mobile



or capable of replacing depletions, their positions are indeterminate in time as well as in space.

(3) Whereas the movements within a static home range are assumed to be determined primarily by positional rules, in the dynamic and amorphous space of search, route decisions are seen as mainly sequential in nature. Position is important only in a relative sense rather than in an absolute one. The organism can only be reasonably certain about the places it has just come from. In choosing a next course of travel, the organism may consider its previous sequence of movements but only rarely must it remember the sites it has visited far back in time.

One result of these assumptions is that the methods of analysis used in the study of search patterns have been directed more towards the features of the routes themselves than towards the spaces in which they occur. They are therefore more generally flexible and process-oriented than are those of home range studies.

The emphasis on spatial indeterminacy and positional forgetfulness has, on the other hand, led mainly to the development of a narrow range of semi-random models. Not only is the possible context of a home range usually disregarded, but the methods themselves are mostly blind to alternative hypotheses involving any sort of positional or directional memory. Although the methods used in search studies are sequential, they are usually only incompletely so. If the home range paradigm views movements as constellations of points, the search paradigm typically chops up a route into pairs of consecutive path segments (referred to here as two-step sequences).

The underlying view of movements that fostered this approach had its origin in studies of relatively simple organisms performing relatively uncomplicated searches. Although some degree of sensation and memory was granted to these subjects, their hypothesized primary feature was an inability to detect their search goals at any significant distance away from themselves. Search was thought of as accomplished solely by trial-and-error probings of the immediate surroundings and brought about by a completely undirected series of movements.

The classic description of this model of search was presented by Jennings (1904) for protozoa encountering a zone of aversive conditions. Upon entering such an area, the organism was observed to increase its rate of turning. If the new path resulted in regaining favorable stimulation, then the turning decreased and a relatively straight path was then taken away from the aversive area. If, on the other hand, the organism continued to experience aversive stimulation, it kept on turning until it either habituated to the conditions or hit upon a path that finally did succeed in taking it away from the zone of unpleasantness.

A more generalized version of klinokinesis (variations in angular velocity in response to differential stimulation) was worked out independently by Ulliyot (1936a, b) and Laing (1937, 1938). It is their models that form the main basis of the search paradigm, although they differ from Jennings' only slightly: the organism is now considered capable of making graded responses to environmental conditions through utilization of information about the concentration of both aversive and attractive stimuli. In this more general view, the

environment need not be divided into sharply demarcated zones but it still must either be patchy in nature or show some more continuous variation over space.

Implicit in these models is the view that there are two separate problems that face any searching organism: 1. how can the length of path taken through unfavorable areas be minimized? and 2. how can its length in favorable areas be maximized? For an organism that is unable to perceive the quality of an area from any distance, its desirability can only be judged according to the rate or the intensity of stimulation received as the organism travels through it. According to Ullyot's and Laing's models, the simplest response the organism need make to solve either of the two basic problems is to adjust its rate of turning as a function of the level of stimulation.

Ullyot's model, for which the term klinokinesis was specifically proposed (Gunn et al., 1937), deals with the negative case, where the rate of turning decreases as positive stimulation increases. The organism changes to a more convoluted path if unfavorable situations are encountered, which serves to minimize entry into the zone of unpleasantness and keep it within the vicinity of the previously favorable levels of stimulation (note the similarity here to Jennings's model). This sort of model only works if the habitat patches are arranged in a gradient. If they are, then organisms possessing sensory accommodation can move up or down these gradients by undirected turning alone. As such, it covers only a limited number of search phenomena, most of which operate over only extremely minute distances. Bacterial "chemotaxis" (Berg and Brown, 1972) and other short-range olfactory searches (Davenport et al., 1960; see Bell and Tobin, 1982

for a review) are the prime examples (Ullyot's, in fact, is no longer viewed as a case of true klinokinesis; Gunn, 1975).

Laing's model, to which the term klinokinesis also applies (although the less informative or more misleading terms "area-restricted" or "convoluted" search are usually employed; see Rowlands and Chapin, 1978, for an exception) treats the case in which turning rate increases with favorable levels of stimulation instead of decreases. In unfavorable areas, which may be judged by either a high or low level of stimulation, the best course of travel is here predicted to be a relatively straight line. By reducing its rate of turning, the organism moves as directly as possible through the area. Once it encounters a more favorable area, it then increases its rate of turning. By doing so it travels in a more convoluted path and minimizes its rate of drift out of the area.

Compared to Ullyot's model, Laing's assumes less about the environment (it need not have a gradient structure) and has proved to be much more widespread in its applicability to search phenomena. It also differs from Ullyot's in that it models environmental stimulation as discrete events or "encounters" rather than as a continuous bath. As such, it has been particularly appropriate for models of foraging, in which context the study of search has been mainly conducted.

As a model for foraging movements, klinokinetic search embraces a number of variants. Although they are fundamentally similar, the slight disparities among them has often prevented a perception of their unifying features and has obscured their differences from other truly distinct types of search. This variation among klinokinetic models is due mainly to two categories of differences in the mathemat-

ical function that relates angular velocity to encounter or reward rate.

(1) The dependent variable has been either the distance separating turns, the turn rate (Dixon, 1959; Chandler, 1969), or the magnitude of the individual turns, their "directionality" (Levin et al., 1971; Cody, 1971; Pyke, 1978b), or a combination of both (Banks, 1957; Heinrich, 1979; Zach and Falls, 1977). In all cases angular velocity (either instantaneous or average) is adjusted in response to some measure of stimulus intensity. In this regard, even apparent examples of "random" search (Zimmerman, 1979, 1982; Hodges and Miller, 1981; Pyke, 1981) actually represent just an extreme form of klinokinesis, where directionality is minimized and turn-rate is maximized as a response to a consistently high level of favorable encounters.

(2) The independent variable has also been treated as having two forms. First, it may represent some approximation to current levels of stimulation, obtained for example from the amount of reward found at each encounter (Pyke, 1978a; Heinrich, 1979), or from some estimate of the instantaneous rate of encounters. In these cases, the response function is often a smoothly varying curve, corresponding to relatively fine-grained variations in the environment. Second, the independent variable may actually be some level of "expectancy" (Gibb, 1958, 1966; Croze, 1970; Charnov, 1976), set either by motivational level (Dixon, 1959; Bond, 1980), learning (Beukema, 1968; Zach and Falls, 1977; Ulliyot's sensory accommodation would also fall under this heading), or natural selection (Jones, 1977). In these models it is

the average or total level of stimulation experienced over past time periods that is important, and the responses usually show little relationship to more immediate fluctuations in stimulation. In this regard, klinokinesis covers even simple two-phase systems where constant levels of high and low angular velocities are separated by on-off thresholds (Laing, 1937; Bond, 1980; Waddington, 1980). In one extreme variant of this model, angular velocities remain constant throughout a patch but jump to a higher or lower level when a boundary is encountered or crossed (Pyke, 1978b). This is essentially the same model of search as proposed by Jennings (1904) and Ulliyot (1936a) and is also formally identical to the home range model of Siniff and Jessen (1969).

That all these are models of klinokinesis can be seen in their use of two-step sequences as the fundamental sampling units. Given a certain level of stimulation or "expectancy", step lengths represent an independent, random sample from one stationary distribution, while the turn angles between steps are likewise selected from another. Under constant conditions these variables, thus, have no interactions with one another. Changes in conditions bring about changes in the parameters of these distributions but not in the number of the variables or in their relationships. These models are therefore distinct from other models that produce similar effects but accomplish them either through spatial rules (for instance, true "area-restricted search", Tinbergen et al., 1967; Croze, 1970) or through higher-order sequential relationships between the steps or turns (for example, simple alternation of turns, Smith, 1974a, b; Pyke, 1978a; or

true klinotaxis, Fraenkel and Gunn, 1961; Bell and Tobin, 1982; Schone, 1984).

The appeal of klinokinetic models of search lies in their parsimony. Simulation models can be built using a minimum number of components and interactions between them (Rohlf and Davenport, 1969; Cody, 1971; Kitching, 1971; Murdie and Hassell, 1973; Jones, 1977a,b; Pyke, 1978b; Sirota, 1978; Yano, 1978; Kitching and Zalucki, 1982a). Mathematical models are likewise tractable (Skellam, 1951, 1974; Hassel and May, 1974; Murdoch and Oaten, 1975; Mackay and Underwood, 1977; Underwood, 1977; Pyke, 1978a). These models are natural hypotheses for the movements of organisms with relatively simple, nomadic life styles (Fleschner, 1950; Banks, 1957; Davenport et al., 1960; Dixon, 1959; Chandler, 1969; Mackay and Underwood, 1977; Jones et al., 1980; Scheibling, 1981). They are also well suited to serve as null hypotheses countering more sophisticated models of migration, navigation, or orientation (Pearson, 1906; Wilkinson, 1952; Mosiman, 1958).

The parsimony of these models, on the other hand, also leads to their major faults. If the organism is believed to be reacting in the simplest possible manner to environmental information, then the investigator may feel free to gather a correspondingly limited amount of data on the routes of travel. Too often, turns and step lengths are treated as independent variables without any real check of this assumption. This is particularly true where observation is limited to brief glimpses of a path but many such glimpses can be obtained. The temptation to use a klinokinetic model in this situation is strong since, assuming similar conditions from observation to observation, the turns can all be pooled to form one large sample, as can the step

lengths. Such pooling can apply to different sections of a single route, to different visits to an area by a particular individual, or, with similar justifications, to the visits of many different individuals. A model based on these samples, however, would be misleading if there were any sort of interactions between turns or step lengths or any positional or directional dependencies governing these variables.

These kinds of complications, unfortunately, have been rarely looked for. As with the Siniff and Jessen model of home range, the main ways of evaluating a search model's fit to actual data rely only on the indirect effects of movement, obtained mainly as population-level measurements: distances of dispersal over some set measure of time (Skellam, 1951; Broadbent and Kendall, 1953; Underwood, 1977; Inoue, 1978; Zalucki and Kitching, 1982); success rates or speeds of animals homing to a particular point or intercepting some other particular target after starting from a set distance away (Wilkinson, 1952; Saila and Shappy, 1963; Kitching, 1971; Jones, 1977a; Sirota, 1978; Cain, 1985); or degree of aggregation in a population or in its response to resources (Hassel and May, 1974; Murdoch and Oaten, 1975; Jones, 1977b; Yano, 1978). While these measures are all appropriate to the problem of search and are predicated upon simple turn models, they do not require that the organism be observed for any time at all between its starting and stopping points.

The use of population level measurements does avoid the autocorrelation difficulties discussed for attempts to validate sequential models of individual home ranges through a spatial analysis of points. Nonetheless the use of indirect measurements in the evaluation of a



search model's fit to actual data raises other questions similar to those discussed for the Siniff and Jessen model. Are indirect measures of movements sufficiently sensitive to differences among various models constructed from a given set of components? Can they tell whether a sufficient number of components or interactions have been included in the model? Are they precise enough to determine even whether movement process is completely homogeneous over time and space or whether it instead shows some degree of dynamism in its basic parameters (as would be expected in classic klinokinesis)?

While there is no real question about the importance in searching behavior of alterations in angular or linear velocity as a response to variations in environmental structure, these alterations are usually not the only kind of response available to the organism; the majority of animals are capable of receiving more information at a point in space than simple stimulus intensity. In many organisms for which klinokinesis has been proposed as a model, particularly vertebrates (e.g., Beukema, 1968; Cody, 1971; Thomas, 1974; Zach and Falls, 1977; Pyke, 1981) and the more advanced hymenoptera (e.g., Levin et al., 1971; Pyke, 1978b; Heinrich, 1979; Zimmerman, 1979; Waddington, 1980), there is also the possibility that some sort of systematic search could be employed. In all the cases just cited, the subject organisms are well known to possess acute sensory capacities and highly specific positional memories. These capabilities are demonstrated not only by the existence of home ranges but also by abilities for navigating complex routes of travel (Manning, 1956; Heinrich, 1976; Zach and Falls, 1976). The question of search in these organisms is thus not only whether their navigational abilities can be used for systematic

forms of search, but also how often the organism actually needs to search at all. It may already know the locations of nearly all its movement goals from previous experience (Thomson et al., 1982).

Even when directional capabilities are considered by themselves, in absence of any long term positional memories, the organism can still travel more efficiently than hypothesized under a klinokinetic model. Simply by adding some form of corrective interactions between turns, the animal will travel a much straighter course than would be possible for pure klinokinesis even with very low angular velocities. In terms of true search, this ability could serve to move the animal through unfavorable areas much more rapidly.

Such sequential relationships among turns have, in fact, been found in the few instances where they have been specifically looked for. Smith (1974a,b) and Pyke (1978a), for example, both discovered patterns of alternation in the signs of turns. This pattern produces routes that are zig-zagging in appearance but hold to a straighter course than would have been expected without these interactions. Smith also found a switch to runs of a given sign (all to the left or to the right) following contact with prey, which served to keep the animal in the vicinity of the capture point. The effect, a more convoluted path, is similar to that in Laing's model of klinokinesis but is more certain in its results.

Even greater efficiency could be obtained through the addition of higher order interactions among the turns, as would be the case in some form of taxis. Such an explanation could, in fact, also account for the results obtained by Smith and Pyke. If there is a flaw in their studies, it is in their lack of serious consideration of this

possibility. They looked only at the transition probabilities among the signs of the turns, ignoring magnitudes. Furthermore, even if they had examined the transitions with respect to magnitude, by treating the routes solely as Markov sequences of turns, of whatever order, any relationships within the routes to fixed frames of reference would have gone unnoticed.

This problem would seem to be particularly important when the analysis of turning sequences leads to the conclusion that the search is "random". The apparent absence of directionality or sequential dependency among the turns, as described, for instance, by Zimmerman (1979, 1982) for bumblebees foraging for "randomly" distributed rewards, might in fact indicate the predominance of positional rules of movement over sequential rules. The animal could be relying completely on memory for recently inspected sites (Gill and Wolf, 1977; Kamil, 1978, 1983; Olton et al., 1981; Soltz, 1986) or on trail markers (Price, 1970) simply to avoid backtracking. These mechanisms could be further enhanced by the addition of some form of true "area-restricted" search (Tinbergen et al., 1967; Croze, 1970). Here the animal uses positional memory to remain within a limited area. Such a process itself, without any avoidance of previously visited sites, can provide a very effective form of search for patchily distributed goals (Croze, 1970). Movements generated by this process would also be difficult to distinguish from a random search, given the information provided by the turns alone.

Although in many ways the problems of the search paradigm are the converse of those of home range studies — hypotheses of search tend to overemphasize simple sequential rules of movement at the expense of

positional rules — their solutions nonetheless are likely to be very similar. Both search patterns and home ranges, if they can even be distinguished, probably involve complex interactions between the two forms of guidance. One cannot be investigated independently of the other, whether referring to the guidance mechanisms or the patterns that result from them.

Two examples illustrating just such combinations are described by Wehner and Srinivasan (1981) and by Hoffman (1983a, b; 1987), both for relatively simple organisms. Although these studies describe a form of search for a misplaced burrow entrance (by a desert ant and isopod respectively), the movement pattern they discovered could serve equally well as an explanation for the bivariate normal utilization distribution used so often in studies of home range (in fact, it is a more realistic model for home range than those of Holgate, 1971; Dunn and Gipson, 1977; or Yang, 1979; which I pointed out previously are inadequate in their treatment of sequential patterns in routes of travel). Except for the fact that they deal only with a specific kind of movement problem, these two studies illustrate the possibilities in a unified approach to movement studies. Their models, which are only slightly different, not only combine simple positional guidance with klinokinetic search, but have systematic and dynamic properties, as well. One final integral and realistic feature of these models is that they link true orientation (in the form of dead-reckoning) inseparably with these other forms of route patterning. While these authors' approaches still do not provide a general prescription for the investigation of animals' routes of travel, they do illustrate the need to integrate all three movement paradigms in the explanation of

even simple tasks.

To finish the arguments in favor of a unified approach to the study of movements, I will next contend that what was true for the studies of home range and search, when considered in isolation, applies equally well to studies of orientation and navigation.

## **L.E. The Orientation Paradigm**

Although true orientation is involved in some forms of search, and kinesis have also been studied as a form of orientation (Fraenkel and Gunn, 1961), directed movements are usually considered as part of the behavior that follows a discovery. In terms of routine activities, if searching behavior corresponds to the appetitive phase of movements, then orientation, and taxes in particular, governs the second major phase, that of consumatory actions.

As such, active orientation must play a ubiquitous role in daily activities. Yet as was true for the study of search, the study of orientation has been conducted mostly outside of the context of everyday routines, either in the laboratory or under controlled environmental conditions. These restrictions have led to a similarly narrow perspective of movements. Where search theory has mainly ignored the possibilities of the positional or directional guidance of movements, the assumptions upon which the orientation paradigm rests ignore the occurrence of factors which make routes of travel at least partly indeterminate.

This limitation is clearly seen in the two main assumptions that underlie the study of taxes:

(1) Movements are made with respect to spatial knowledge, either that supplied by direct perception or that provided by memory of past experiences with particular routes or places. "To orient oneself means to place oneself into a particular relation to known facts (or principles)" (Schone, 1975). Whatever its source or mode, this knowledge provides a directional referent for movements (a sollwert, Mittlestaedt, 1964a, b) that remains

unchanging during the animal's own changes in location. It provides an absolute frame of reference rather than the relative one usually assumed in the study of search.

(2) The space over which a particular referent acts, consequently, can be represented by a vector field (e.g., Cartright and Collett, 1982; Wallraff, 1974). Unlike the simpler scalar fields governing kinesis, tactic fields possess some preferred direction at each point in space (and in some cases a magnitude associated with the level of stimulation).

The goal of the orientation researcher holding these assumptions is to discover the specific referent and mode of action of the vector fields. From Loeb (1918) onward, the tendency has been to view orientation problems as if they were a matter of Newtonian physics, with ultimately deterministic solutions. Given an understanding of the field and given the position of the animal within it, an exact trajectory of travel is predictable under these assumptions (Cartright and Collett, 1982).

This viewpoint has, in turn, fostered a rigorously experimental approach to the investigation of orientation. Whether in the laboratory or in the field, conditions are made as replicable as possible, with all potentially extraneous variables suppressed. This procedure usually involves controlling the sensory input into the animal, plotting several trajectories from particular points within the presumptive field, and averaging the observed behavior over many trials and individuals.

The analytical methods that have been developed to accompany these procedures are likewise rigorously simple. The basic variable

in the study of taxes is the azimuth or compass bearing, a simple directional quantity without even a magnitude associated with it (Batschelet, 1965, 1981; Mardia, 1972). The goal in any orientation study is to relate a sample of azimuths obtained at a particular point in space to the direction of the hypothetical referent at that point. Given sufficient experimental controls, the sample values should all coincide. Two classic examples of this approach to the study of movements are the use of Kramer cages and the recording of vanishing bearings in the study of avian navigation (Kramer, 1950; Schmidt-koenig and Keeton, 1978; Gauthreaux, 1980).

These examples also indicate that the paradigm of orientation studies, like those of home range and search, has evolved around observational limitations on the recording of the details of animals' routes of travel. As with the other two divisions of movement study, the methodology for orientational analysis has not kept pace with the technology that has made possible the long-term tracking of particular individuals. This problem was stated clearly by Batschelet (1972). Although he believed that stochastic models could be developed to handle long sequences of movements made by single individuals, he did not believe that the prevailing statistical tests for azimuthal samples were adequate for this task. The problem is that all these tests depend upon the assumption of independent sampling from stationary distributions. Batschelet felt that this assumption was not a safe one to make for the tracks of single individuals, where the possibility of serial correlation among the path azimuths is high.

Despite Batschelet's hopes for the development of more powerful models, however, most orientation studies have been content to take



his lesser suggestion that azimuthal samples be tested only for the null hypothesis of randomness (e.g., Schmidt-Koenig, 1975; Emlen and Demong, 1978; Ireland et al., 1978). If a significant departure from uniformity is found, then random movements can be ruled out, but it still cannot be determined whether the organism is performing a taxis or, more simply, a kinesis of some kind. Azimuthal samples can thus be used only descriptively, without any guarantee that they can even be used to compare the movement tendencies of different individuals.

For whatever reason, the orientation paradigm has not produced any significant form of route analysis as such. This situation is unfortunate since much of the data obtained from tracking the everyday movements of individuals do not lend themselves easily to the traditional experimental approach; referents cannot always be identified even where a wealth of contextual data has been gathered along with the surveys of the routes.

For example, the referent direction may be determined with respect to an unmarked point in space. Such a spot may be set by the organism relative to a constellation of external cues (Tinbergen, 1932; Tinbergen and Kryt, 1938; Collett and Land, 1975; Cartwright and Collett, 1982) or with respect to some form of "cognitive map" and the use of internal dead reckoning (Tolman, 1948; Barlowe, 1964; O'Keefe and Nadel, 1978; Morris, 1981). Some combination of both internal and external referents is also possible (Gorner, 1958, 1972; Wehner and Raber, 1979). With respect to routine movements, such referents should be especially important to any animal that "traplines" (Manning, 1956; Janzen, 1971), caches food (Vander Wall, 1982; Cowie, et.

al., 1981; Sherry et al, 1981), or possesses a home range generally.

Futhermore, even where a target has been correctly identified (as for example in well-motivated homing pigeons released far from their lofts) detours or other temporary departures from course can also occur (Michener and Walcott, 1967; Wagner, 1972). While in some cases these deviations represent only course errors, in others they could correspond to sub-targets or temporary referents. Generally speaking, it is not always possible to determine how many directional referents are involved along a particular route, or even whether the movements are always under the influence of a referent. A homing pigeon, for instance, might periodically have to search for information (klinokinetically or otherwise) before it can resume its homeward taxis (Hodge, 1894; Michener and Walcott, 1967). In all these cases, Batschelet's skepticism about the usefulness of azimuthal samples is more than justified. Even without the problem of serial correlation, if the referent direction is misidentified or more than one exists, then even simple tests for randomness (e.g., the Rayleigh Test or V-Test; see Batschelet, 1981) could well give falsely negative results.

It is an irony of the orientation paradigm that, although an oriented route of travel possesses more information than a merely klinokinetic one, the methods traditionally used to analyze oriented movements extract even less information than do those used in the search paradigm. Instead of examining the relationships among three or more steps (displacements), which is necessary if taxes are to be distinguished, the standard methods do not examine sequences at all! They are content with the information provided by single steps, and

by only their directional components at that.

While these limitations are typical in most studies of taxes, at least one branch of orientation studies has developed a more useful viewpoint and a methodology based on three-step sequences rather than on isolated azimuths. Mittlestaedt's (1962, 1964a, b) concept of orientation as a control system underlies this work; the nature of a taxis (or a kinesis) is best seen in the way an animal adjusts its course or heading in response to some measurable deviation from a target value. With respect to route studies, this concept implies that course deflections supply important information about orientation and should not be simply removed or ignored in an experimental setup. Furthermore, it suggests that course control is best studied as a process, observable only over a number of successive steps.

Either directly or indirectly, this concept provides the basis for a series of elegant "detour" studies (e.g., Dingle, 1964a, b, 1965; Barnwell, 1965; Burger, 1971; Mittlestaedt-Burger, 1972; Mittlestaedt et al., 1979; Merkel and Fischer-Klein, 1973, 1978; Merkel, 1978; Moore, 1982; Seyfarth et al., 1982). In these strictly laboratory investigations, the subject is allowed an initial free choice of heading but is then forced to detour through some variably complicated passage, at the end of which it is once again free to choose its course. The questions addressed are: how similar are the initial and final free choices in direction; and how do variations in the detoured path affect that relationship?

This approach has proven particularly useful in investigating the role of stored information (memory) in course control. In the studies mentioned, the subjects were able to compensate for the sign as well

as the magnitude of the deflection at least partly on the basis of an internal accounting of the effects of the detour. The role of this kind of "idiothetic" course control (Mittlestaedt-Burger, 1972; Mittlestaedt and Mittlestaedt, 1972) and its interactions with externally based orientational components (Barnwell, 1965; Burger, 1971) can perhaps be assessed only by these sorts of studies (as opposed to the more traditional approaches of azimuthal mapping).

By measuring the angular correlation between pre- and post-detour steps, these studies also go beyond the simpler demonstrations of sign-alternation between turns (e.g., Schneirla, 1929; Dashiell and Bayroff, 1931; Warden, et al., 1940; Dember and Fowler, 1958; Dingle, 1961; for a review of these studies, see Barnwell, 1965). Investigation of these possibilities has relevance not only for the study of taxes as such, but also for the study of search. Recall that Smith (1974a, b) and Pyke (1978b) discussed the importance of sign-alternation or sign-repetition in controlling the convolutedness of a search path. They did not, however, employ methods for examining the degree of turning compensation. Their organisms might, in fact, have been doing something more sophisticated than simply storing the signs of their turns and then turning to the opposite side at the next opportunity.

In Kleerekoper et al.'s (1969) model of goldfish movements, for example, simple turn-compensation provides a more efficient model of linear progression out of an area than does turn-alternation alone, but still does not require any fixed orientational referents. The organism only needs to match the magnitude of the immediately preceding turn while changing the sign. A similar control of turning magni-

tude can also aid an animal trying to make its path convoluted in order to stay within an area (Kleerekoper et al. also observed turns to occur in runs of the same sign). In either case, Kleerekoper et. al. provide a straight-forward statistical test that examines the turning behavior over a series of steps. Turn-matching implies that large turns will follow one another in a sequence more than expected by chance, as will small ones. Simple intra-class correlation can be used to test this prediction (but treats the variables as linear rather than as circular; Watson and Beran, 1967, provide a more appropriate test of this relationship and one that does not involve arbitrarily dividing the segments into classes).

Even though simple turn-compensation represents an advance over pure klinokinesis or turn-alternation, it is still relatively inefficient compared to the higher forms of taxes. While a turn-compensator may have a very specific target direction at each step, any deviations that occur during the commission of that step will be incorporated into later course decisions. Unlike taxes governed by fixed frames of reference, simple turn-compensation cannot hold to a particular heading even though it does correct to some degree for deflections. Furthermore, it lacks the higher taxes' ability to damp out the effects of deflection. For example, a single large detour can "waste" the animal's forward motion in subsequent series of wide zig-zags.

For reasons such as these, turn compensation has often been hypothesized to play only an adjunct role relative to more precise taxes governed by fixed directional or positional referents (Gorner, 1958, 1972; Barnwell, 1965; Mittlestaedt-Burger, 1972). Where dead-reckoning systems are hypothesized to play a more important role, they

are assumed to involve memories for a longer series of rotations as well as for their accompanying translations (Barlowe, 1963; Wehner and Srinivasan, 1981; Hoffman, 1983a, b; Seyfarth, et al., 1982). These sorts of systems duplicate, by internal means, the abilities of taxes governed by external and directly perceived orientational cues.

Unfortunately where these more complicated mechanisms apply, the serial correlation methods of Kleerekoper et al. (and Watson and Beran) no longer work. The effects of any deflection are immediately damped out at the next step and there are no runs of larger or smaller turns. More generally, the analytic methods developed in detour studies suffer the same problems when taken out of the controlled laboratory situations and into the field as do the more standard methods of azimuthal mapping. Additionally, even where the orientational referents are known to the observer, the deflecting agents are often unknown or completely stochastic. Whereas in a series of compensatory turns any three-step sequence will fit the detour paradigm, in a higher taxis this will not be the case. Each step in a particular series can contain some degree of deflection, not simply the second. If the largest deflection occurs in the first or third step then there will be no exactly predictable relationship between the turns, compensatory or otherwise.

On the other hand, any adjunct, compensatory responses to deflections confirm Batschelet's suspicions about serial azimuthal sampling. Compensatory turning, for example, could be used by the animal to minimize its drift perpendicular to the target heading. Here, even where the referent direction is constant over all steps, as in menotaxis, biases among the deflections would prohibit treating the azi-

muths of the steps as independent samples from a single population.

Other stochastic features of the deflections also make their study just as important in route analysis as the study of the more deterministic, directional referents. In this regard, Mittlestaedt's cybernetic concept of orientation can still provide the underpinnings for a general theory of routes of travel. It is the nature of the animal's steering responses to a series of deflections that gives a particular character to its movement patterns, not simply the physical nature of any orientational cue or the sensory mode by which it is perceived. This perspective applies no matter if the movements are organized as a search kinesis, a consumatory taxis, or part of a home-range routine. The key feature of routes is that they represent processes of adjustment to naturally occurring, everyday vagaries of existence. They cannot be studied when taken completely out of context, which includes any attempt to analyze small fragments of a route in isolation. What was true for point-fixes, turn-angles, and azimuths also applies to three-step sequences. Only a method that deals specifically with long sequences of movement can hope to unravel the control processes that govern animals' routes of travel.

## **I.F. Stochastic Walk Models**

The paradigms of home range, search, and orientation collectively cover the subject matter of route studies. There is, however, still a fourth body of work that has developed more-or-less independently, the primarily mathematical and biophysical theory of stochastic walks. Although this area has its own distinctive approach to the study of movements, its interests are more abstract than those of the three previously considered areas. For that reason, rather than treat it as a separate paradigm, I will discuss it here as a possible basis for unifying the investigation of routes, both theoretically and analytically.

The archetypal model of a walk process is the random walk described by Karl Pearson (1905). The question he posed was: how far will a moving organism travel, on the average, over a given number of discrete, straight-line steps, when after each step a new direction of travel is chosen at random? As simple as it appears, this problem has given rise to much productive research, incorporating as it does all the essential features of stochastic walk models, as follows.

(1) Discreteness. The term "walk" refers to any series of discrete steps, where the term "step" refers to a finite, straight-line displacement rather than to any physical locomotory action (throughout the rest of this paper "step" and "step-vector" will be used interchangeably).

(2) Stochasticity. In all models of this type, it is assumed that a particular trajectory (route of travel) of an individual cannot be predicted with any certainty. The direction of travel of any given step is considered to be a random vari-



able, as is the step length in most models. These assumptions in turn imply that the organism's position at any particular time is also indeterminate. The average behavior of the trajectories, on the other hand, is assumed to be quite predictable. Behavioral rules of movement are believed to have some statistical constancy, making the probability distributions of the step-vectors and the turn angles between them stationary, unchanging over time and space. Furthermore, the relationship among these variables is also assumed to be constant; usually the length and direction of any step are considered to be independent of one another, as is each step in relation to the next one in the sequence.

(3) Sequentiality. Given the simple statistical features of a series of steps, predictions can be made about the overall properties of the walks themselves, no matter what their lengths. The estimated variable is some property of the sequence, usually a measure related to the net displacement or the position of the organism relative to a point of origin.

With respect to at least these three features, it is clear that there is a close correspondence between abstract walks and several of the more specific behavioral models that have been previously discussed. This resemblance is particularly clear with regard to the form of data that are used. In the majority of animal movement studies, especially those done in the field on wide-ranging animals, data are collected in the form of positional fixes, or, in terms of vectors, discrete steps. Even where continuous tracings of a route are obtained, paths are usually partitioned according to some rule prior to analysis, partly for the sake of convenience but also, more impor-

tantly, because movement decisions are often presumed actually to occur at discrete intervals. In most studies, step-lengths, azimuths, and turn angles are all thought to have some real behavioral meaning (as discussed in greater detail in Chapter III).

Beyond the discrete nature of the information, many behavioral models share with the theory of stochastic walks its assumptions about the simple statistical nature of the rules of movement. Examples include the home range models of Siniff and Jessen, Holgate, Yang, and Dunn and Gipson; the models of klinokinetic search of Cody, Smith, and Pyke; and most explicitly, the models of purely random search of Wilkinson, Skellam, and Zimmerman.

Other behavioral models, however, do not meet all three of the criteria given above. There are, in fact, a large number of movement models that hypothesize behavior to change in a complex way over space and time. These include, most obviously, the classic models of klinokinesis, where either the distribution of step lengths or of turn angles varies according to the level of stimulation experienced at each point in space. They also include movements within home ranges possessing multiple foci of activity and taxes that are governed by complex spatial arrays of cues. Such spatially or temporally heterogeneous processes often require more complex and sophisticated stochastic modelling techniques than currently exist.

On the other hand, many of these processes can be mathematically transformed into a simpler model if the spatial determinates are known and can be corrected for. It may also be possible to approximate the behavior of a more complex model by means of a simpler one, at least over limited regions of time and space. These approximations can

furthermore come closer and closer to reality if changes are made in the scale by which the steps are measured. In any case, it will often be possible to find a reasonably simple walk that can serve at least as a null hypothesis for the actual behavior, if not mimic it exactly.

More than any of the mathematics discussed in previous sections, the equations relating the average behavior of the sequences to the average behavior of their components provide a means for using all the information potentially present in a route. Certain walk models in particular require no contextual information for their analysis. The relationship among the route variables alone is sufficient to characterize the process. Nothing need be assumed about the position or even the existence of any orientational target or other spatial influences acting upon the movements. The presence of any such additional factors becomes revealed by departures from the relationships predicted under the null model.

These non-contextual walk models can thereby have great heuristic value in the initial investigation of routes and can be extremely important where the precise behavioral or environmental circumstances in which a route occurs is difficult or even impossible to assess, as for instance in most remote radio-telemetry studies. Where contextual information does exist, these models are still useful, since they are the ones to which more complex processes are most easily transformed. The rest of this section will be devoted to this class of models. Particular emphasis will be given to finding a suitable measurement for characterizing these walks for statistical hypothesis testing as well as for indicating the nature of any departures from them.

Pearson's classic random walk is the best known model possessing the desirable property of self-contained, relationships. The solution to his basic question only requires measurements that can be obtained from routes considered in complete isolation from their surroundings. The power of this model can be seen in the great number of applications it has spawned, especially with respect to the behavior of populations. Pearson's approach itself, predicting the distribution in space of net distances of displacement from a point of origin, over a given number of steps, leads directly to number of models for dispersal (e.g., Pearson and Blakeman, 1906; Brownlee, 1911; Skellam, 1951). More importantly, its generalization to diffusion processes by Einstein (1905, 1906), Smoluchowski (1906), and others allows for even more powerful predictions to be made about the changes in a population's distribution over time (see Okubo, 1980, for a review).

However, this approach is more cumbersome when applied to the routes of individuals rather than to the mass fluctuations of a population. Ideally, instead of the prediction of a distribution function relative to a given number of steps, there should be only a single dependent variable to measure. The functional relationship between this variable and the number of steps in a series would then permit a graphical representation of a route-generating process and the use of statistical analyses similar to regression. Each particular kind of walk should theoretically be identifiable by the parameters of the curve it produces.

For a stochastic process, this dependent variable will take the form of some average value or statistical expectation. For a walk model in particular, this variable must also change as a function of

the number of steps in a sequence. Under these two requirements, it can be seen that Pearson's measurement of the simple net displacement will not serve this purpose: its average value (a function of the vector sum of all possible displacements) will be zero for all numbers of steps. This situation is directly analogous to the parametric characterization of Gaussian distributions (indeed, Pearson's solution to his random walk question is a two-dimensional normal distribution). The average deviation from the mean (equivalent to the point of origin) will always be equal to zero, and it is the expected square of the deviation that provides the best measure of the spread from the center.

Indeed, it can be shown that the mean squared distance (MSD) of travel as a function of step number is easily related to the expected values of the individual steps and the turn-angles between them (see Feynman, 1963). For a random walk in two-dimensions, where the step lengths,  $s$ , have a stationary distribution but any arbitrary form, and the distribution of turns between steps is uniform,

$$E( D_n^2 ) = n E( s^2 )$$

where  $n$ , the independent variable, is the number of steps in the series. A plot of MSD against  $n$  is thus for a random walk a straight line with origin at zero and slope equal to the average of the squared individual step lengths.

Without knowing anything about the step variables themselves, such a straight-line plot in itself implies the behavioral properties of a random walk and can be further used to estimate the average step length. Three examples can be cited to illustrate the value of this

function as a test of the null hypothesis of a random walk:

(1) In a study of granulocytes moving in an isotropic medium, Peterson and Noble (1972) found no differences from the predictions of the null model. The observed MSD's showed no clear trend in their deviations from those expected under a random walk (the use of a t-test to evaluate the significance of the deviations, however, was possibly not appropriate; see Chapter V).

(2) A clear difference from the null model was found for movements of granulocytes in the presence of a chemo-attractant (Peterson and Noble, 1972) and for the movements of dissociated sponge cells in the presence of other sponge cells (Noble and Peterson, 1972). In both cases, there was an obvious trend for the observed MSD's to be greater than expected under the random model.

(3) An opposite but also clear difference from the null model was discovered by Waser (1976) in the movements of troops of mangabey monkeys. Although their ranging patterns appeared to be fairly nomadic, the observed MSD's were consistently shorter than expected.

These examples, covering the three general outcomes of this test, indicate the general applicability of this approach to movement studies, the common problem of which is to rule out random movement first. The first two examples have relevance to the problem of search and possibly to that of orientation. The third example likewise may hold a key to the problem of detecting spatial constraints within an other-

wise protean ranging pattern. The authors, in fact, all interpret their findings along such lines.

This approach, however, is only the first step in the process of investigating routes. The next would be to try to fit the observed data to some more elaborate stochastic model. The studies mentioned above stop short of this step; the authors relied on intuition alone to interpret the departures they found from the random walk.

All three departures from random could, in fact, have been produced by another commonly investigated stochastic model, the "correlated" or "persistent" walk. The only difference between this model and the purely random walk lies in the form of the distribution of inter-step turns. In the random walk, this distribution is uniform but in the correlated walk it can take on any other shape. The term "correlated" refers to the fact that this non-randomness in the turns ensures some sort of relationship among the successive directions of travel in a series of steps.

In the case of Peterson and Noble's non-randomly moving cells, the observed "directionality" could have been due simply to a unimodal distribution of turns about  $0^\circ$ , the angle representing no change in direction. Their speculation about inter-cellular interactions or orientation towards any external stimulus was premature. In the case of Waser's mangabeys, a tendency for circling movements could have been imposed upon an otherwise random pattern by simply biasing the likelihood of turning toward one side from step to step. His interpretation of the results as an indication of spatial constraints was probably correct, but, like Peterson and Noble's educated guesses, is not conclusive.

These possibilities are, fortunately, also easily checked by means of a relationship between mean-squared displacement and the number of steps in a series. For this model, unlike that for the purely random walk, predictions about the characteristic curve depend upon information about the distribution of turn angles as well as of step lengths.

Two early versions of this type of walk were described by Furth (1920), who applied it to the movements of paramecia, and by Tchen (1950), who was interested in the more general mathematical problem of correlated movements. Both models were restricted to the case of equal length steps and of a distribution of turns that was symmetric about  $0^\circ$  (Furth only examined the possibility of turns of  $0^\circ$  and  $180^\circ$ ). Under these restrictions, Tchen provided a measure of the directional correlation between steps as a function of the cosines of the turn angles (this function will also be seen later to have importance beyond the correlated walk).

A more generally realistic model, not restricted to equal length steps but still requiring a symmetry of turns relative to  $0^\circ$ , was described by Gail and Boone (1970) and elaborated by Hall (1977). Their formula for the MSD curve is

$$E(D_n^2) = n E(s^2) + 2 E(s)^2 \sum \lambda_k$$

where  $\lambda_k$  is the expected value of the cosine of the angle between steps that are  $k$  steps apart in the series (a more detailed discussion of this equation will be presented in Chapter IV). Instead of a straight line, this curve is initially concave upward and only straightens out asymptotically. From the addition of the last term,



which will always be positive, it can also be seen that a correlated walker of this type will always move farther than a purely random walker over a given number of steps.

This type of stochastic walk is actually more general than the random walk. For one thing, it possesses a more inclusive formula: if the distribution of turns is uniform, then  $\lambda_k$  is equal to 0 and the equation reduces to that of the simple random walk given earlier. More fundamentally, as Furth first pointed out, all moving objects, at a sufficiently fine scale of measurement, should show some correlation in direction between steps. Random walks will emerge when each measured step actually incorporates the result of a large number of correlated steps (in living organisms random walks might also reflect the operation of some true, internal random generator). This effect was quantified by Gail and Boone for the movements of fibroblasts and by Hoffman (1983) for the searching behavior of a desert isopod.

A correlated walk itself can also emerge from more elaborate kinds of processes. The counter-turning models of Smith (1974a, b) and Pyke (1978a) and the compensatory turning model of Kleerekoper et. al. (1969), for example, all show accumulations of "error" over time and distance. If this error is unbiased towards right or left, then at increasingly larger scales of measurement the steps first describe a correlated walk then, ultimately, a random walk.

While such models of unbiased turning cover a wide range of the movements actually observed in animals, only recently has the formula for the correlated walk been made general enough to cover side-biased movements as well. Using a more complicated mathematical approach than that of the previously mentioned studies, Kareiva and Shigesada

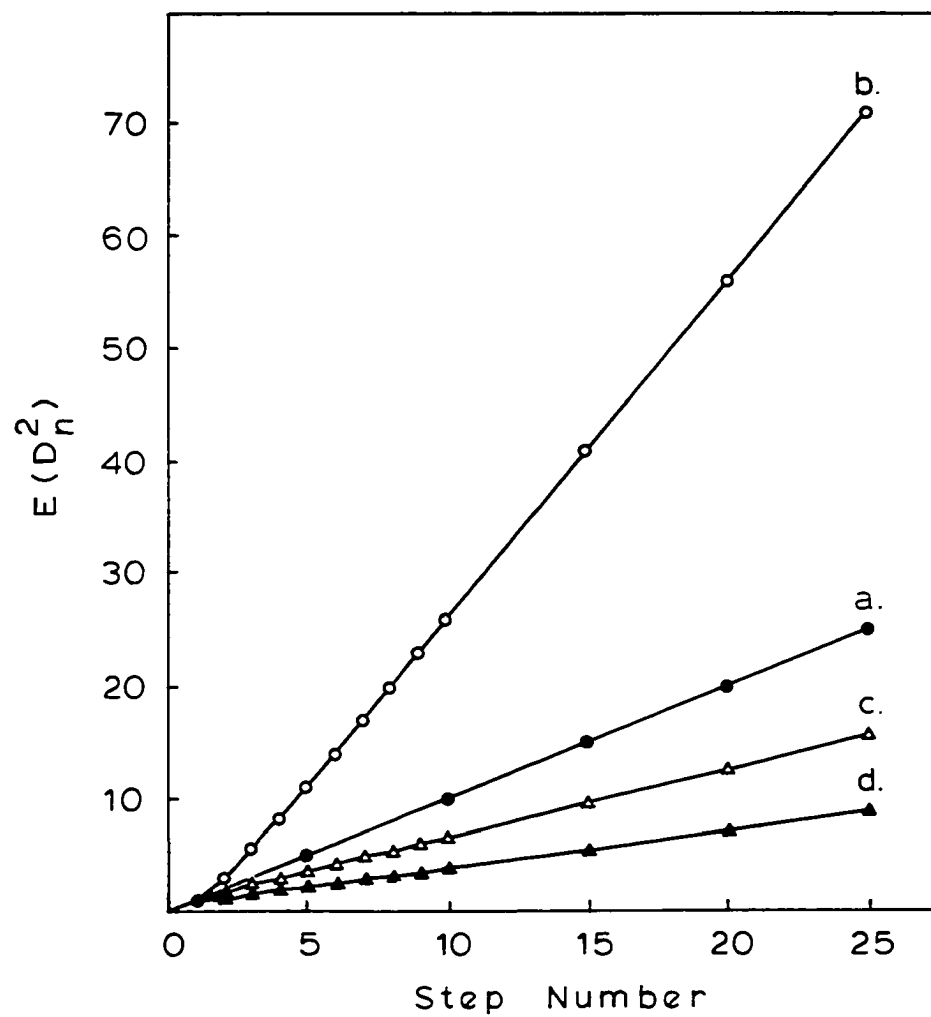
(1983) have succeeded in removing all restrictions on the form of the turning distribution. They do so by incorporating into the MSD equation the expected value for the sine of the turns (the equation is too lengthy to be reproduced here; it is, however, easily programable and is the one I used in the analysis of the data presented in Chapter V). Where the sine is zero, as it is for the unbiased models, the equation reduces to that given above (Hall, 1977). Where this is not the case, as in stochastic circling movements, the curve that is generated will fall below that of an unbiased walk for all step numbers greater than one and can even lie below that of the purely random walk. Figure 1.1 illustrates these possibilities, the same as those mentioned as alternative explanations for the findings of Peterson and Nobel and of Waser.

This figure also illustrates a general feature of correlated walks: no matter what the form of the distribution of turn-angles, the relationship between step number and the mean squared distance of travel becomes linear with a positive slope as the number of steps becomes large. Since the purely random walk is also a special case of this kind of process, such asymptotic, positive-sloped linearity can be interpreted as a general indication of a failure of the organism to compensate actively for drift away from a chosen course.

There are, naturally, different degrees of course regulation, as reflected in the number of steps required for the curve to straighten out. A random walk possesses no control whatsoever and its curve, consequently, is straight from the beginning. A correlated walk shows less drift, even if its course is circling, and its curve straightens only after some initial curvature. The greater the correlation bet-

**FIGURE 1.1** A comparison of the squared distances of travel expected over a given number of steps for the random walk and the biased and unbiased correlated walks.

- a. Random walk;  $\rho_{\delta} = 0$
- b. Unbiased correlated walk;  $\rho_{\delta} = 0$ ,  $\mu_{\delta} = 0^{\circ}$
- c. Biased correlated walk;  $\rho_{\delta} = 0.5$ ,  $\mu_{\delta} = 90^{\circ}$
- d. Biased correlated walk;  $\rho_{\delta} = 0.5$ ,  $\mu_{\delta} = 180^{\circ}$



ween steps, the greater the number of steps before the curve becomes rectilinear.

A corollary of this effect is seen in the way the curve changes with increases in the scale by which the steps are measured. If there is no control for drift, larger partitions of a path should possess more accumulated "error" than smaller divisions. Consequently, increasing the scale of measurement should cause the MSD curve to straighten out in a smaller number of steps than it took at the finer scale (unless, of course, the walk was random to begin with).

Conveniently, this effect holds true for walks that allow some accumulation of drift but for which the MSD curve is presently unknown. Examples include the counter-turning and compensatory-turning models of search behavior and higher-order Markov models generally. Although these processes represent more control than simple correlated walks, and hence generate travel either farther or less far in a given number of steps, they also lack any external frame of reference or feedback mechanism by which drift can be detected and adjusted for. When partitioned over larger and larger distances, their behavior will tend to become indistinguishable from that of the true correlated walk.

Organisms that possess absolute frames of orientational reference, conversely, should produce walks that do not have the above features in their MSD curves. No matter what scale of measurement, an absolute control over drift should be reflected in an MSD curve that never becomes positively linear, even asymptotically.

One major way to regulate movements is to control for positional drift through the use of spatial constraints. As was suggested by

Waser, the MSD curve for a site-tenacious walker should lie below that of a purely random walker, at least after some number of steps have been traversed (the exact figure depends on the extent of the area of confinement). But a conclusive demonstration of positional control lies in the shape of the curve, not simply in its location relative to a random walk. Such a demonstration was given by Hoffman (1983a) for the searching behavior of Hemilepistus. He first fitted the sequential data, using Tchen's (1950) method, to a walk possessing significant correlations between both adjacent steps and those once removed in the sequence. Calculating the variance around a MSD-related curve, he showed that the animals returned significantly more often to a point of origin than would be expected under the purely correlated walk model. While this result will not hold true for all kinds of spatially constrained movements, the important thing is that some definite limit can be detected in the distances the animal will travel from some arbitrary point of origin.

The other major form of route control, correction for directional drift, has received more attention from modelers of animal movements. Ullyot's model of directional klinokinesis in particular has received a good deal of consideration in studies of the movements of cells within chemical gradients (Patlak, 1953a,b; Nossal and Weiss, 1974a, b; Lovely and Dahlquist, 1975; Boyarsky, et al., 1976). Recently even a quasi-tactic model for cellular movements in a gradient was formulated by Nossal (1976; Nossal and Zigmond, 1976).

For the most part, however, these studies make use of diffusion-related equations rather than ones given in terms of discrete steps made by individual walkers. Their usefulness as a general means of

orientational analysis is further hampered in that they all require for their predictions prior knowledge of the directional target. They do not possess the desirable feature of self-contained predictions described above for the correlated and random walks.

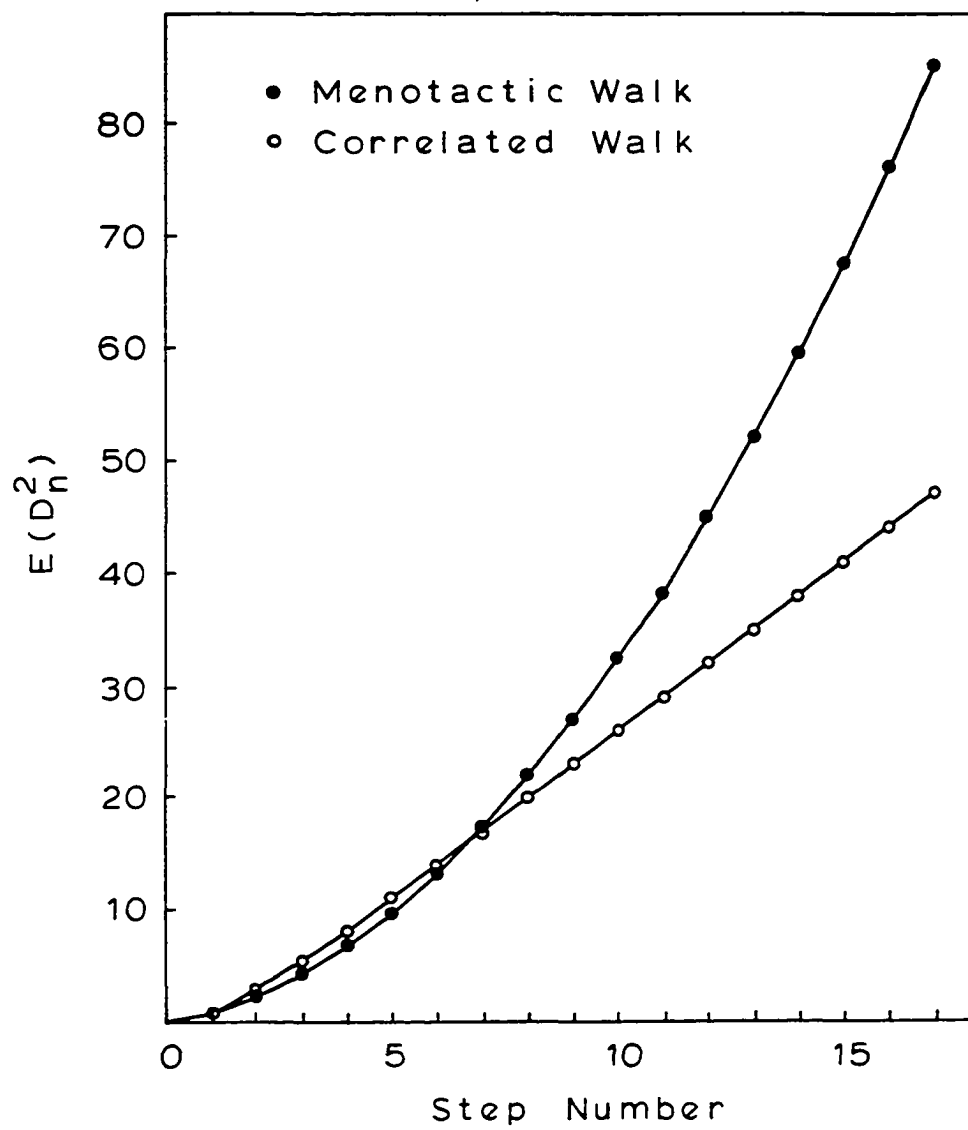
In this study, I will introduce a new formula for a large class of common tactic movements, one that is completely analogous to the MSD equations given earlier. Where directional drift is measured and adjusted relative to a fixed azimuthal referent (as in menotaxis and some forms of inertial guidance, anemotaxis, and pharotaxis; see Chapter III), I will show that

$$E( D_n^2 ) = n E( s^2 ) + 2 E( s )^2 \lambda_1 ( n^2 - n )$$

As in the correlated walk, all that is needed to characterize this process are the distributions of the step lengths and turn angles; no prior knowledge of the directional target is necessary. Again, the data from walks having different targets can all be pooled provided  $\lambda_1$  is the same for all of them. Figure 1.2 illustrates the different curves produced by these models given the exact same information about turn angles and step lengths. Given additionally the knowledge about the target headings at each step, this formula applies to the stochastic components of any form of walk, tactic or otherwise, as will be discussed in Chapter IV.

**FIGURE 1.2** A comparison of the expected squared distances of travel for the menotactic and unbiased correlated walk given the same distribution of deflection angles:  $\mu_\delta = 0^\circ$ ,  $\rho_\delta = 0.5$ . Note the initial advantage in terms of distance traveled by the correlated walk. This holds true for at least the first five steps no matter what the distribution of deflections (other than biased or uniform), as will be discussed in Chapter V.





### **L.G. The Box Turtle as a Subject for Route Studies**

Although outwardly a rather simple-seeming organism, the box turtle (both Terrapene carolina and T. ornata) has proved to be a challenging subject for movement studies. In several ways it is the ideal candidate for the relatively complex approach to route analysis I have been proposing.

First, the disparity between the quality of the movement data that has been collected on this genus and the sophistication of the methods used in its analysis is, perhaps, the greatest for any organism. Using the spool-trailer method (see Chapter II), which has recently been supplemented by radio-telemetry, researchers of box turtle movements have been obtaining accurate, continuous, and abundant data on actual routes of travel for over fifty years — longer than for any other organism (Breder, 1927; Stickel, 1950; Legler, 1960; Metcalf and Metcalf, 1970; Schwartz and Schwartz, 1974). The treatment of this data, in contrast, follows the usual paradigms founded on mere glimpses of movements. Home-range patterns have been examined mainly in terms of minimum area polygons; only Madden (1975) has even tried an utilization distributional analysis. Orientation and homing treatments have viewed the data exactly as if it had been obtained from a rapidly vanishing pigeon or honeybee (Breder, 1927; Gould 1957, 1959; Lemkau, 1970; Madden, 1975; Metcalf and Metcalf, 1970) or a migrant warbler fluttering in a Kramer cage (DeRosa and Taylor, 1982).

Second, while falling short of what they could have accomplished, these studies at least succeeded in demonstrating a diversity in box turtle movement patterns that is as great as has been found in any

other animal. Ranging patterns vary from long-term site-fidelity (Stickel, 1978; Schwartz et al., 1984) to long-term transiency (Kiestler et al., 1981), with all other possibilities lying in between (Stickel, 1950; Schwartz and Schwartz, 1974). Box turtle navigational abilities are also quite complex, resembling that of birds and hymenoptera in the number of possible mechanisms that have been suggested. Explanations for homing include simple pilotage (Breder, 1927), olfaction (Metcalf and Metcalf, 1970; Madden, 1975), vector-navigation (DeRosa and Taylor, 1982), and even true celestial navigation (Gould, 1957, 1959). Furthermore, there are indications that box turtles possess highly specific positional memories that may persist over an entire year without obvious reinforcement.

Third, these studies reveal a fundamental paradox to box turtle movements. Although the existence of positional or directional constraints on their routes of travel has been well established, their exact nature or function remains a mystery. Indeed, examination of basic box turtle biology makes it unclear why they should possess home ranges or homing abilities at all, let alone the great range of individual differences in ranging patterns that has been observed. The question this paradox raises is: does this apparent complexity in route patterning reflect a true complexity in the behavior of these animals or does it simply reflect a failure of the traditional paradigms of movement study to provide a general enough model for route behavior?

Box turtle ecology does, in fact, appear to be quite different from that of other, more traditional subjects of movement study. Compared to a vole, pigeon, or bumblebee, the box turtle lives accor-

ding to a slower-paced, more generalized, and less constrained lifestyle. As a member of a line that has re-adapted to full terrestriality in comparatively recent times (the Miocene; Milstead, 1969), the box turtle appears to be exploiting a niche that has been either overlooked or long-abandoned by other organisms more specialized in their adaptations to a land existence. The box turtle uses a unique combination of extreme longevity, opportunism, and low-energy requirements to exploit conditions that racier organisms would find too impoverished to sustain either individual or population. Even compared to the tortoises, whose specializations to terrestrial conditions have had much more time to evolve (since the Cretaceous), box turtles employ such a generally different sort of strategy that it fails in many ways to conform to the postulates of the various movement theories, particularly those of search and home range.

The box turtles' non-conformist approach to life is clearly seen in the nature of their foraging adaptations. They take the generalist tendencies of the emydid turtles to an extreme, becoming the most omnivorous of all reptiles and perhaps possessing a dietary range greater than any other organism. They eat things even a human would disdain! As dwellers on the abyssal plains of forest, grassland, or marsh ecosystems, a great part of their diet is composed of whatever rains down from the more productive layers beyond their reach. Such items include fruit, carcasses, dung, and even oak galls (for reference to the last item, see Latham, 1972). The other major portion of their diet is made up of their fellow detritivores: fungi, annelids, gastropods, and arthropods. Additionally, some foliage is consumed as well as an occasional smaller vertebrate or its eggs. In short, they

consume whatever comes their way that they can overpower and tear apart with their horny jaws (for lists of their foods see Moore, 1943; Barbour, 1950; Bush, 1959; Klimstra and Newsome, 1960; Legler, 1960).

The box turtle's dietary opportunism, in turn, leads to flexibility in the nature of its foraging movements. Since a major part of its diet is composed of food items that are sparsely, widely, and unpredictably scattered, the box turtle must be at least partly a searcher. On the other hand, since another large component of its diet is made up of items that are both more concentrated and predictable in time or space (berry and mushroom patches, or concentrations of detritivores around decaying logs), the box turtle could also make use of positional guidance in foraging. This orientation might take the form of direct telotaxes towards likely feeding sites or more indirectly with respect to remembered positional information about past feeding successes. The optimal foraging pattern would thus seem to be a mixture of strategies, involving varying proportions of kinesis, taxes, and positional constraints. This mixture itself can be expected to vary depending on environmental circumstances, individual experience or current motivational state.

Mixed strategies could also characterize the box turtle's relations to other of its resources. Water, for instance, might be obtained during the course of a generalized search or through more specific movements. On my ridgetop study site, individuals made most frequent use of transient rain puddles, while only a few utilized the one spring found in the area or an irregularly filled vernal pool. Other studies have reported much greater reliance on permanent sources of water (Culbertson, 1907; Overton, 1916; Latham, 1916; Cahn, 1937).

In some of these cases, large numbers of individuals were observed to congregate in isolated pools, sometimes remaining partly submerged and immobile for weeks at a time. Such behavior has been hypothesized to be a response to summer drought.

Shelter from environmental inclemency, however, can also be more opportunistic. During the 1976 drought in Chapel Hill, none of my subjects sojourned in pools but, on the contrary, remained for lengthy periods in their dry-land forms (shallow burrows in the leaf litter). Similar behavior was reported in another population of Terrapene c. carolina by Stickel (1950) and in the more xeric T. ornata by Legler (1960). Although form sites are likely chosen with respect to micro-climatic features (Reagan, 1974), suitable conditions are generally widespread and forms are typically dug wherever the turtle winds up at the end of the day (Legler, 1960). Forms occupied for longer periods during unfavorable conditions do not appear to be exceptional in this regard. Even hibernacula may simply be the deepened forms made at the end of whatever day happened to be the last active one of the season. The Schwartzes (1974), for example, reported no evidence that turtles moved to any special hibernating grounds.

As with foraging for food and water, however, this seemingly hapazard pattern of finding shelter also seems to be mixed with a more determinate strategy, at least for some individuals or certain populations. Both Stickel (1950) and the Metcalfs (1970), for instance, reported several cases of turtles re-using forms following intervening travels of up to several days. This behavior suggests at least some kind of positional determinacy governing the movements. They also reported that certain areas, such as thickets or tree falls, seemed to

be more intensively used than others, and that turtles would also utilize the forms abandoned by other individuals. This pattern, in turn, suggests some form of habitat selection, but whether it is strictly related to shelter-seeking or also due to foraging is unclear. Furthermore, I have observed that scats are almost invariably left behind in the forms at the start of a day's travels. Revisitation of form sites, particularly by different individuals, could also involve some communication function. But in any case, such re-usage is not obligatory nor even particularly frequent, and this pattern at most suggests yet another complex strategy.

The Metcalfs also reported a more striking case of recurrent site usage. They found that individuals of T. ornata would, at least on occasion, congregate at certain preferred hibernation sites and that they would even share the same hibernacula. Such denning behavior is characteristic of other reptiles, notably Viperids, where winter mortality may be high and secure hibernation sites at a premium. While winter cold is very possibly the most significant limiting factor in some box turtle populations (Legler, 1960; Schwartz and Schwartz, 1974), such congregations have not been observed in any other population of either T. ornata or T. carolina. Most probably, suitable hibernation sites are normally widespread.

On the other hand, Madden (1975) found individual site-specificity in hibernacula in his Long Island population of T. c. carolina. Although these sites were indeed widely dispersed throughout wooded habitats, individuals would return to hibernate close to where they had overwintered the previous year. I also observed this behavior in my population. In the two turtles I followed to hibernation in suc-

cessive years, one (T7) spent the second winter only about 10 ft from where it had spent the first, and the other turtle (T16) chose sites only 5 ft apart, at least after she established a definite home range (her first recorded hibernaculum was located far from the area of her subsequent movements). Unlike the situation described by the Metcalfs, where even experimentally introduced individuals chose to hibernate in the same places as the natives, a general habitat preference or social function does not provide an answer for this kind of site-specificity. In my own two examples, for instance, one turtle chose its two sites on a steep south-facing slope in an oak-hickory stand, while the other spent its winters near the bottom of a north-facing slope covered with pines. The reason for site fidelity in these cases more likely involves positional memory for sites that have proved successful to the individual in the past.

If this is the case, then box turtles have at least the potential for highly accurate place-learning that can persist over months without reinforcement. Another possible example is nest site selection. Madden (1975) observed clustering of individuals' nest sites between years, all within what he considered to be normal home range boundaries. Stickel (1950) also suspected that off-range sites are similarly returned to year after year, and I also observed one possible case of this behavior (see Chapter II). Legler (1960), on the other hand, found no such evidence for site fidelity in nesting and believed that only haphazard searching was involved. Once again, the answer is possibly that individuals employ mixed, opportunistic strategies in their nest site selection, with a large range of individual variability. In some habitats nest sites are hard to come by and memory



for them is favored. In others a general search for appropriate and widespread sites can suffice.

Such individualistic adaptations enable box turtles to make use of nearly all habitats within their geographic range. At the same time, existence within certain of these habitats requires individuals to be both wide-ranging and sparsely distributed. Coupled with the box turtle's low rate of movements, these factors make encounters between individuals of the opposite sex so infrequent that in most other species the population would wither away. Three other box turtle adaptations allow their populations to persist at extremely low densities.

First, as in all other things, the box turtle is an opportunist when it comes to mating. There is no set breeding season; mating is possible whenever a male and female encounter one another (Ewing, 1933; Allard, 1949; Legler 1960; Schwartz and Schwartz, 1974; Madden, 1975). Such encounters may occur either during a generalized search, or, again, at more predetermined rendezvous. Evidence for the latter possibility exists in the greater incidence of mating that has been observed to occur both preceding and following hibernation (Ewing, 1933; Legler, 1960; Schwartz and Schwartz, 1974). There is also the aforementioned possibility of form-site marking and re-visitation. In neither of these cases, however, is there enough evidence to rule out the possibility that these represent only spurious encounters, reflecting the general mating opportunism in company with some other, more regular pattern of resource exploitation.

On the basis of a second reproductive adaptation, that of sperm storage, Mosiman (1958) theorized that even a completely random stra-

tegy of mate-finding would suffice to maintain a population of box turtles. Ewing (1943) and Finneran (1948) had earlier demonstrated that female box turtles could remain fertile for several years following isolation from all male contacts, and seminal receptacles have since been confirmed by Hatten and Gist (1975). Ewing watched two of his subjects lay normal-sized clutches of five or six eggs even after four years of isolation from male contact, all but one egg of which subsequently hatched (two years of continued fertility appeared to be more the rule, however). On the basis of these findings and on the rates of movements obtained from Stickel's study, Mosiman concluded that "box turtles could at least maintain a stable population, as regards problems of mate-finding, at a density as low as one per four acres without other special mate-finding traits". While his random model does not do justice to box turtle movement patterning (they can travel either farther or less far than he predicted in a year's time), the existence of sperm storage must at least permit the prolonged mating season that has been observed. Together these two adaptations support his basic hypothesis that the box turtle is adapted to low encounter rates between individuals.

Mosiman also noted a third adaptation in support of his hypothesis: the extreme longevity commonly observed in box turtles. A number of anecdotal accounts of shell-carved individuals place the box turtle near the top of longest-lived animals, if not at the very summit. Estimated ages for elderly turtles are often put at over fifty years up to an extreme of 130 years (Schenk, 1886; Flower, 1937; Nichols, 1939; Edney and Allen, 1951; Price, 1951; Graham and Hutchison, 1969). On a firmer foundation are the nearly twenty and thirty

year population censuses conducted by the Schwartzes (1974, Schwartz et al., 1984) and Lucille Stickel (1978), respectively. Both studies are in agreement with the earlier anecdotal records in estimating minimum ages for certain individuals to lie between 50 and 80 years. They also show that sizable proportions of their populations are composed of individuals over thirty years old.

Whatever the maximum age, the well-documented longevity of box turtles was viewed by Mosiman as yet another way of increasing lifetime fecundity for individuals whose yearly mating opportunities are infrequent. Another possibility is that low rates of survival of eggs or juveniles creates selection for multiparity. Predation pressure on box turtles does, in fact, appear to be highest on individuals under three years of age, as a result of the wider array of predators capable of dealing with smaller turtles (Legler, 1960). Legler also believed that nest mortality was an even greater factor in limiting box turtle populations. As a supporting example, Minton (1972) mentions observing during only a single day's walk twenty box turtle nests that had been dug up and destroyed by predators.

Box turtles, even the very young, are not helpless, however, and two aspects of their defensive system gives their freewheeling approach to life its most unhampered expression. In dealing with both potential predators and intra-specific rivals, the box turtle relies on a supremely passive, on-the-spot defense that requires no evasive movements or combat. It is, in fact, the basic chelonean defensive features, retained and modified by the box turtle, that have pre-adapted it for its peculiar approach to terrestrial existence.

Like most Emydids, the box turtle is extremely wary of the approach of larger animals. I was seldom able to surprise a turtle in the act of doing anything but apparently waiting for my approach. Legler (1960) also noted that his subjects would freeze in apparent response to his movements when he was still up to 200 feet away. In addition to their excellent vision (Hertzler, 1972), box turtles probably also rely on their acute auditory sensitivity to low-pitched sounds or ground-borne vibrations (Wever and Vernon, 1956) to detect the approach of potential enemies. Unlike their aquatic relatives, however, which can dive to safety at the least disturbance, the box turtle's most effective response to an approaching predator is simply to stay put and to rely on its cryptic coloration, its highly domed and tight-closing shell, and, ultimately, its remarkable healing powers to escape destruction (Cahn, 1937; Legler, 1960; Metcalf and Metcalf, 1970; Schwartz and Schwartz, 1974). Furthermore, the box turtle's very sparsity and scattered distribution possibly contribute to its defense by preventing any predator from cuing on their patterns (Tinbergen et al., 1967) or from otherwise specializing on these prey that are incapable of effective flight or active resistance (however, biting, musk discharge, and even running have also been reported as infrequent means of defense; Pope, 1939; Neill, 1948; Legler, 1960; Minton, 1972).

The longevity of adult turtles, most of which bear the scars of unsuccessful predatory attacks, is eloquent testimony to the fitness of their defensive system. Only in turtles under three or four years of age is the system incomplete, due to their small size and undeveloped carapacial dome and plastral hinge. In their situation, the

safest strategy is to remain under cover, and this age class is, in fact, almost never observed in the wild even where adults are abundant (Cahn, 1937; Pope, 1939; Anderson 1965; Minton, 1972). Only at this stage of life do the box turtle's movements show any sign of obligatory restrictions. Madden (1975) found through radio-telemetry that hatchlings show no tendency to disperse from the vicinity of the nest site during their first year of life, and that they led a highly secretive existence beneath the leaf litter. The Schwartzes (1974) also found slightly older turtles to occupy fairly restricted ranges.

Once the individual attains a certain minimum size and its shell has assumed the adult form, it is then free to wander much as it chooses. These same defensive features are equally good at negating any possible agonistic restrictions on movements. Although instances of apparent fighting have been reported (e.g., Latham, 1917; Allard, 1935, 1949; Boice, 1970), these can usually be related to conflict over specific food items, particularly in the abnormal conditions of captivity. There is also the possibility that these instances were really mistaken cases of courtship: biting at the female's shell is a normal part of the male's display (Evans, 1953; Madden, 1975).

Whatever the true situation regarding combat, the combination of effective defense, low encounter rates, and the diffuse nature of their resources and mating opportunities makes territoriality untenable (Brown, 1964). Ranges of different individuals, not surprisingly, are found to overlap broadly under natural conditions, and reports of peaceful coexistence far outnumber records of combat (Stickel, 1950; Legler, 1960; Schwartz and Schwartz, 1974; Madden, 1975).

Altogether, these basic adaptations to terrestriality of the box turtle form a consistent, if distinctive pattern. In the pursuit of any one of the goals to its movements — food, water, shelter or mates — it uses the same sort of strategy: a general opportunism employing possibly both search and foreknowledge; a mixture of kineses, taxes, and positional memories. These similarities among the strategies of resource utilization further suggest a second sort of mixture: routes of travel governed by a single, multipurpose set of rules. With the possible exceptions of nesting excursions and journeys towards hibernacula, both of which sometimes appear single-minded, box turtle movements throughout the rest of the year seem adjusted to meeting several of its needs simultaneously.

Taken alone, either of these two possible mixtures pose crucial problems for the traditional paradigms of movement study. If both kinds of mixtures are present, it must be doubted that even a combination of all three paradigms can deal with just routine patterns of movement, let alone distinguish the routine from the extraordinary. The shortcomings of piece-meal, context-dependent methods are obvious enough in their inefficient handling of the organisms for which they were designed. In dealing with the variegated yet paradoxically simple movements of box turtles, can they reveal anything beyond the barest qualitative features that have already been so well described by Breder (1928), Stickel (1950), and others?

Consider what is known just about box turtle residency patterns. Box turtles do indeed possess what anybody who believes in the concept would call home ranges. That they display some degree of site-fidelity is not, perhaps, surprising given the evidence mentioned above for

their use of positional memory. What is surprising are the extremes of ranging behavior shown by these animals. Among terrestrial vertebrates, box turtles are candidates for records both for the longest home range tenure and for the greatest duration of individual dispersal.

The observed lengths of residency within individual ranges (or small study areas; evidence for individual range constancy is not always mentioned) appears to be limited only by the amount of time allotted for the investigation. Short-term studies report high percentages of individuals occupying the same ranges over periods of several years (Nichols, 1939; Stickel 1950; Williams, 1961; Yahner, 1974; Madden, 1975). Longer-term studies likewise report at least some individuals residing in the same areas over periods as long as 13 years (Metcalf and Mecalf, 1970), 19 years (Schwartz et al., 1984), and 30 years (Stickel, 1978). Two anecdotal records indicate a potential for essentially life-time residencies in these very long-lived animals: Price (1951) reported a case in which a box turtle was found within the same woodlot (dimensions not give) 46 years after it was first marked there; Schenk (1886) reported a net displacement of only 0.5 miles for an individual over a period of 61 years!

In contrast, Kiestler et al. (1981) followed three dispersing adult males over nearly straight courses of two, three, and ten kilometers. The last one of these turtles took nine months to travel that distance (interrupted only by hibernation), and is perhaps the only individual of any species that normally occupies home ranges to have been observed in transit for that length of time. Possibly even longer distances could have been recorded if these animals had not

been lost or abandoned. It appears that only the persistence of the investigator determines the observed lengths of transiency in these animals.

While the existence of such transiency is clearly established, the well-known difficulties in studying this phenomenon (not just in box turtles) make vagrants seem like wraiths slipping through the more corporeal populations of resident animals. The numbers of vagrant individuals are always much harder to estimate than those of the more easily found and tracked inhabitants of stable home ranges. Furthermore, it is also difficult to distinguish true dispersers from round-trip excursionists. The nestward movements of females, the homing movements of turtles following any sort of excursion, and the routes of displaced individuals generally are all similar in their lengthy straightness to those of the true dispersers described by Kiester and the Schwartzes (Breder, 1927; Stickel, 1950; Legler, 1960; Lemkau, 1970; Metcalf and Metcalf, 1970; Schwartz and Schwartz, 1974; Madden, 1975). Although some form of transiency is commonly observed in box turtle populations, its true nature is hard to assess.

More surprisingly, the same is true for the patterns of movements associated with residency, although not because of mere problems with observability. The diversity of ranging patterns within even a single population of box turtles is as great as, if not greater than, has been reported for any other organism. Stickel (1950) found that, while many of her subjects traversed most parts of their ranges fairly evenly and frequently, others commonly moved through a series of intensively used patches. At one extreme were animals that moved more-or-less regularly between widely divided ranges, the intervening



ground being scarcely utilized. Similar findings are reported in the other studies of box turtle movements.

There does appear to be one glaring omission in the box turtle ranging repertory, the bivariate normal utilization distribution so beloved of students of home range (only Madden, however, actually looked for this pattern statistically and failed to find it). But to simply describe the observed patterns as "patchy" and to resort to non-parametric methods (as Madden did) fails to capture what is going on. The most characteristic features of box turtle movements (individual dynamism and populational diversity) cannot be conveyed by any sort of static, area-based models.

The range of variability in box turtle movements is so great, in fact, that the patterns associated with residency appear to grade smoothly into those associated with transiency, forming a continuum. Not only do normally resident animals occasionally make off-range excursions lasting for periods up to weeks, and transients briefly exploit resource patches through means of convoluted movements, but the entire patterns of movement of certain individuals appear to fall in between the extremes. Is it then even possible to define categorical home ranges or vagrancy for box turtles?

In the absence of either rigid boundaries, networks of fixed paths, or statistical tailings-away of activity out from foci of activity, the home range paradigm is silent about the mode of operation of positional constraints. Without any apparent absolute reliance on spatio-temporally predictable resources, the paradigm also provides no clear expectations about the function of long-term positional memory. While the pessimistic view of Brant (1962) concerning

the very concept of home range also seems too extreme to apply to animals capable of showing decades of faithfulness to particular areas, a more dynamic and less categorical concept is clearly desirable.

The more process-oriented paradigms of search and orientation, however, also have their problems with flexible, opportunistic patterns of movement. Even more than studies of home range, these paradigms are context-dependent and the movements of box turtles seem to be especially difficult for which to define the governing circumstances. Not only does the box turtle's basic biology suggest a polyfunctionality and multimodality for any particular route of travel, but a continuum of ranging patterns would further suggest that only quantitative differences exist in the control of widely dissimilar-looking patterns of movement.

In terms of routine activities — the normal, daily travels in search or in pursuit of food, water, shelter, mates, and so on — the routes of travel taken by transients and residents may be governed by much the same mixture of kineses, taxes, and short-term positional memories. Both transients and residents have been observed in the performance of all the above functions. For example, Kiester et al. (1982) observed all three of their dispersing males to mate en route. Others, including myself, have recorded matings both within the normal ranges of the participants and during the course of round-trip, off-range excursions. Even though these animals' routes differed in their relative straightness (or convolutedness), it would be difficult to assign a specific context to each variation, at least based on "normal, routine" behavior.

In the same way, even extraordinary movements, such as nesting or other "off-range excursions", possibly do not differ fundamentally from the more routine movements of particular animals. Again, the same sorts of kineses, taxes, short-term positional memories, and now long-term positional memories could be employed in traveling to rarely visited sites off range. Here, even knowing the specific context of a particular route — travel towards a nest or hibernaculum — might not be of aid in differentiating the types of control mechanisms that govern the routes.

Without a one-to-one correspondence between contexts and specific kinds of control over the routes, the interpretation of the distributions either of turns or of azimuths becomes hazardous, at best. While such correspondences can be made (in theory) for single-minded searchers, such as bumblebees or thrushes, or one-track ballistic missiles such as homing pigeons, is it really worthwhile to look for them among organisms as multifarious as the box turtle?

## **I.H. Thesis and hypotheses**

I contend that analysis of the features of the routes in themselves will provide more information about the nature of their underlying control, at least initially, than can any method using more external sources of information. In contrast, attempts to establish experimental controls on the variables of the route processes defeat the very purpose in studying the overall movement patterning of free-ranging animals. Equally fruitless seem efforts to define a context for every twist and turn of a path, especially in terms of a static utilization pattern, before some understanding of the route processes is acquired, by whatever method.

I further believe that stochastic walk models provide the best means of analyzing the features of routes as such, at least where they represent the action of a single control process. This belief holds whether the routes are considered in or out of their environmental context. More than any use of route fragments (point fixes, turn angles, or step azimuths), extraction of the relational information contained only in long sequences of movement has any chance of deciphering an animal's routes of travel, through whatever contexts they may lead.

The power of this approach can be gauged by the way it opens up new avenues for testing the apparent diversity of ranging patterns. My primary working hypothesis regarding box turtle movements is that only quantitative differences among the route-control parameters need be invoked as an explanation for the observed range of route patterns. These differences form a continuum, not a set of qualitatively distinct categories. After first ruling out a completely random walk as

a model for movements, it seems reasonable in any study of ranging patterns to try next to fit as parsimonious a set of control models as possible to the observed range of route behaviors. Only after this procedure has been carried out does it then become time to hypothesize why either the parameters of the models vary or why different models replace one another in changing contexts.

To test the hypothesis of a continuum, however, is not all that easy; instead I have chosen only an approximate approach, by attempting to show that the extremes of ranging patterns observed in box turtles do not differ in any qualitative way. This procedure does require at least a minimum of contextual information for distinguishing the groups to be compared; the distinctions I make between residents and transients are provided in Chapter II. There are further limitations on this approach according to how finely the various route processes can be distinguished. While relatively few in number, there are at least enough kinds of stochastic walk models to test two major subclasses of my working hypothesis against the alternatives supplied by the more traditional paradigms of animal movements.

The specific null hypotheses ( $H_0$ 's), their alternatives ( $H_a$ 's), and their respective predictions ( $P_0$ 's or  $P_a$ 's) are outlined as follows. Details will be provided later on.

$H_{01}$ : The differences between "Residents" and "Transients" (see Chapter II) are explainable simply in terms of the parameters of a purely sequential model.

$P_{011}$ : "Residents" are more easily deflected from a course than "Transients" and hence tend to travel

in a more convoluted path and stay within a particular area for longer periods of time.

P<sub>o12</sub>: "Residents" show a greater tendency towards path curvature, which would also have the effect of keeping them within a particular area for longer periods of time.

H<sub>a1</sub>: The differences between "Residents" and "Transients" are at least partly due to differences in the kinds of sequential rules that govern their movements.

P<sub>a11</sub>: "Residents" movements are convoluted due to absence of directional control mechanisms (as in random or klinokinetic search) while those of the "Transients" are governed by an active orientation process (either a true taxis or some form of turn alternation or compensation).

P<sub>a12</sub>: "Residents" movements are more area-intensive than a random walk due to some form of systematic search patterning; "Transients" are then simply those animals moving according to a purely random walk or to some form of directional model.

H<sub>o2</sub>: If positional constraints are found to exist in box turtle movements, then both "Residents" and "Transients" show them but differ only in their strength.

P<sub>o21</sub>: "Residents" show the operation of spatial constraints over much shorter distances than "Tran-

sients"; "Transients" either have especially large ranges over which they wander widely or they are excursionists on their way to or from a more typical home range.

P<sub>o22</sub>: "Residents" and "Transients" show the same spatial scale of operation of the constraints but "Transients" have a higher rate of drift of their entire "home range".

H<sub>a2</sub>: True Residents exist and are distinguished by their possession of positional constraints on movements; true Transients lack such spatial constraints.

P<sub>a21</sub>: Residents and Transients are otherwise similar in the nature of their directional rules of movement, either showing a definite sequential pattern or not.

P<sub>a22</sub>: They can also differ according to both sequential and positional control of movements. This prediction is further subdivided similarly to P<sub>a11</sub> and P<sub>a12</sub>; the major distinction here is that true spatial constraints have been established for the residents only.

Although this outline is somewhat sketchy, it does indicate a rough progression from the simplest models (including the completely random walk) to the most complex (such as represented by a true home-range). While even finer subdivisions would be desirable, these should be quite enough to challenge any approach to studying animal movements.

Furthermore, this plan may represent the only way of grasping the protean nature of box turtle movements, at least for the time being. Whereas in other organisms many of the steps can be bypassed (as is the rule for the hypothesis of completely random movements), in the case of the box turtle nothing should be assumed in advance! Indeed, the diverse ranging patterns of the box turtle provide an ideal proving ground for this entire approach to the study of movements. If this program is at all successful in handling the box turtle, then surely it can be generalized to many other organisms.



## **CHAPTER II. METHODS, MATERIALS, STUDY SITE, AND POPULATION**

### **IIA. Trailing**

The method I used to record box turtles' routes of travel antedates radio-telemetry by about three thousand years. Greek mythology credits the Minoan princess, Ariadne (or, in some accounts, the archetypal scientist, Daedalus) with inventing a simple and elegant method whereby the subject of a study lays down a trace of his own passage. One end of a ball of thread carried by the subject (originally Theseus, Prince of Athens) is staked at the beginning of the investigation and unwinds as the subject moves along. All the labyrinthine twists and turns involved in search, orientation, and homing can then be later studied at the leisure of the investigator. Occasionally, even the remains of past behavioral interactions, such as a slain Minotaur, can be detected.

In more recent times, this method has come to be associated preeminently with studies of box turtle, although it has also been successfully used for other species (as in Breder, 1927; Dole, 1965; Emlen, 1969; Grubb, 1970 ; Gibbons, 1979; and Miles et al., 1981; Boonstra and Craine, 1986). For its introduction into animal movement studies, particular credit is due to two modern Ariadnes: Ruth Breder (1928), who pioneered its use for studying both box turtles and toads, and Lucille Stickel (1950), who greatly improved the design of the housing device and used the method to obtain the best data on animal movements prior to radio-telemetry. In addition to these two classic studies other investigations of box turtle that have made use of the

spool method include Gould (1957, 1959); Legler (1960); Lemkau (1970); Metcalf and Metcalf (1970, 1978); Dolbeer (1971); Reagan (1974); and Schwartz and Schwartz (1974).

In more recent years the use of radio-telemetry has begun to supplant Ariadne's method even in studies of box turtles (see for instance Schwartz and Schwartz, 1974; Madden, 1975; and Kiestler et al., 1982). As a means of finding a subject for periodic sampling of location or behavior, the use of portable radio-tracking equipment is unquestionably the superior method. The investigator does not have to worry about thread running out and his subject becoming tethered or breaking free. He only needs to handle his subjects at rare intervals for battery changes rather than having to handle them every day or so for spool changes; a given animal need be checked only every couple of weeks.

For these reasons Madden, in particular, argued that radio-telemetry is the superior method. However, I disagree, at least where routes rather than point-fixes are the main interest. Compared to radio-tracking, Ariadne's technique is more efficient in its use of time; the observer does not have to locate the turtle repeatedly in order to monitor its changes in position. Furthermore, since the production of data is not dependent upon the presence of the observer, the use of this method can actually result in less biasing of behavior by the observer.

Even compared to the much more sophisticated (and much more expensive) method of automated, remote radio-triangulation, Ariadne's method still has advantages. Although in this case less efficient in use of time, it is more accurate. A big radio-tracking installation,

such as the well-known University of Minnesota station at Cedar Creek (Cochran et al., 1965) can monitor the movements of many animals simultaneously and without an observer ever setting foot in the field except to tag an animal or to change its batteries. But while potentially thousands of fixes of an animal's location can be gathered daily by this method, the error of any one fix is often quite high (Heezen and Tester, 1967). For example, the error polygons for fixes in a study of squirrel movements at Cedar Creek were 15 meters on a side (Connolly, 1979). Only on even, unforested terrain (where signal reflection is minimal) and where the angle of triangulation is 90 degrees, can tracking stations reduce their error to that of the average for the spool method, approximately 0.5 square meters (e.g. Banks et al., 1975).

The other advantage automated radio-triangulation has in fixing the animal's position in time as well as in space is offset by the thread-trail follower's ability to study a track in situ. The investigator examining a physical trace of the actual route of travel is free to divide it up into a series of "natural" segments, if the route is marked by sharp alterations in course, or other behavioral markers. Or he can divide it into uniform length segments if such distinctions cannot be made. Either method of sampling has advantages over the time-dependent method of remote radio-triangulation.

Materials. Another obvious advantage Ariadne's method has over radio-tracking is in the availability and simplicity of its trailing devices. While radio-transmitter packages are more compact and lightweight, the spool packages are only slightly less so, and are more easily constructed from simple household materials. Of the several

models that have been developed, I chose to use the one invented apparently independently by Reagan (1974) and the Schwartzes (1974). This device makes use of discarded 35mm film containers to house the spools and plastic tape to attach the housing to the turtle's carapace. The only modification I made to this design was to push a nail through the cannister to serve as an axle for the spool.

Unlike the earlier trailers or open-ended spool mountings used by Breder and Stickel, this housing completely encloses the spool. The thread feeds out of the film container only through a small hole melted into its side; the spool, consequently is more protected from both the weather and snags. The flexible attachment of the cannister to the rear of the turtle's shell by means of waterproof tape also has the advantage that females wearing these devices are supposedly still able to mate. Reagan reported observing several occasions in which males had successfully pushed the housing forward as they had climbed onto the females' shells. Although I myself never observed any such successful matings (but did see several apparently unsuccessful attempts), it is certainly true that this design is less likely to interfere either with mating or nesting than the earlier rigid designs.

In any case, normal daily activities are not hindered in any important way by the spool housings. The cannister is taped to hang below the top of the carapace, and its width is only slightly greater than the turtle's shell, if at all. During the entire course of my study I never observed any turtle entangled in thickets or stuck under logs because of the housings. Some individuals even used burrows without any apparent difficulty.

For construction of the spools I followed the design used by Emlen (1969) in wrapping thread onto sections of plastic drinking straws. To keep the thread from unraveling from the ends of these spindles, I added conical end-pieces constructed from laminated note cards. Each spool thus fashioned was able to hold up to 300 yds. of thread wound onto them by means of a modified egg-beater. The life-time of one of these spools was on the order of several months.

My choice of thread material was 100% polyester. This proved to be much stronger and more durable than cotton. Thread-trails of polyester could be uncovered more-or-less intact from the leaf litter a year or more after having been laid down, whereas cotton would rot after only a few months. Polyester also had the advantage of not being too strong. Unlike the nylon monofilament used by the Schwartzes and Legler, polyester trails will break after having been snagged by an animal's (usually a human's) foot and dragged only a short way from its original position. Although such breaks were occasional nuisances, they allowed the greater part of the trails to be preserved without distortion.

The overall weight of the housing plus a loaded spool was about 25 g, between 4% and 12% of my subjects' body weights. The turtles seemed to be in no way encumbered by these loads. A much more serious problem was the turtles' becoming tethered when their thread ran out or, much less frequently, when they became entangled in the thread itself. To prevent this from happening the turtles needed to be checked and the spools replaced every day or so depending on the level of the turtle's activities. Only rarely would a turtle use up one or more spools within the course of a single day's travels.

Whenever possible, I checked each turtle after it had dug its form for the night, both to avoid disrupting the course of their normal daily activities and to make use of their usual quiescence at that time of the day in order to change spools without handling the turtles themselves. At other times of the day, certain individuals had to be restrained during the respooling operation.

These disturbances, as well as tethering, were more-or-less unavoidable drawbacks of the spool method, but I do not believe that either of them resulted in any serious distortion of the turtles' behavior. Both Stickel (1950) and the Schwartzes (pers. comm.) found that the ranging patterns of individuals provided with spools were similar to those of other individuals studied by simple mark-and-recapture. Furthermore, the Schwartzes' use of Labrador retrievers to locate turtles would seem to be a much more serious form of harassment, yet their subjects' movement patterns seem in no way different from those of other populations. Indeed, they have now followed certain of their subjects using this method over the entire eighteen years their study has lasted to date.

## **II.B. Surveying**

Upon inspection of my first thread trails, I found that I could not easily divide them up into "naturally" defined segments. Although form sites and occasionally obvious feeding sites and detours did punctuate the trails, they were too few and far between to represent the behavior over a trail as a whole. The alternative method I chose was to divide each day's movements into a series of segments of uniform length plus any remainders needed to fix the terminal form site (or, more rarely, any other possible point of discontinuity in the sequence).

Surveying the trails in this way was most naturally carried out by means of traverses. Rather than locating each point to be surveyed relative to a grid of fixed referents, I would start at one end of a section of trail and work forward along it, dividing it successively into straight-line segments characterized by distance, azimuth, and slope. This method has the advantage over the more traditional methods of home range studies or even of those used in remote radio-triangulation, in that the polar coordinate form of the data is obtained directly from the surveys instead of secondarily from the resulting maps. The direction and distance of any step in a traverse are subject to less error in measurement, since the relationship between a segment's endpoints is measured only once and directly instead of being obtained indirectly and from two separate measurements. The traverse method has an additional advantage in being able to follow the movements of a subject no matter where it strays.

Fixed referents were still needed, however, both to locate separated trails relative to one another and to allow the measurement and

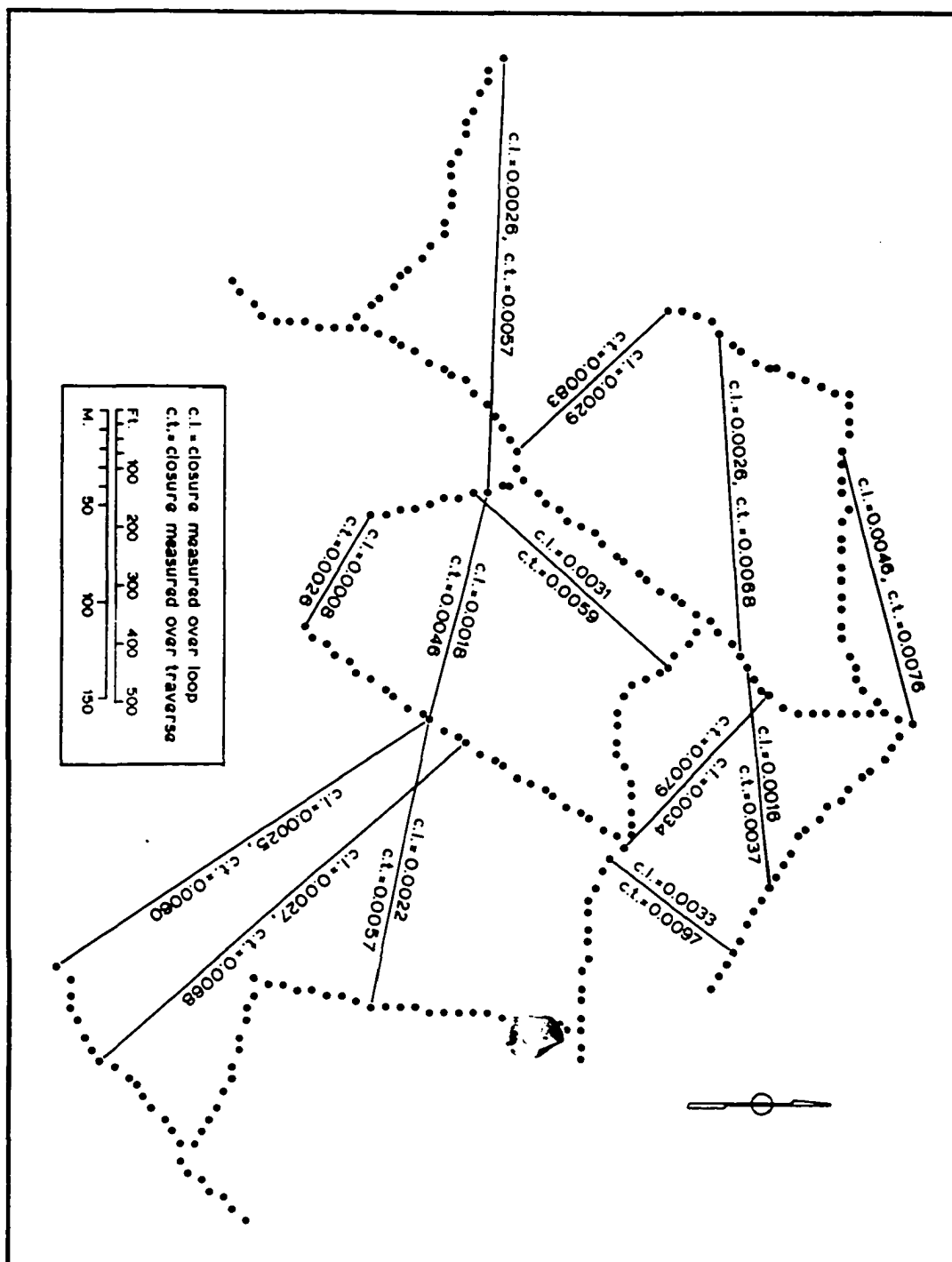


adjustment for closure, a form of error unavoidable in any survey. For my purposes, however, I only needed to connect my traverses into the system of control lines at infrequent intervals. Consequently, the system of referents could take on the form of an open, expandable network rather than that of a tightly bound group of cells.

The final form of the control net (Figure 2.1.) was itself obtained by means of traverses, which for the most part followed the course of old farming and logging roads. As can be seen, the ends of these traverses are not all connected and the control network was not itself adjusted for closure. I can justify this only by the fact that the errors of closure I did obtain in the route traverses did not seem to require the extra labor that would have been needed to join all the widely separated ends of the control lines. Furthermore, I added sections to the control network throughout the course of the study.

Equipment and measurements. I chose my surveying instruments with regard for the exigencies of solo surveying, for manageability and portability as well as accuracy and precision. I made all angular measurements using a Brunton Pocket Transit mounted on a jacob staff. Azimuths were read to the nearest degree and slope to the nearest ten minutes. I measured distances in the traverses using a range-finder (Optical Tapemeasure). Its specified accuracy at 25 ft was 99.2%, or about 2.5 inches. Sightings with the rangefinder were made either onto the jacob staff or onto an eight-foot-long ranging pole. Both of these were plumbed with the use of a staff level. For extremely short distances (eight feet or under) the ranging pole itself was used for measurements since it came conveniently marked in feet. All distances in the surveys of the turtles routes

**FIGURE 2.1** Control network and illustration of selected closures  
obtained over widely separated parts of the system.



were read to the nearest foot. For the control lines, greater accuracy was obtained by use of a tape measure and the aid of a second person. Distances in the control lines were accurate to the nearest inch.

The standard unit of length I chose to employ for all traverses was 25 ft. Although this was an arbitrary choice, I considered this distance to be both long enough to minimize the importance of any imperfections in the thread trace and still short enough to capture the details of the movement patterns at the scale of measurements I was interested in. This distance was also the maximum at which the rangefinder could be read to the nearest half foot.

I also occasionally needed to use longer or shorter length segments in order to detour around obstacles. I also used non-standard lengths to record the location of form sites, obvious detours, and sites where the turtles had either been handled or had become tethered. All these places represented possible points of discontinuity in the sequences, the influences of which I originally wished to examine. Altogether, these non-standard segments amounted to only about 15% of the total. Even when they are pooled with the standard segments, which I have done for the analysis of day-ranges, any bias they introduce by being of different length I believe to be negligible.

### **II.C. Traverse Adjustments and Cartography**

For the analysis of either the directions and distances of the surveyed segments, or the angular relationships between different segments, the raw form of the data provides the most accurate information. While all measurements contain some error, for any analysis that treats the segments as isolated units this error need not be corrected unless it is excessive. On the other hand, for analyses that deal with changes in position over a series of steps, this is not the case; where the calculations of location are concerned, the errors in a traverse are cumulative. Small errors average out over a series, but any unbalanced error made during the course of a traverse will throw off the calculated positions of all subsequently surveyed points.

Analyses affected by these errors include any that involve calculation of the distance traveled in a number of steps or of the square of this distance, in other words, two of the most important methods for dealing with sequential data through the use of walk models. Also affected are any analyses that make use of segments obtained indirectly from the maps produced from the surveys. These include analyses of the overall lengths and directions of the day ranges and of any relationships between these segments.

This problem could prove an important drawback of the traverse method when compared to the use of grids: when each point is surveyed relative to fixed referents, positional errors are non-cumulative. However, the traverse method provides a way of measuring the error in a series of positional measurements that is not possible when each point is fixed independently. When a traverse is brought back to its

starting point and forms a closed loop, or when the last point in a traverse coincides with a referent of known location, then the amount of positional error in the series can be found approximately in what is termed the error of closure, the gap between the calculated position of the last point in the traverse and the position required to close the loop or match the site of the referent. Similarly, any angular discrepancy between the direction of the last segment and the angle required to intersect the desired point is termed the angular error of closure. Once such errors are detected, the route can either be re-surveyed or the error apportioned over the entire route to force the calculated position of the last point in the survey to match its known last coordinates.

It should be clear that detection of such error is possible only in the traverse method. Where points are each fixed independently relative to a fixed grid, errors can only be detected by eye and usually go unnoticed. While these errors in themselves are often small, they result in more important errors in the calculated lengths and directions of the indirectly obtained path segments, as was mentioned above.

While errors of closure can be determined for each route separately, by simply connecting its endpoints by way of an intermediate traverse of one or more steps, that method would be highly inconvenient. A fixed control network saves this effort by allowing the endpoints to be tied into an already existing system of intermediate traverses. These control lines are, however, themselves subject to cumulative errors in position, but since they involve fewer steps than the actual routes, more effort can be economically expended in

making them as accurate as possible. I did that by using a tape measure to set the distances between the the control points.

Given the accuracy of the control network, all error within a closed loop created by a route plus the control lines can be can be assigned with some justification to the route alone. That error needs to be eliminated anyway if separate routes are to be plotted with respect to one another on a grid of fixed reference points. While a certain amount of irreducible error will remain in both the routes and the maps, if care is taken this error will be relatively unimportant. Some idea of the accuracy of my surveys can be gained from inspection of Figure 2.1. This shows selected closures obtained from route traverses linking widely separated points in the control network. In calculating these closures, error is shown relative both to the total length of the loop, control lines included, and to just the length of the turtle's route.

All the routes of turtles residing on the study area were tied into the control network, either directly or through the use of supplementary traverses that were considered to contain error comparable in magnitude to the surveyed trails. The routes traveled by transient animals, on the other hand, usually terminated far from the study area and were not tied back into the control lines. From estimates of closure obtained from the residents, however, I do not believe there is much problem in treating the routes of the transients as though they were error free.

The average errors of closure for the Residents are presented in Table 2.1. The errors during 1975 are shown separately since the surveys during that year were done before the control lines had been

**TABLE 2.1. AVERAGE ERRORS OF CLOSURE**

		No. of Segments	Total Distance	Error		
				Angular*		Length**
				Horiz.	Vert.	
Residents						
	1975	1425	31056 ft. (9466 m.)	0.062	0.018	0.027
	1976 & 1977	2022	41932 ft. (12781 m.)	0.041	0.012	0.008
	Total	3448	72988 ft. (22247 m.)	0.050	0.015	0.016
Transients						
		601	12930 ft. (3941 m.)			
Experimentals						
		576	13049 ft. (3977 m.)			

\* Sum of the angular errors divided by the total number of segments

\*\* Sum of the length errors divided by the total distance traveled



put in place. Until the end of 1975 I was not certain how far the study area would extend nor in what directions. The first lines of the network itself were laid down primarily to connect stakes that had been placed to mark these previously surveyed routes. By the time the closures for these routes were determined, it was too late to re-survey sections that contained large errors. Out of a total of 62 closures, I had to let stand 10 that had errors larger than 4%. In subsequent years, errors of this magnitude were always quickly caught and the routes re-surveyed. Since all but two of the transients were studied after 1975, the closures for the Residents after that year are presumably typical for them as well.

Once the closure within a particular section of a traverse had been obtained within acceptable limits (1% error), the calculated positions of the traverse were adjusted by apportioning the error over all its individual steps. The method I followed was the well-known Transit Rule, which assumes that the angular measurements were made more accurately than the distance measurements, as was clearly the case in my surveys since I made use of a rangefinder rather than the more standard tape-measure.

Angular error is apportioned first, equally over all the steps. This brings the heading of the last segment directly in line with the known location of the last point in the survey. The distance error is next apportioned in a way that does not disturb the already corrected bearings. Instead of equal apportionment over all the steps, the transit rule adds greater correction to the longer steps on the assumption that they are the ones more likely to be in error. Each dimension is considered separately according to the following formula:

$$\frac{\text{correction to be added to step i along dimension x, y, or z}}{\text{length of step i along x, y, or z}} = \frac{\text{total closure along x, y, or z}}{\text{total length of the traverse along x, y, or z}}$$

It should be noted that I have departed from surveying tradition (Brinker, 1969) by treating the vertical components of the steps analogously to the horizontal components. I likewise adjusted the vertical angular error of closure (in the slopes). The more usual approach in traverse adjustment is to deal only with the projection of the traverse onto the horizontal plane. This flattening of the traverse is normally done even before the closure, both angular and distance, is determined.

The main reason for my departure from the standard approach is that I wanted to use my traverses to collect data not normally obtained by this method. Ordinarily traverses are used for boundary surveys rather than for leveling; both the approach and the instruments used in the two methods are different. In my study, however, I used the vertical components obtained by the traverses to produce contour maps by means of the SYMMAP computer program. This package takes the corrected coordinates of the traverses and smoothly interpolates elevations between them, completely covering the area to be mapped. Since the traverses criss-crossed back and forth over the study area, the density of fixes was quite high over most of its extent and the interpolations of elevation between them are correspondingly accurate (see Figure 2.4).

The output of this program is a contour map showing any specified interval between elevations (see Figure 2.3). SYMMAP also gives a

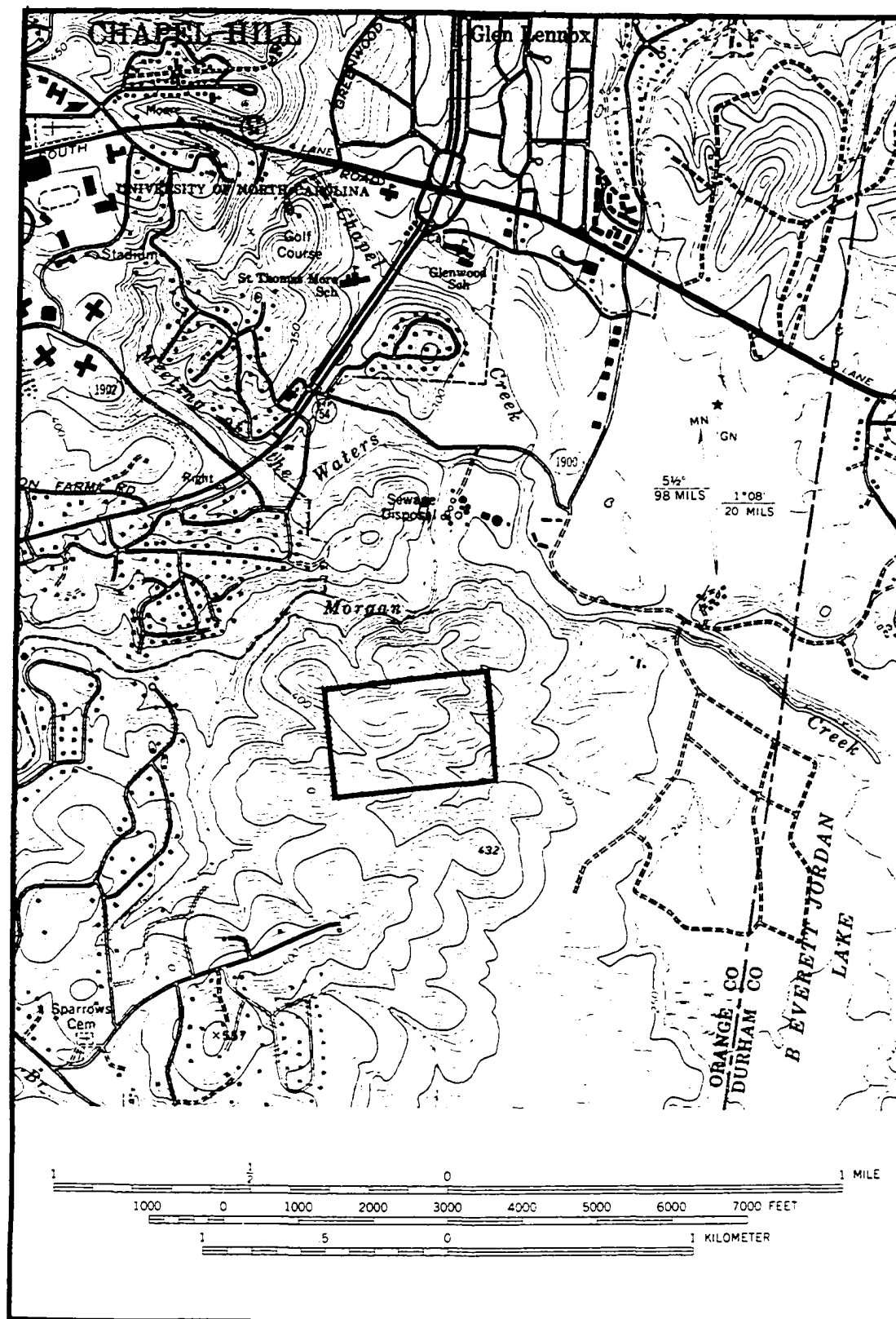
base map of all the plotted positions of the segment endpoints projected onto the x-y plane. The results of this last operation are shown in Figures 2.4, 2.5, 2.6, and 2.7. The corrected Cartesian coordinates that were used for making the maps were also used for all analyses that involved vectors not directly obtained in the surveys (such as day-ranges and higher scale re-partitioning of the routes). While I did not actually make use of the elevations in this study, mapping my routes in this way at least gives me the option of doing this sometime in the future. I highly recommend this entire approach to surveying and map-making for anyone interested in any sort of study of movements, especially where accurate, detailed topographic maps do not already exist.

## II. D. Description of the Study Site

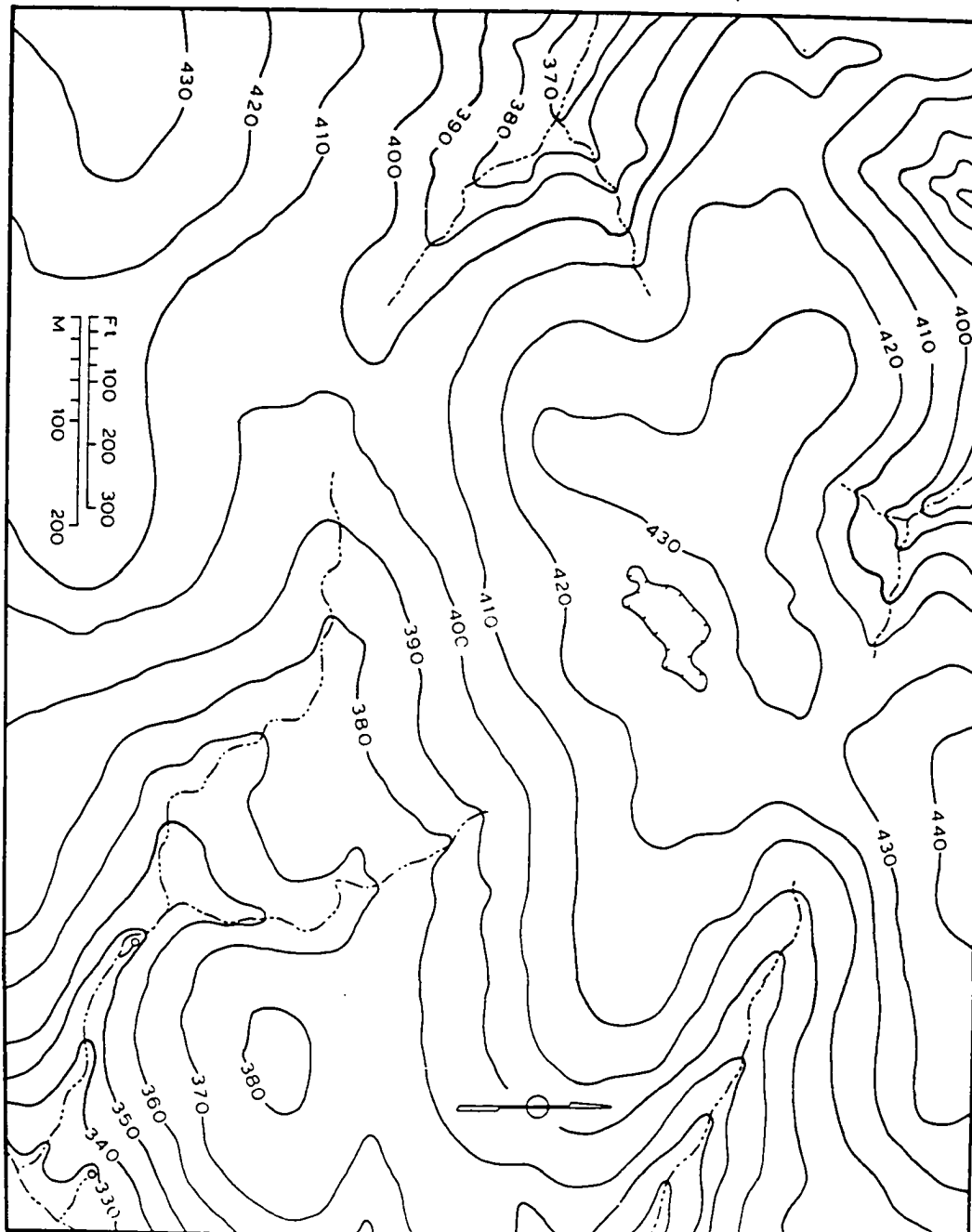
The area in which I worked is located in southern Orange County, North Carolina, approximately two miles south of the University of North Carolina campus (see Figure 2.2). Although my base of operations was at UNC's Mason Farm Biological Reserve, most of my study was conducted on adjacent land owned by Mr. William Lanier Hunt of Chapel Hill. This property was somewhat more remote from foot traffic than the Reserve, an important consideration for anyone using Ariadne's method of tracking. It also was more representative of the prevailing Piedmont Biological Province surrounding Chapel Hill than was true of the more unusual lowlands of the Triassic Basin in which Mason Farm is situated.

The topography of the site is characteristically upland; it was situated atop a northeast-pointing ridge approximately 400 ft. in average elevation (a detailed contour map of the area, produced by the SYMMAP program, is shown in Figure 2.3). The area is well-drained by four moderately steep watersheds (feeding separately into Morgan Creek), and surface water was normally present only at a few seeps and springs located in the Yancey Brook drainage at the site's southeast corner. More irregularly and temporarily, standing water also occurred in a large vernal pool (a breeding site for Ambystoma maculatum and A. opacum) located near the highest point on the study site. In normal years this pool holds water through May and into June, but is dry through the rest of the summer. In the wet year of 1975, however, it filled again in August, while in the dry year of 1976 it dried out earlier than usual.

**FIGURE 2.2** USGS topographic map for the Chapel Hill Quadrangle,  
Orange County, North Carolina, 1978 (photo-revised in  
1981).



**FIGURE 2.3** Contour map generated by SYMMAP from the three-dimensional coordinates corresponding to the points shown in Figure 2.4. Contours for areas outside the limits of the core area were adjusted somewhat to match those of the University of North Carolina's property map. Broken lines represent surveyed stream channels (intermittant); circles represent springs; and the one contour line with inward pointing projections represents the boundary of the vernal pool.





Also characteristic of the Piedmont is the site's history of human occupation. Prior to the early 1900's, the entire ridge was settled and under cultivation; three farms divided its length. Today, however, only traces of two of these farms remain and the third has been deeded to the University. As is true for the Piedmont generally, farming on the thin, rocky, and residual soils of the ridge-tops was marginal, at best, and erosion along with well contamination led to its abandonment over wide areas.

On the study site itself, the main signs of past human presence are deeply rutted wagon tracks, old furrow marks and stone piles, and a few catchement dams that were built within erosion gullies in a futile attempt to save the soil. Just south of the study site stand the stone chimneys and collapsed outbuildings of one of the long-abandoned farms. The last major disruption of the area occurred in 1949, when Mr. Hunt selectively timbered part of his property. This operation left behind a large sawdust and slab pile, providing one of the most prominent landmarks of the study site.

The cycle of clearing, cultivation, and abandonment has given the Piedmont forests a characteristically patchwork appearance. Although the climax community is hardwoods dominated by oaks and hickories, numerous interspersed stands are in earlier stages of succession dominated by a pine overstory. My study site was typical in this regard. A fairly mature stand of loblollies and short-leaf pines with a hardwood understory of red maple, dogwood and sourwood was located mostly south of the Yancey Brook drainage and surrounding the old farm site. Over the rest of the study area, a diversity of oaks and hickories prevailed, with an understory similar to that of the pine

stand. In the lower areas there was also a moderately dense shrub layer dominated by viburnums, while on the more xeric slopes and ridge crests, shrubs and ground cover were sparse.

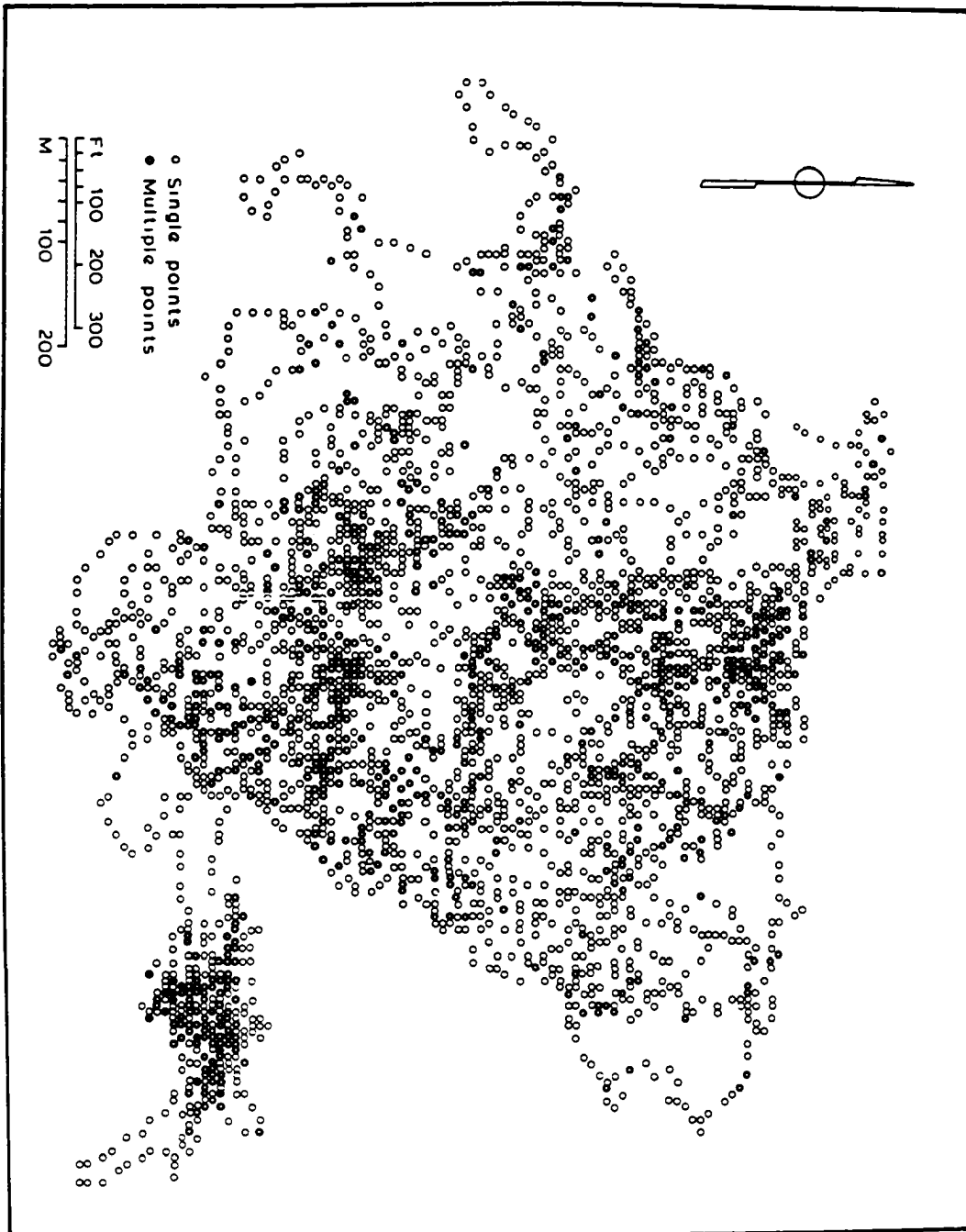
## II. E. Description of the Subjects

Perhaps because of the exhaustion of its soils (from which it is still recovering), its dryness, its lack of extensive edge habitat, or its recency (for box turtles) of human occupancy, the study site appeared to support an especially sparse population of turtles. The core area of the study site, shown in Figure 2.4, comprised the "normal" ranges (plus possibly a few short excursions) of eight animals considered to be "Residents". It also encompassed the points where all other subjects of the study were spooled. Eighteen of these animals appeared to be "neighbors"; their ranges either overlapped the core area for lengthy periods within any one season or they reappeared within it at widely separated intervals over the six years of the study. If these animals are considered to be, on the average, "half-resident", then the overall resident density is estimated at 0.5 per acre (1.2 per hectare).

In contrast, Stickel (1950) used a similar reckoning to estimate a density of 4.6 residents per acre on her bottomland site. Other estimates of the overall adult population, arrived at by less comparable methods and assuming transients to be a minor component, include the following, all for upland populations of Terrapene carolina: 3.6 per acre (Williams, 1961), 7 - 9 per acre (Dolbeer, 1969), and between 7.3 to 10.7 per acre (Schwartz and Schwartz, 1974).

Stickel also agreed with these studies that true transients, although difficult to identify and count, made up only a small part of her population at any one time, roughly 6.7%. In contrast once again, my study population appeared to have a high proportion of "transients". Fifteen turtles were seen only once on the study site, and

**FIGURE 2.4** Core area of the study site, consisting of all surveyed points within the home ranges of resident subjects. The points were plotted as part of the SYMMAP output.



the eleven of these that were trailed for any distance, moved straight out of the area, some quite far before being lost or released. Following Stickel's definition of "transiency", their proportion in my population was approximately 37%. Even if these animals were actually just distant "neighbors" rather than true vagrants, their contribution to the figure for population density is still only slight.

It is likely, however, that any attempt to measure the proportion of transients in a population will produce gross underestimates. Furthermore, without the standard use of trained dogs to census even the resident population (used with great success by the Schwartzes), and without even any standard definitions of "residency" and "transiency", comparisons among these populations appears to be hazardous at best. Nonetheless, the low densities of residents and high numbers of apparent transients do appear to represent actual differences in my population from those of other studies.

In any event, it is the ranging patterns of individuals that are of interest here, rather than the population structure, and the diversity within my population appears to be quite similar to that described by the other studies. There was certainly enough representation at the extremes of ranging behavior, and the conditions of the null hypotheses under examination do not require much more than fairly arbitrary division into general "residency" classes. For the purposes of this study only two such classes need be defined for the naturally occurring population, while a third group was brought in from outside the area for the sake of testing a secondary hypothesis, as will be explained below.

"Residents." The maps shown in Figure 2.5 illustrate the movements of the eight animals whose ranges collectively compose the study site's core area. By nearly anyone's definition, these animals appeared to reside within "home ranges". All of them were tracked within the study site for months at a time and found within this area over spans of from two to five years (not all records are illustrated). However arbitrary, these temporal criteria will be used to separate this class of turtles from the others to which they will be compared.

Other indications are also present that this class was behaviorally similar to other animals believed to inhabit home ranges. Within several of the maps, there appear to be patterns of re-use of certain sites, areas, or trails (similar to findings by Breder, 1927; Stickel, 1950; and Metcalf and Metcalf, 1970). Most of the maps also show fairly long excursions out and back from the more "normal" ranges. The longest of these, in the maps of Turtles 1, 4, and 8, were all probably nesting excursions, although only Turtle 1 was actually observed in the act. The southeastern projection of Turtle 16's range represented a visit to a spring, and excursions for other unknown purposes are indicated in the maps of the male turtles. In all these cases, whatever their function, returns to the normal ranges can be interpreted as instances of "homing", which presupposes the existence of a home-base or range.

These maps also show the characteristic, "normal" pattern of convoluted movements often associated with the phenomenon of home-range. At the same time, it is evident that the degree to which this convolution is shown (as well as of the other more patterned features)

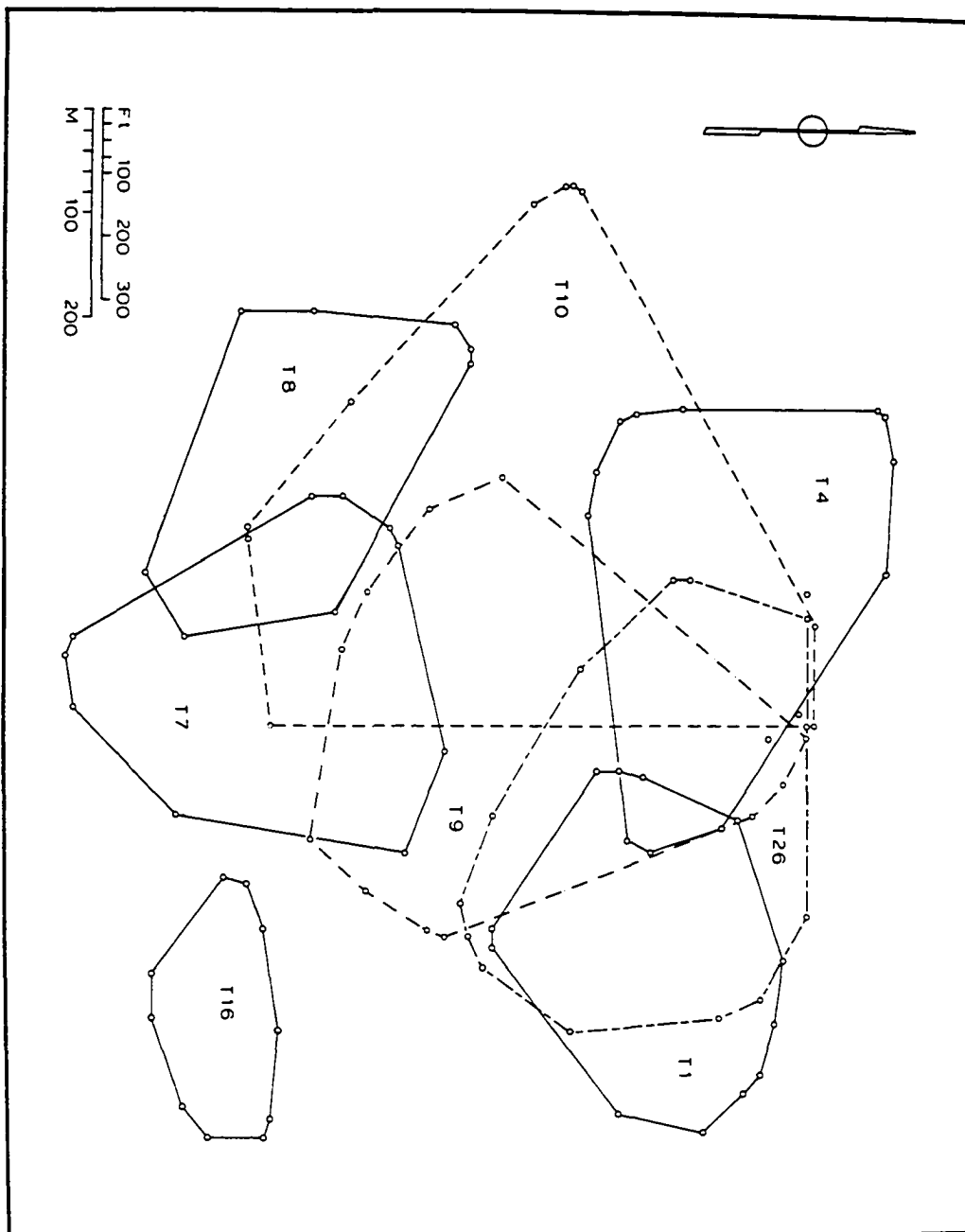
**FIGURE 2.5** Movement records for the Residents.

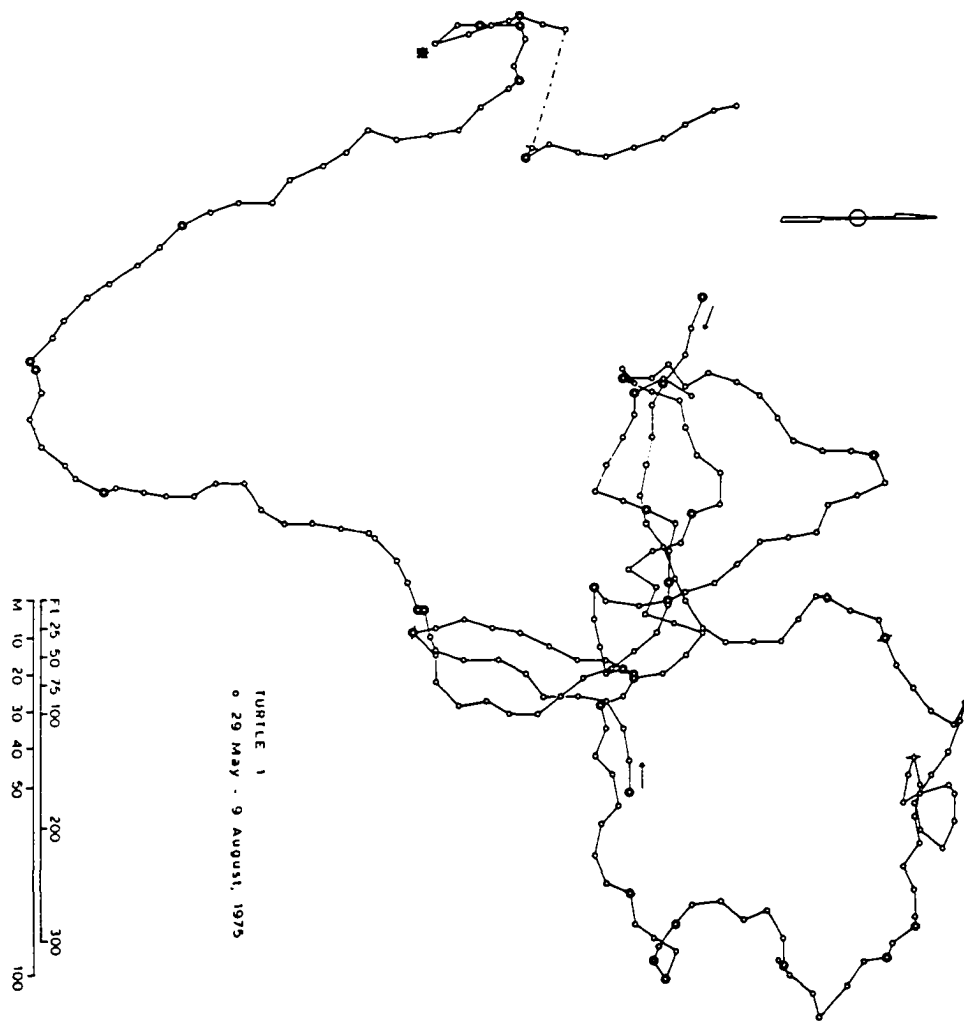
- a. Symbol legend
- b. Relative positions of the Resident's home ranges (excursions excluded). Females' ranges are indicated by solid lines, males' by broken ones.
- c. Movements of Turtle 1 (female). The extended u-shaped route towards the bottom of the map represents an egg-laying excursion; the nest site is indicated by an asterisk.
- d. Turtle 4 (female)
- e. Turtle 7 (female)
- f. Turtle 8 (female). Shown to the left are the convoluted routes representing the home range; to the right are two extended excursions that probably represent egg-laying trips.
- g. Turtle 8; movements within the home range.
- h. Turtle 9 (male)
- i. Turtle 10 (male)
- j. Turtle 16 (female); initial linear movements, possibly representing dispersal, followed by the much more convoluted routes that comprised the home range occupied for the next two years
- k. Turtle 16; movements within the home range
- l. Turtle 26 (male)



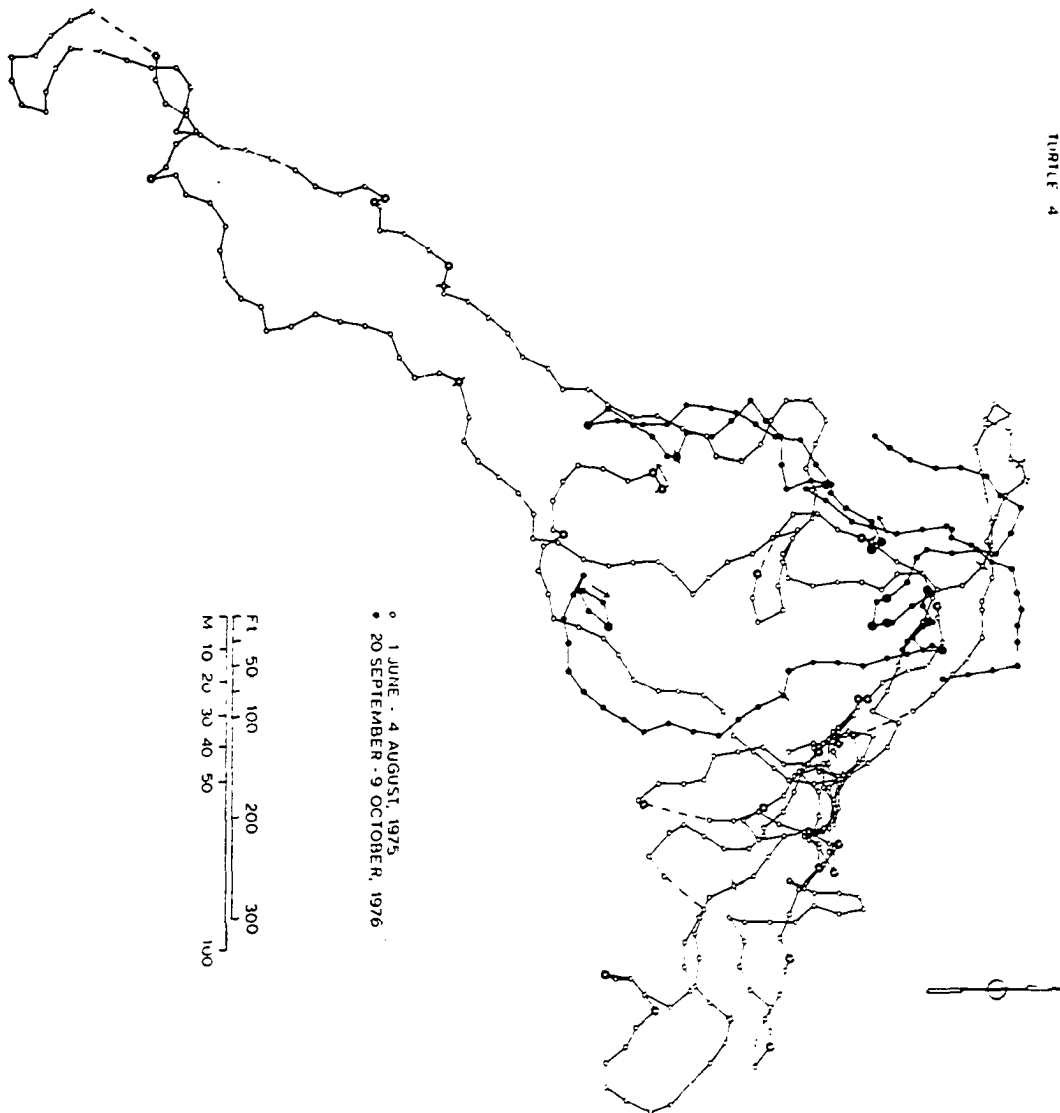
Legend:

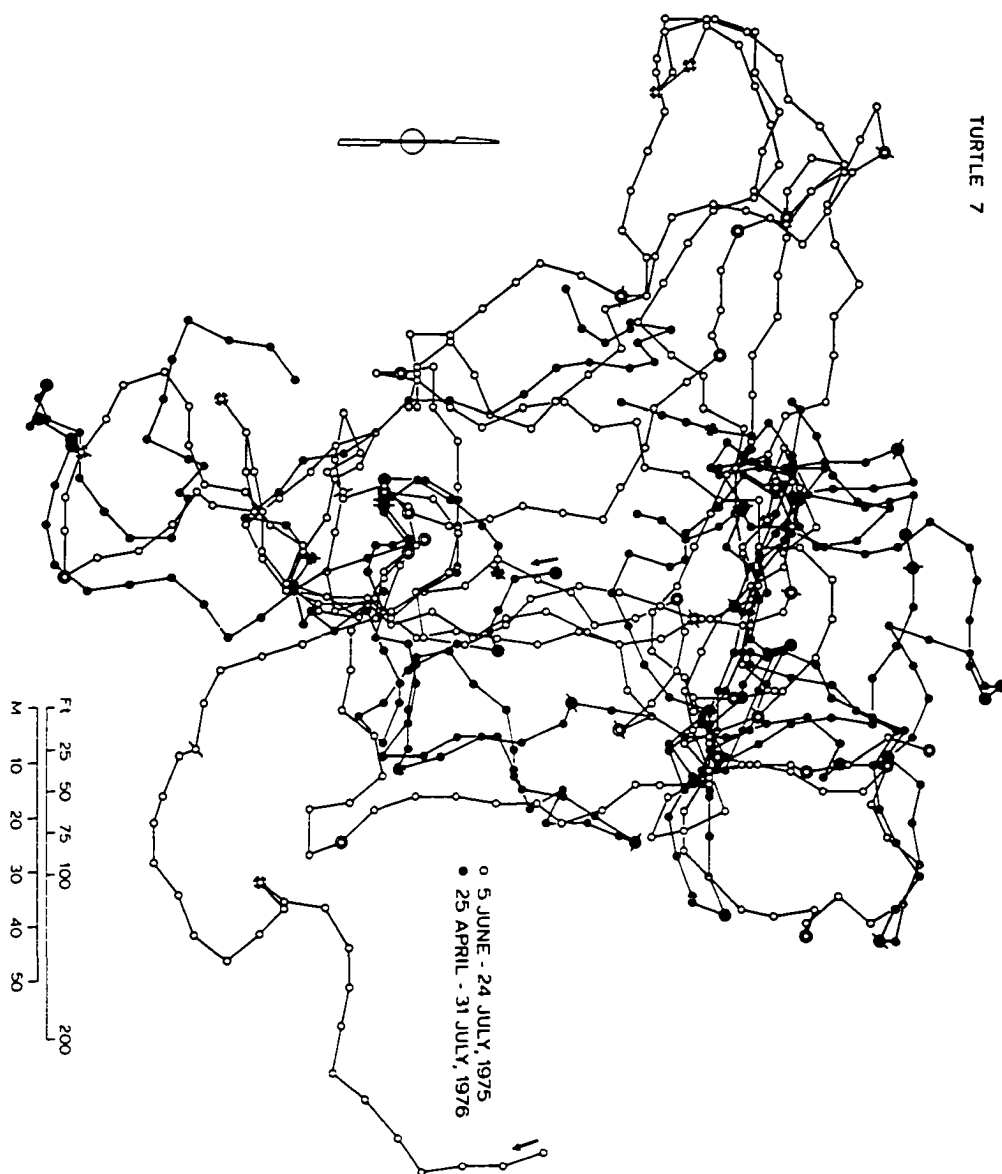
- Survey points
- ⊙ Form sites
- ⊙ Suspected form sites
- ⊙ Hibernacula
- ⌘ Tether points
- Starting points (shown only where not prohibited by the  
density of the lines)



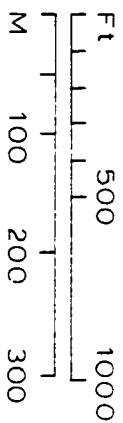
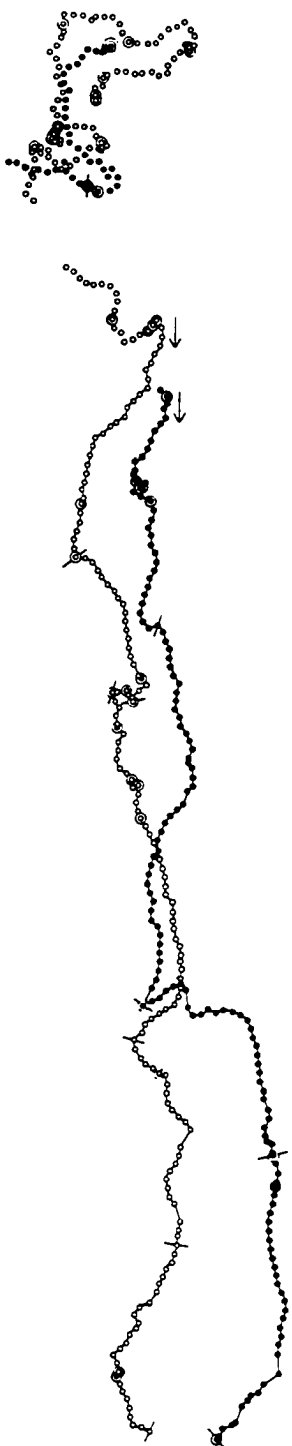


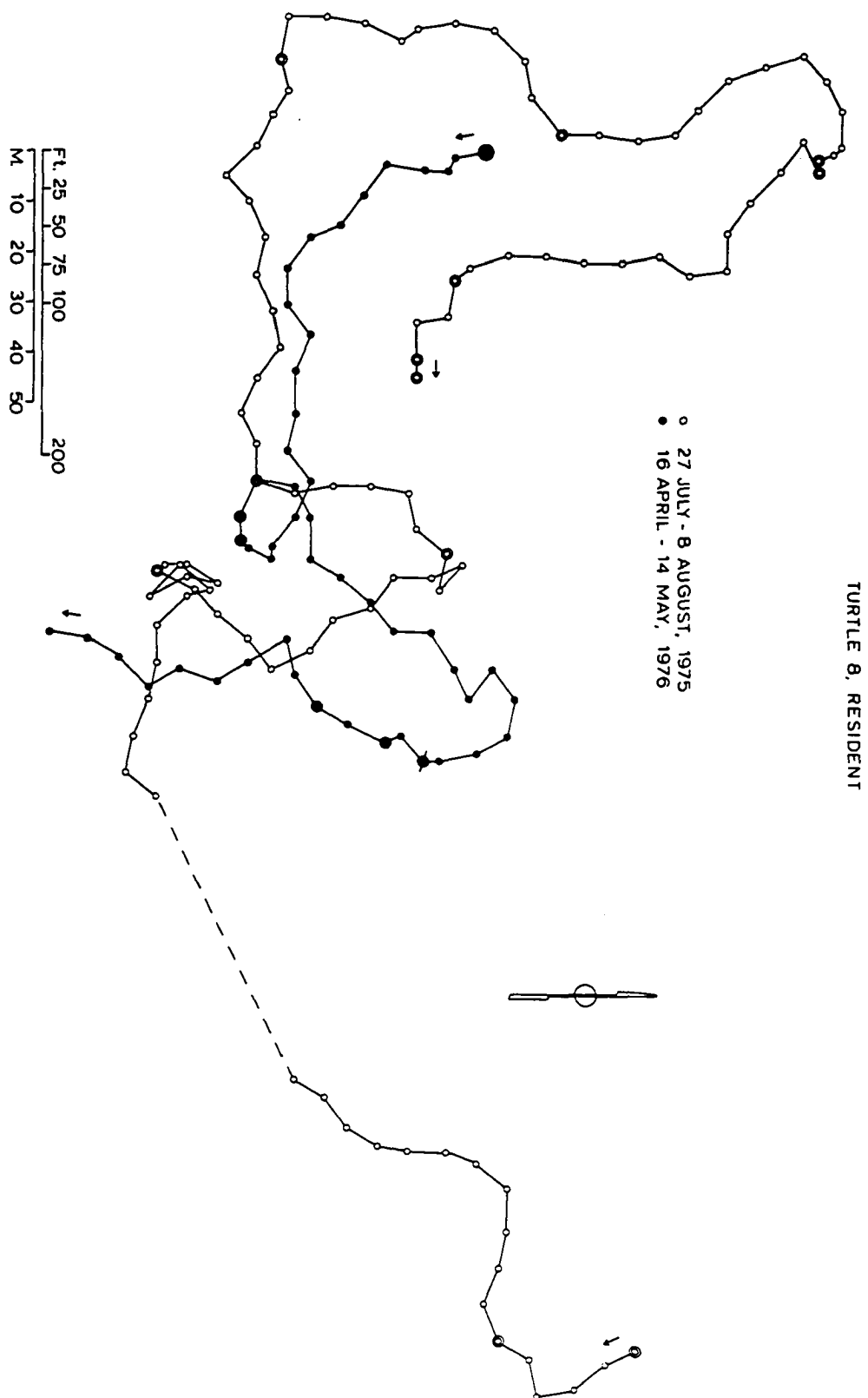
TURTLE 4



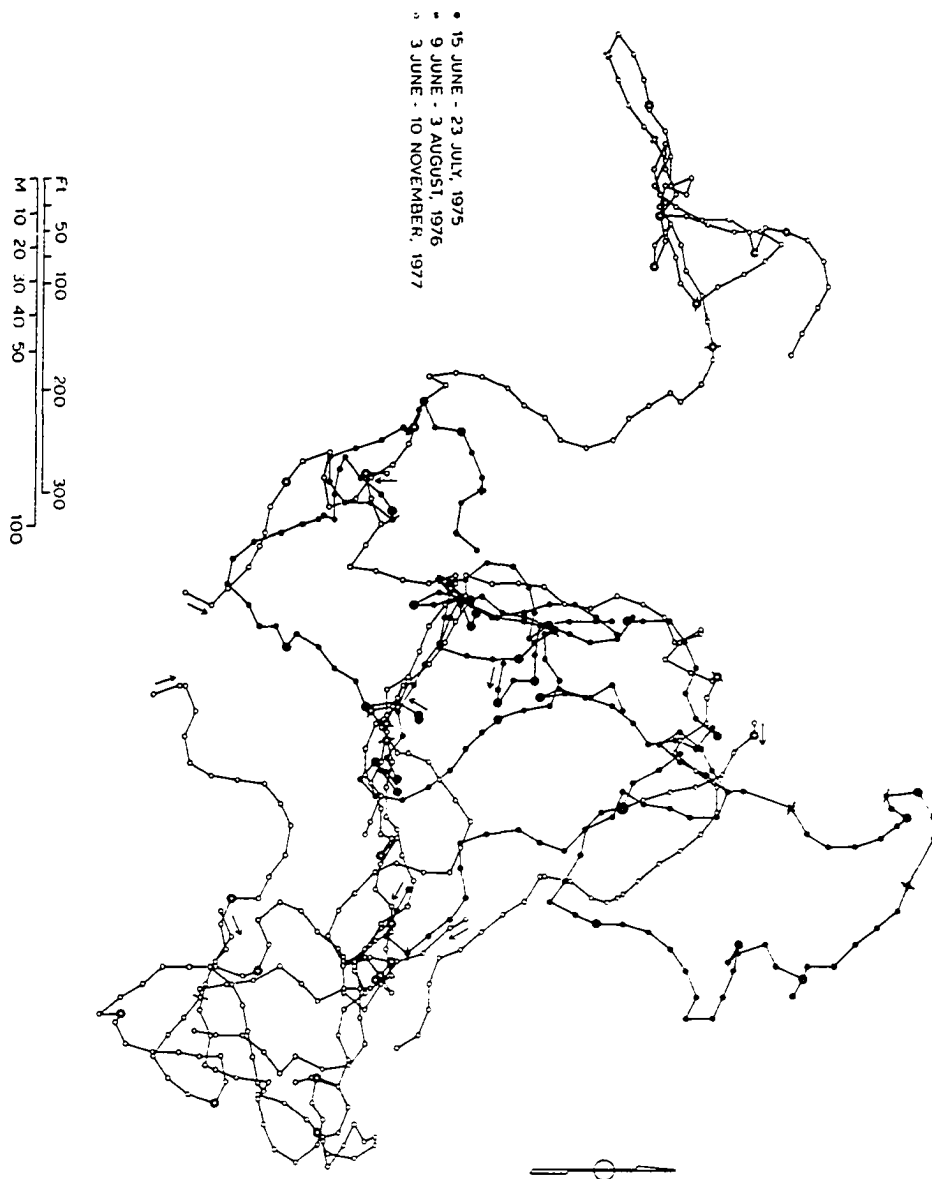


TURTLE 8  
• 1975  
• 1976

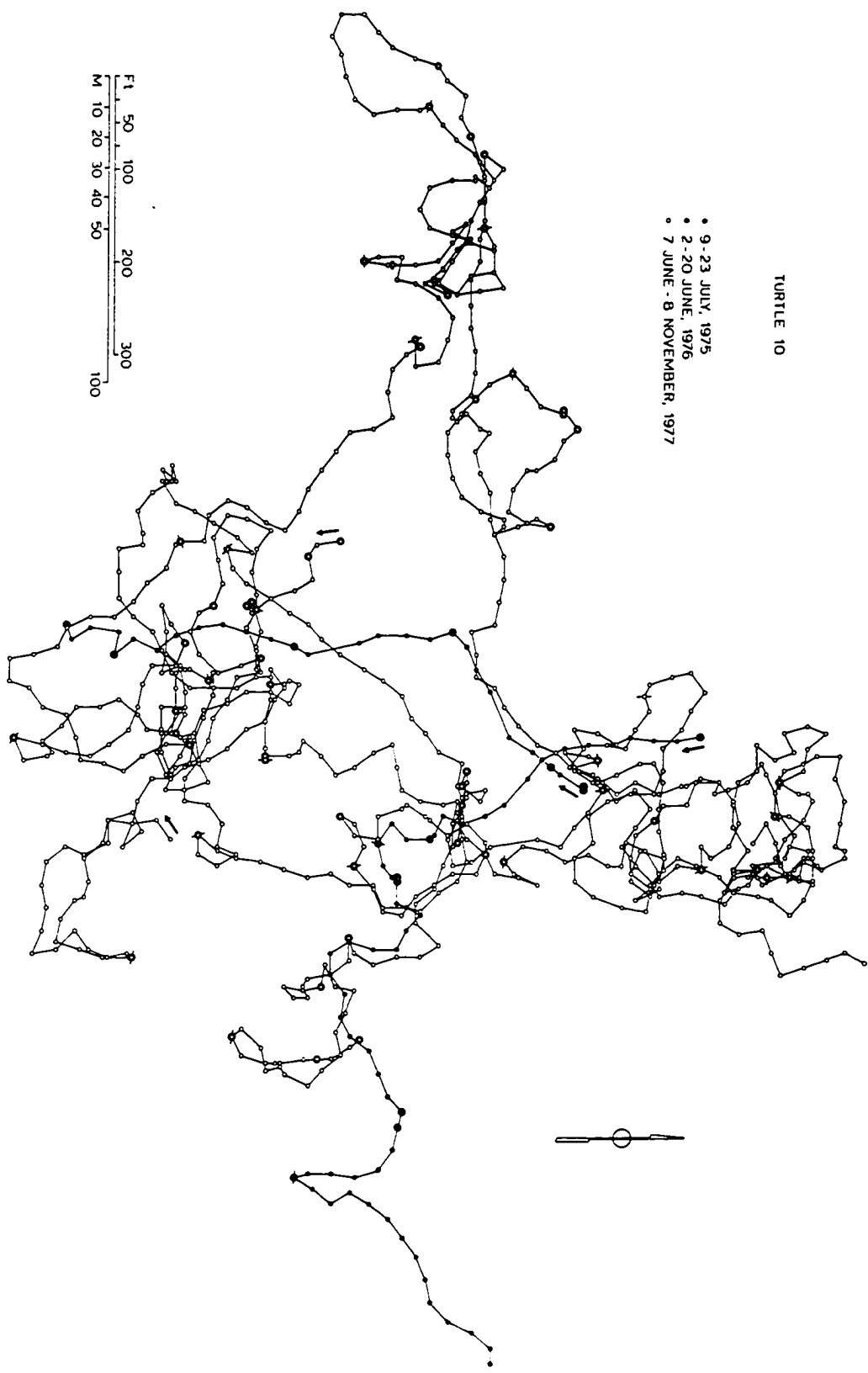




TURTLE 9



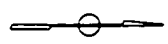




TURTLE 10

- 9-23 JULY, 1975
- 2-20 JUNE, 1976
- 7 JUNE - 8 NOVEMBER, 1977

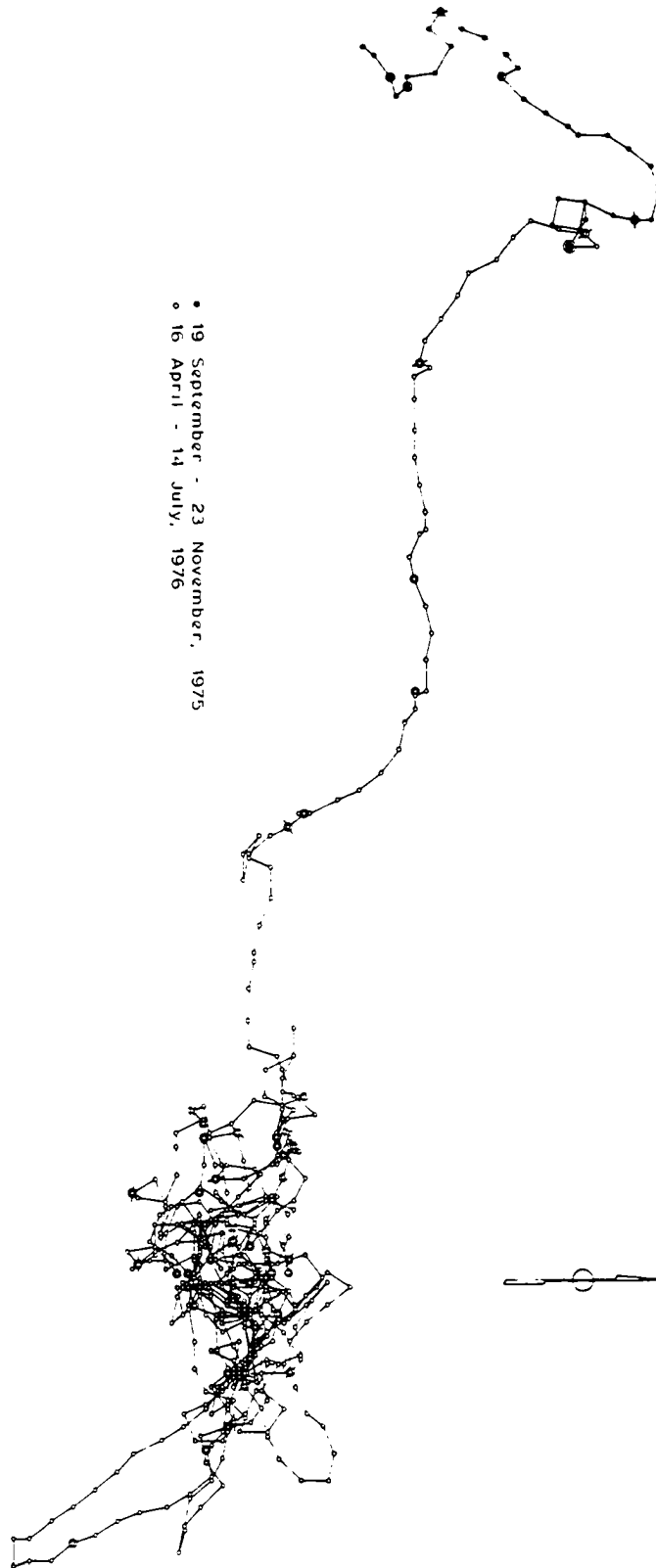
FI 50 100 200 300  
M 10 20 30 40 50 100

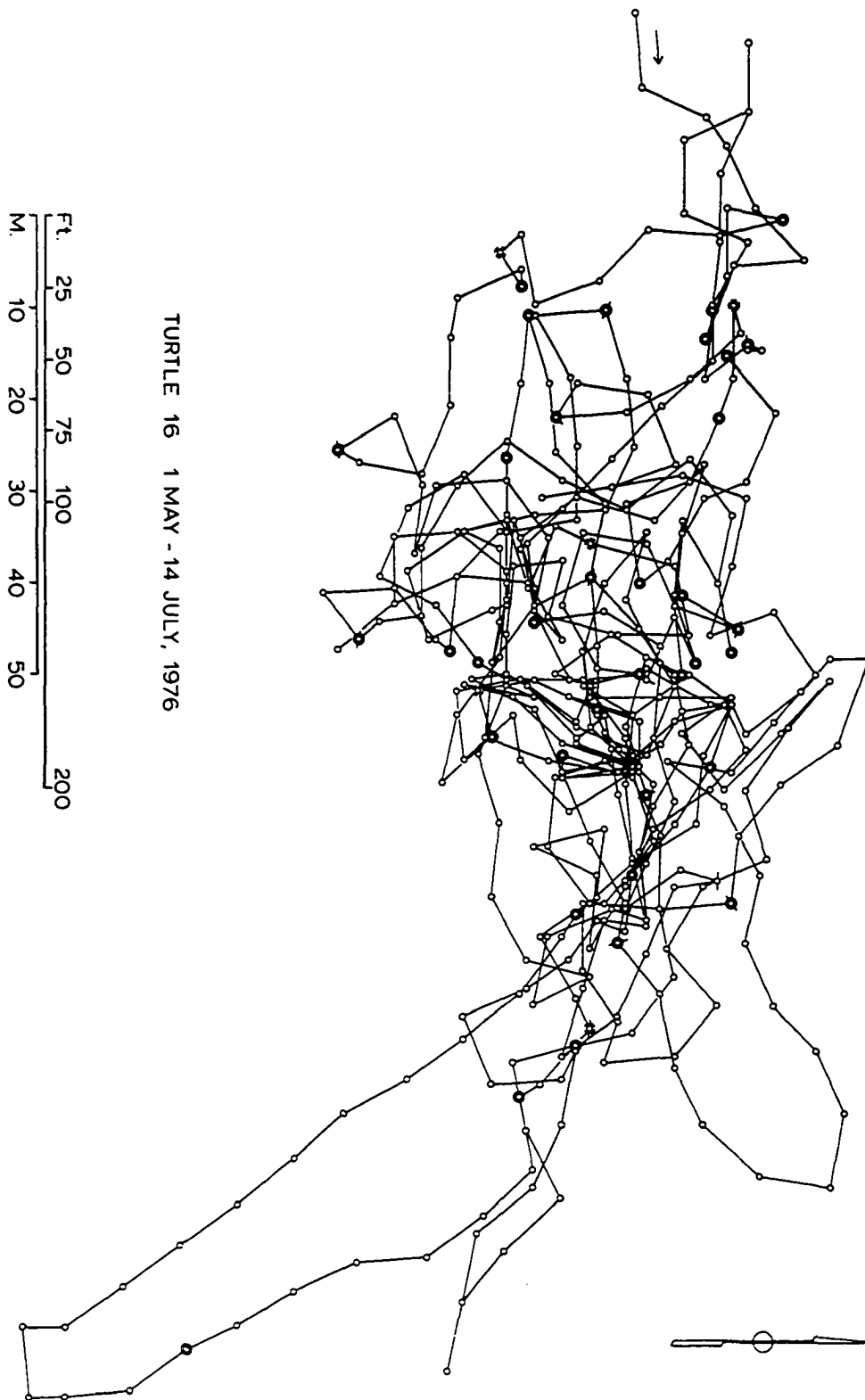


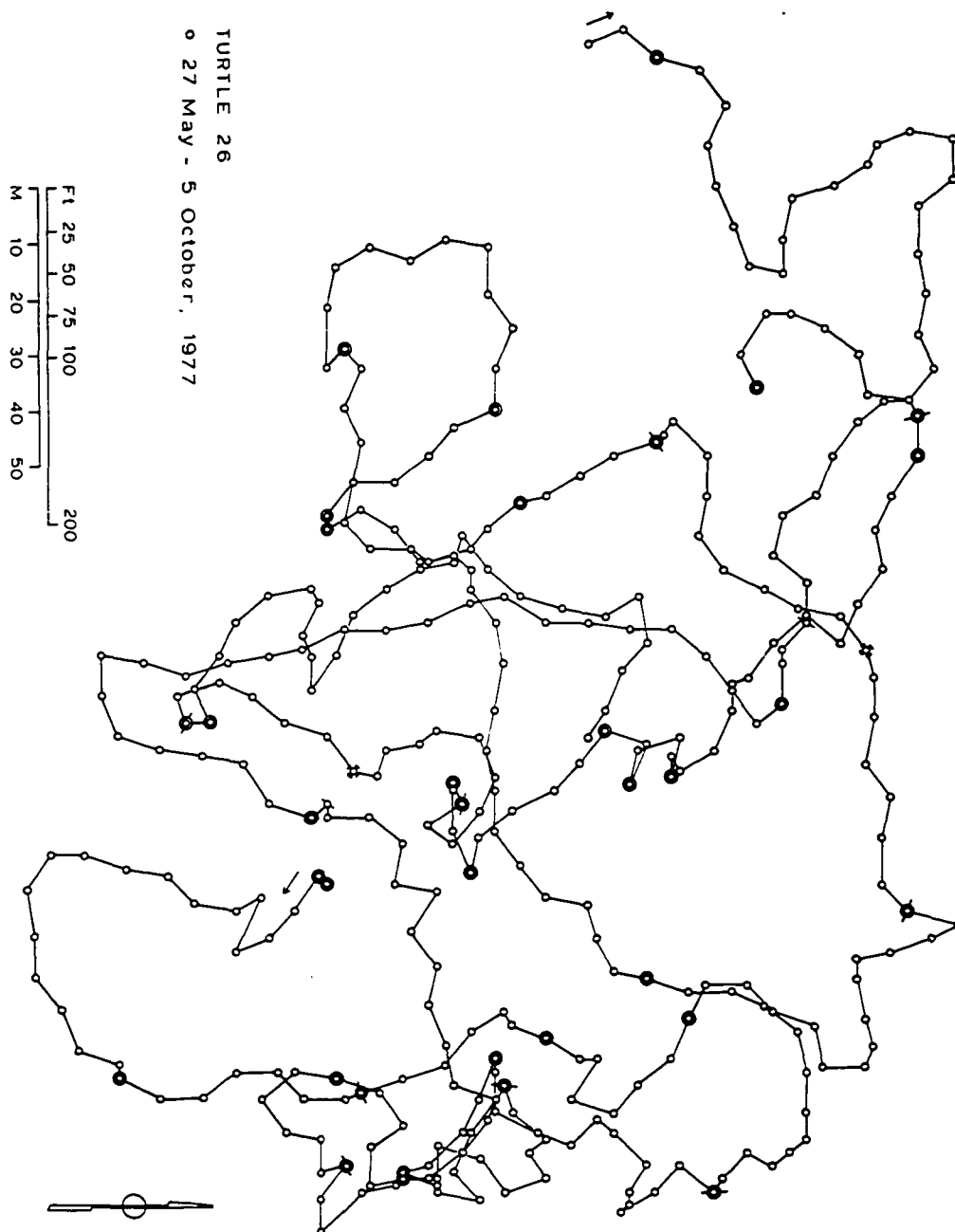
Turtle 16

• 19 September - 23 November, 1975  
◦ 16 April - 14 July, 1976

Ft 50 100 200 300  
M 10 20 30 40 50 100







varies greatly from turtle to turtle. Turtles 7, 16, 26 all show patterns of fairly even use of all parts of their ranges, but differ in the apparent tightness of their coverage. Turtles 9 and 10, on the other hand, show a more patchy pattern; small areas are intensively used then left by way of fairly straight passages. The movements of Turtle 10 were particularly wide-ranging, and during the course of the study he visited nearly all parts of the core study area (not all of these movements were surveyed). Again, this overall diversity of ranging patterns is similar to that described in other studies of box turtles. In addition to suggesting a continuum of ranging patterns, it indicates that the significance of quantitative differences between members of this class should be examined, or even that qualitative differences should be looked for if the working hypothesis fails.

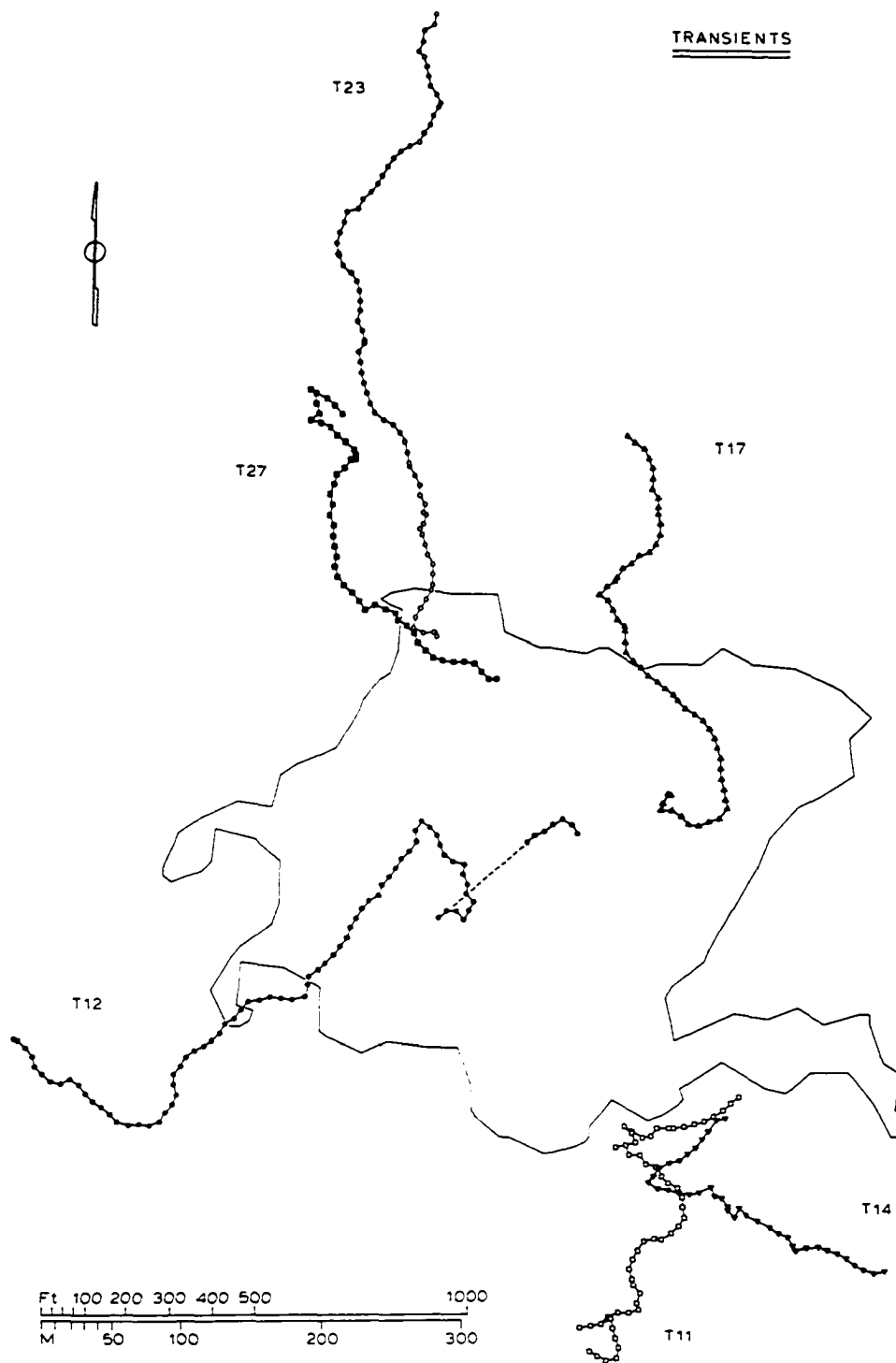
"Transients." Markedly different from the normal ranging patterns of the preceding class are the movements shown in Figure 2.6. The striking linearity of these routes of travel was not, however, the primary defining feature of this class of turtles. As with the "Residents", it was their length of visitation to the study site that distinguished them. For the purposes of this study, a "Transient" was any animal whose stay on the study site at any one time was brief (on the order of days, but not including periods of inactivity), and whose returns, if any, were made only at widely separated intervals (on the order of months or years).

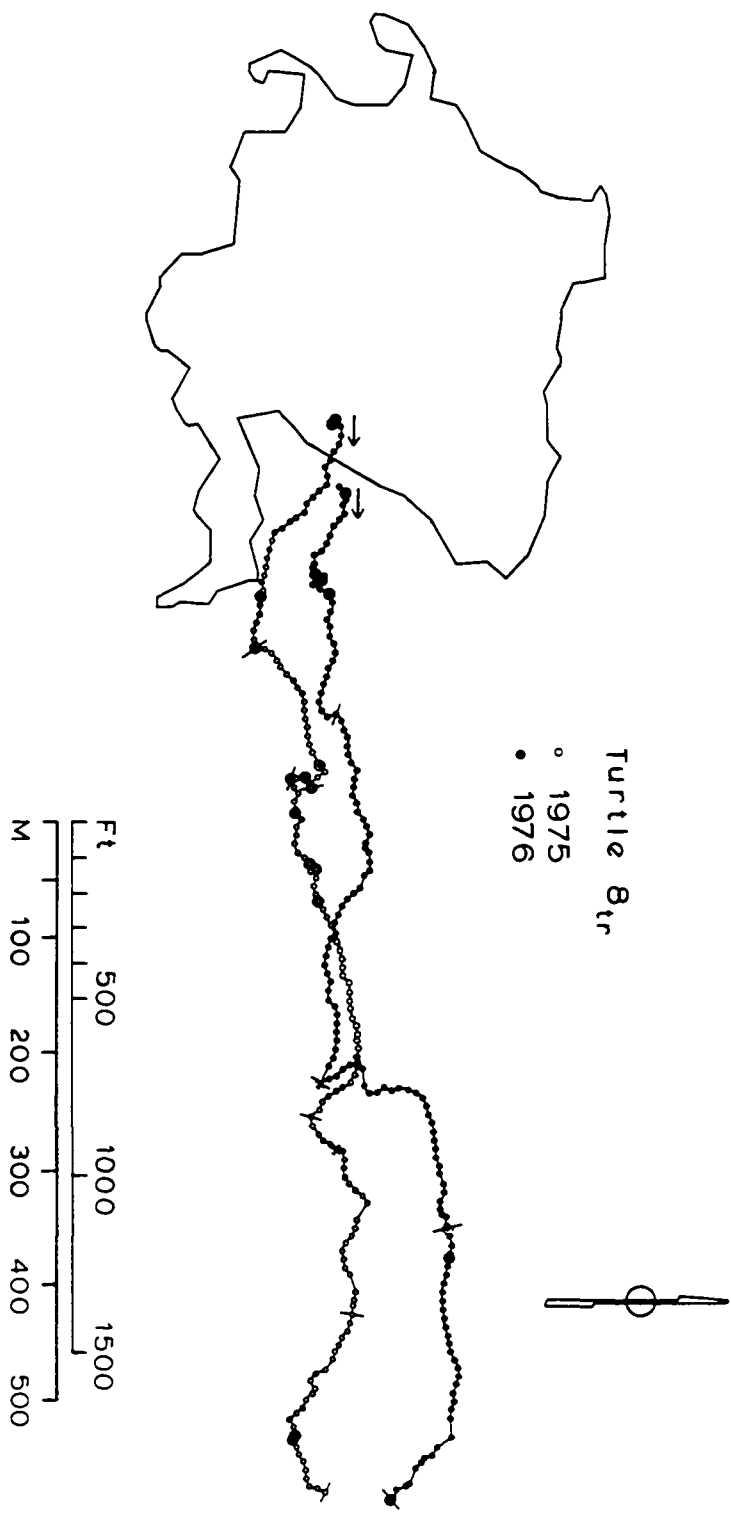
This class of turtles, of course, could well be heterogeneous. I made no attempt to distinguish true vagrants from distant "neighbors" on excursion. For the purposes of testing the null hypotheses that no qualitative differences existed between the turtles, such distinctions

**FIGURE 2.6** Movements of the Transients.

- a. Relationship of the Transients' movements (except T8tr's) to the core area of the study site (shown in outline)
- b. Relationship of Turtle 8's excursions to the core area of the study site
- c. Turtle 8tr's excursions shown in greater detail
- d. Turtle 11 (female)
- e. Turtle 12 (male)
- f. Turtle 14 (female)
- g. Turtle 17 (male)
- h. Turtle 23 (female)
- i. Turtle 27 (female)

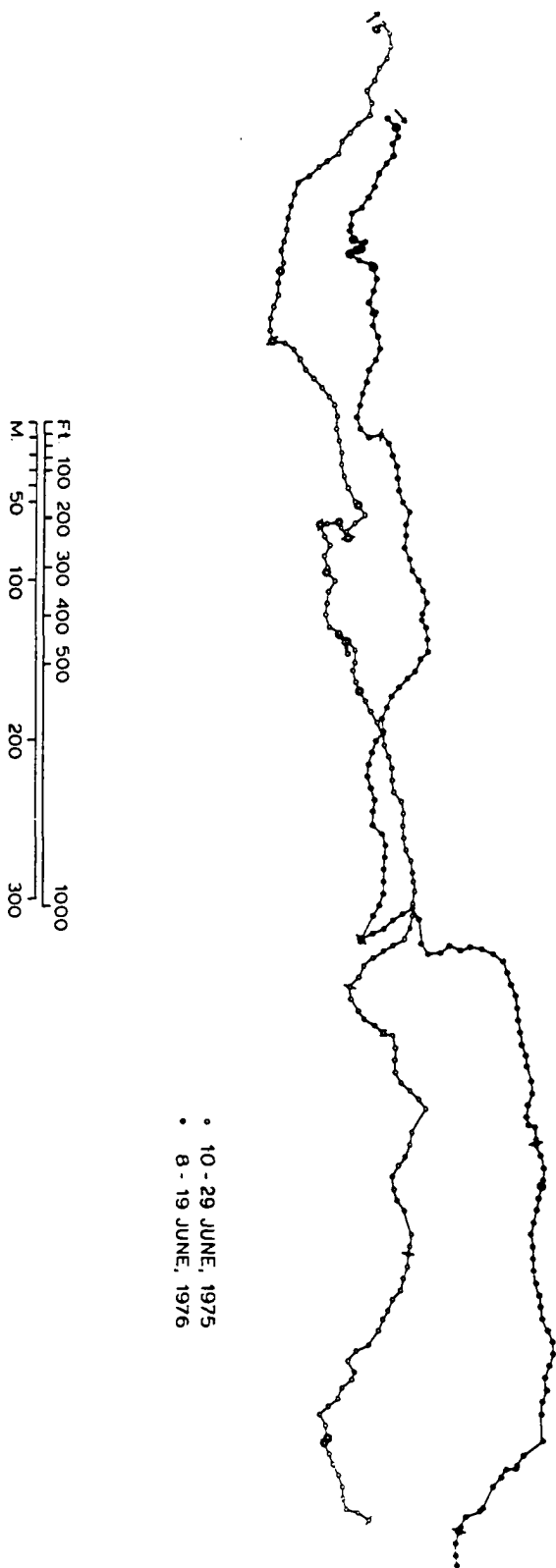
(The movements of Turtle 2, a male, are not mapped. They all occurred during 1974, the first year of the study, when I did not record slopes and did not have the control lines in place. Lacking corrected coordinates, his data are used only in analyses involving the compass directions measured directly from one 25 ft step to the next.)





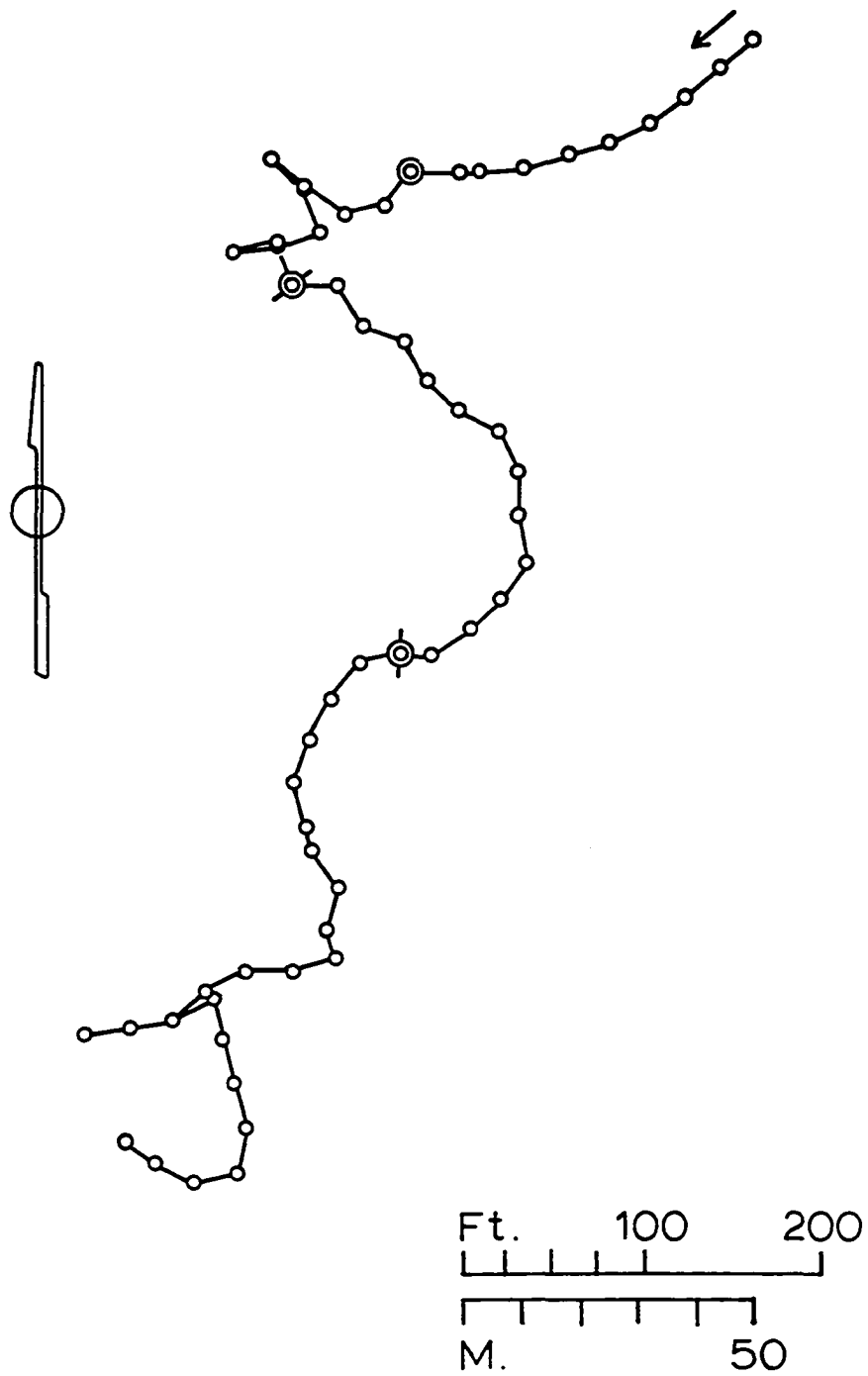


# TURTLE 8, TRANSIENT SEQUENCES



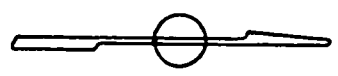
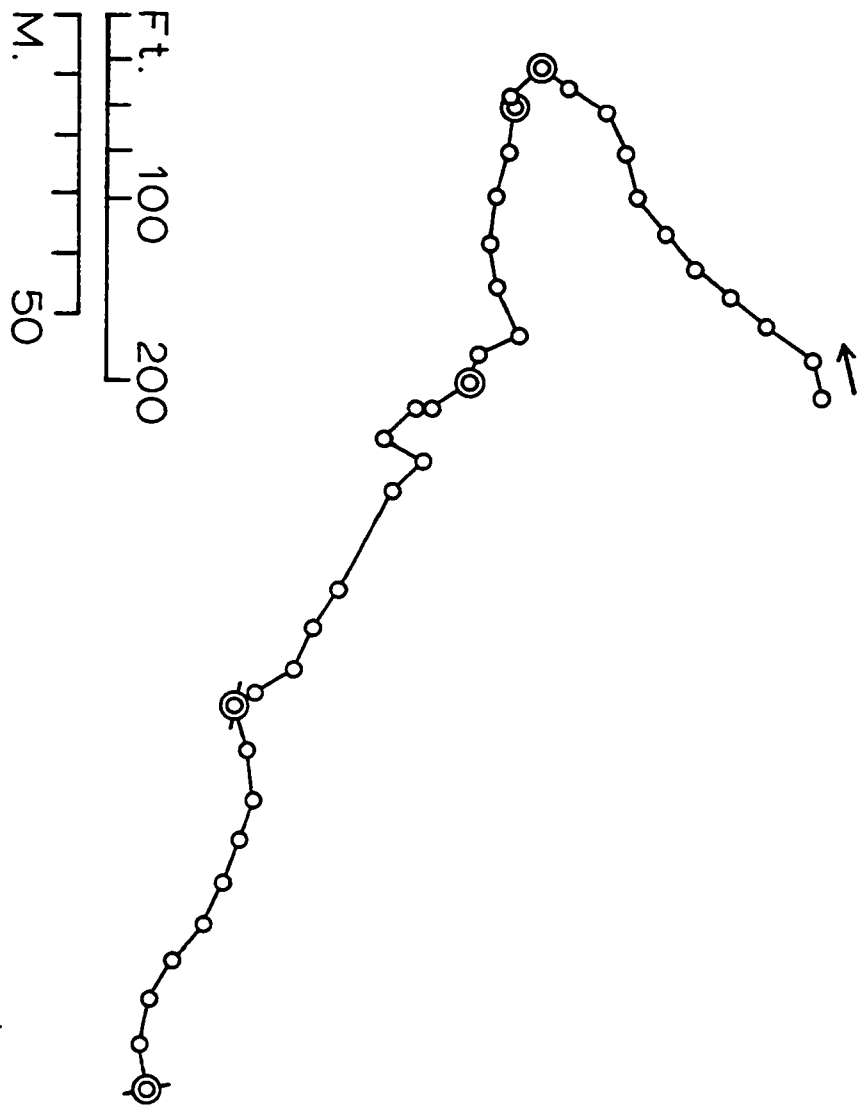
- 10 - 29 JUNE, 1975
- 8 - 19 JUNE, 1976

# TURTLE 11



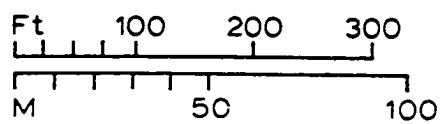
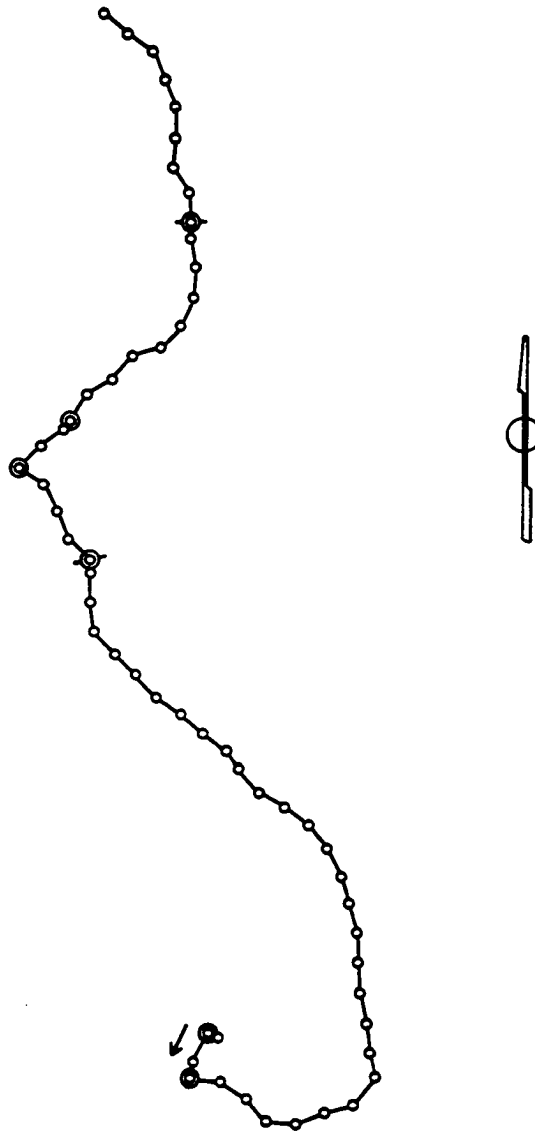


# TURTLE 14

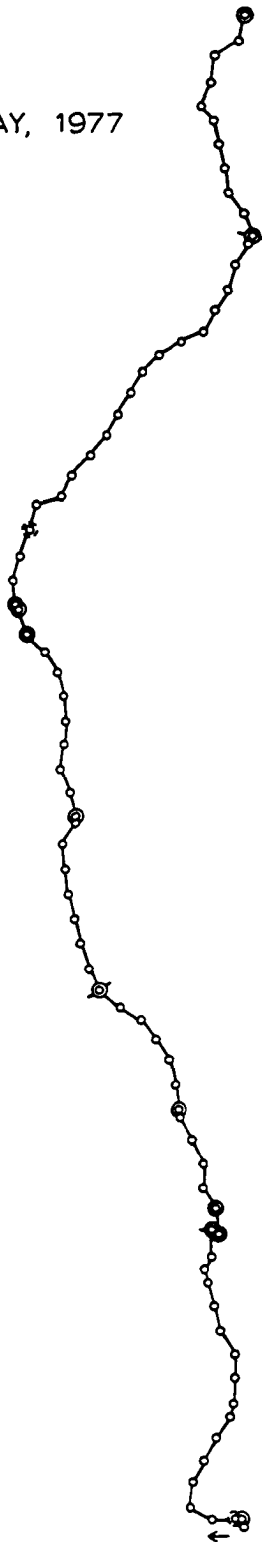
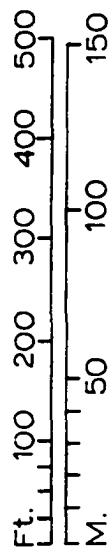


TURTLE 17

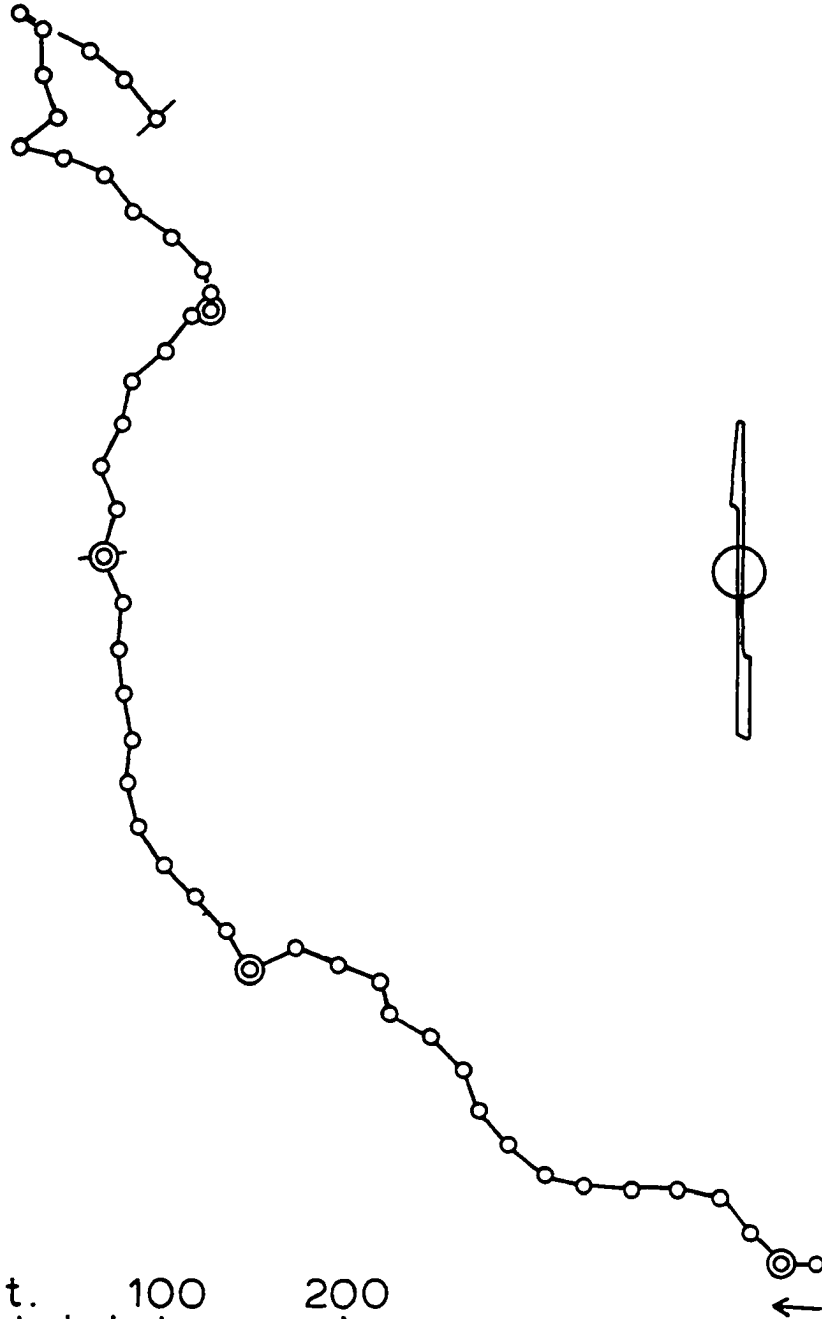
27 MAY - 14 JUNE, 1977



TURTLE 23  
14 APRIL - 1 MAY, 1977



# TURTLE 27



seem secondary. For that reason, I have also included in this class the long and apparently off-range movements of Turtle 8. Turtles 11, 12, 14 were also almost certainly on excursion when they visited the study site, having shown up there twice or more during different years. Excluded from this class, however, were the animals that appeared to be closer "neighbors", those whose normal movements overlapped the core study area or whose visits to it were fairly regular. If the study area had been enlarged to include their movements, they would have been considered "Residents".

"Experimentals." Doubts about the possible confounding of vagrants and excursionists in the class of "Transients" led to my introduction of a third, experimental group. My concern was that if most of the "Transients" were actually excursionists, then perhaps I was not testing the difference between the extremes of ranging patterns as rigorously as I wished. The differences between on-range journeys and rarer trips to more distant but also "known" sites might not be so different as between the movements of residents, either on or off their ranges, and those of true dispersers.

In an effort to push a group of box turtles artificially towards the extreme of vagrancy, I brought in turtles from an area located approximately 17 miles from my study site. The idea was at least to remove the possibility of their guidance by familiar surroundings. These turtles might still be able to use either vector-orientation or true navigation to attempt to return home, and in that case, they would probably resemble excursionists to some degree, since such capabilities would most likely have evolved in this species only to meet the needs of relatively short-distance migrations.

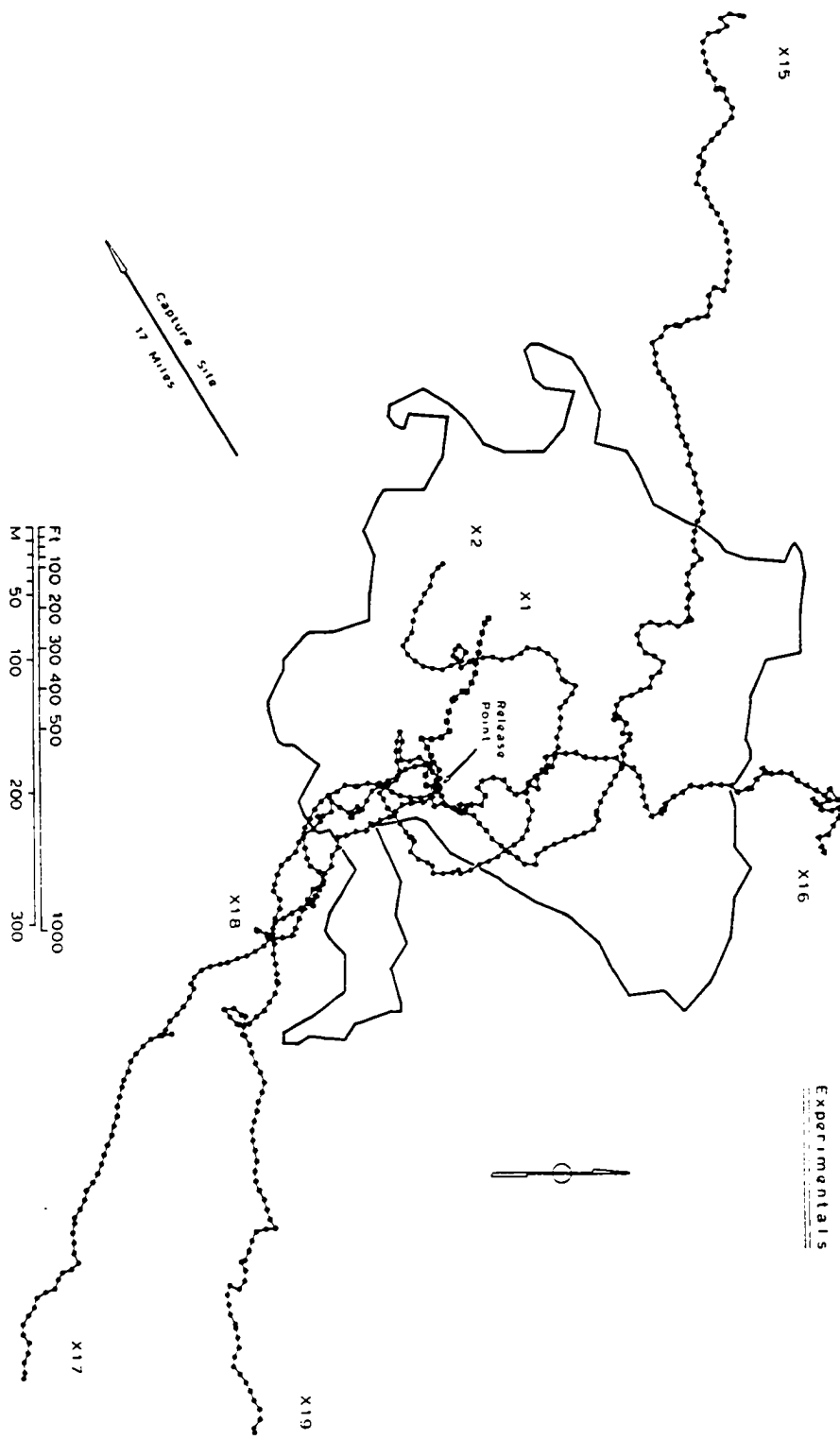


On the other hand, long-distance translocations might also remove those abilities as well, in which case the experimental group could come to resemble natural vagrants. An additional resemblance could have also resulted from any tendency to leave the study area as a result of the overall disturbance created by their being moved to a completely unfamiliar area. At any rate, my expectation was that this class would either be similar to the "Transients", in which case both classes could be combined to produce a larger pooled sample, or that they would show even more extreme differences from the "Residents".

Figure 2.7 shows the movements of seven "Experimentals" that behaved like the "Transients" after being released on the study site. Two other individuals appeared to settle on the area, becoming essentially like the "Residents", but these were excluded from further consideration. The maps also show the approximate distance and direction of the initial capture site of all members of this class. They were all collected from roadways within a black vulture study area during the course of an investigation on that species by Dr. Patricia Rabenold. When the "vanishing" bearings were examined using the V-test (Batschelet, 1972), no significant homeward orientation was indicated, nor is any hint of it displayed in the maps ( $u = 0.15$ ,  $n = 7$ , n.s.).

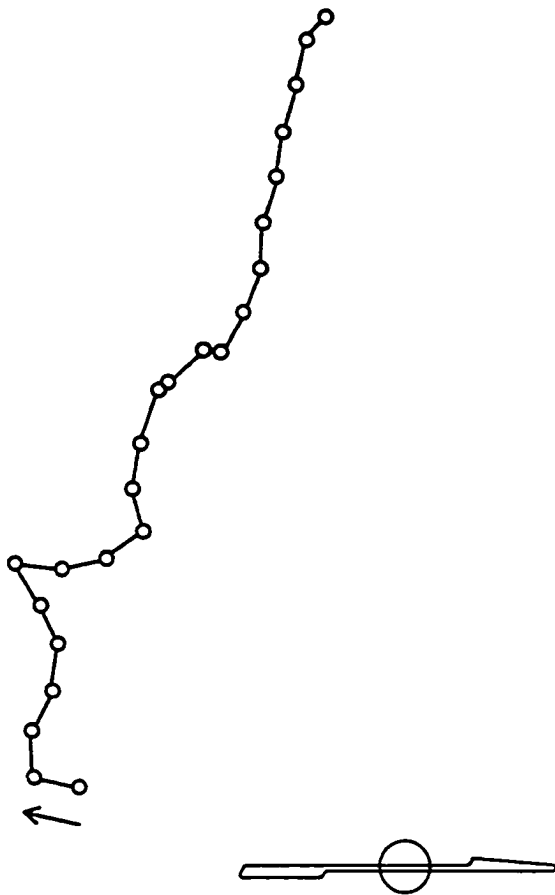
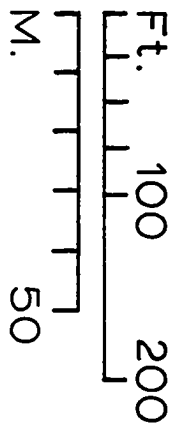
**FIGURE 2.7** Movements of the Experimentals.

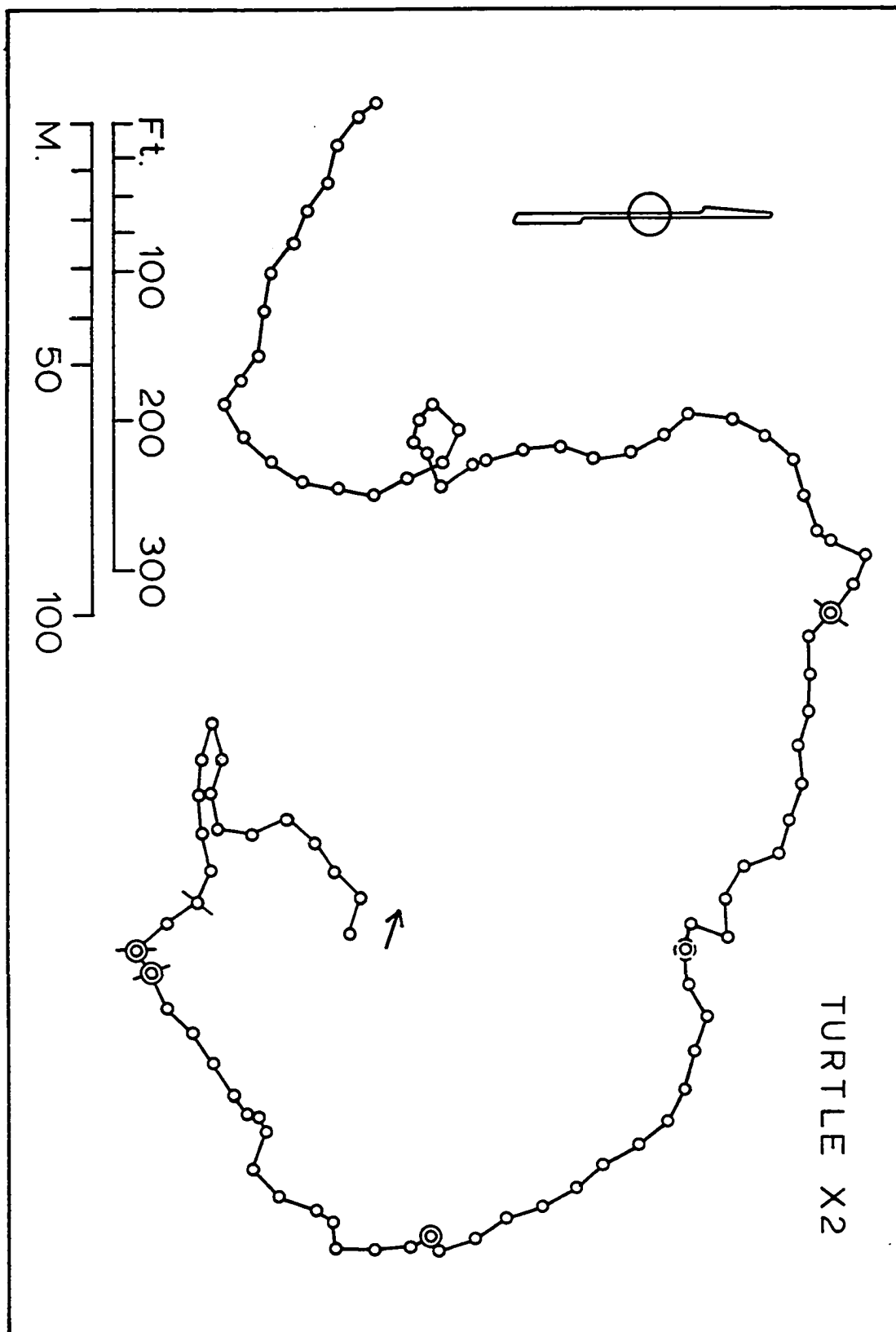
- a. Relationship of the Experimentals' movements to the core area of the study site and to the location of their original capture
- b. X1 (female)
- c. X2 (female)
- d. X15 (female)
- e. X16 (female)
- f. X17 (female)
- g. X18 (female)
- h. X19 (female)



Experimentals

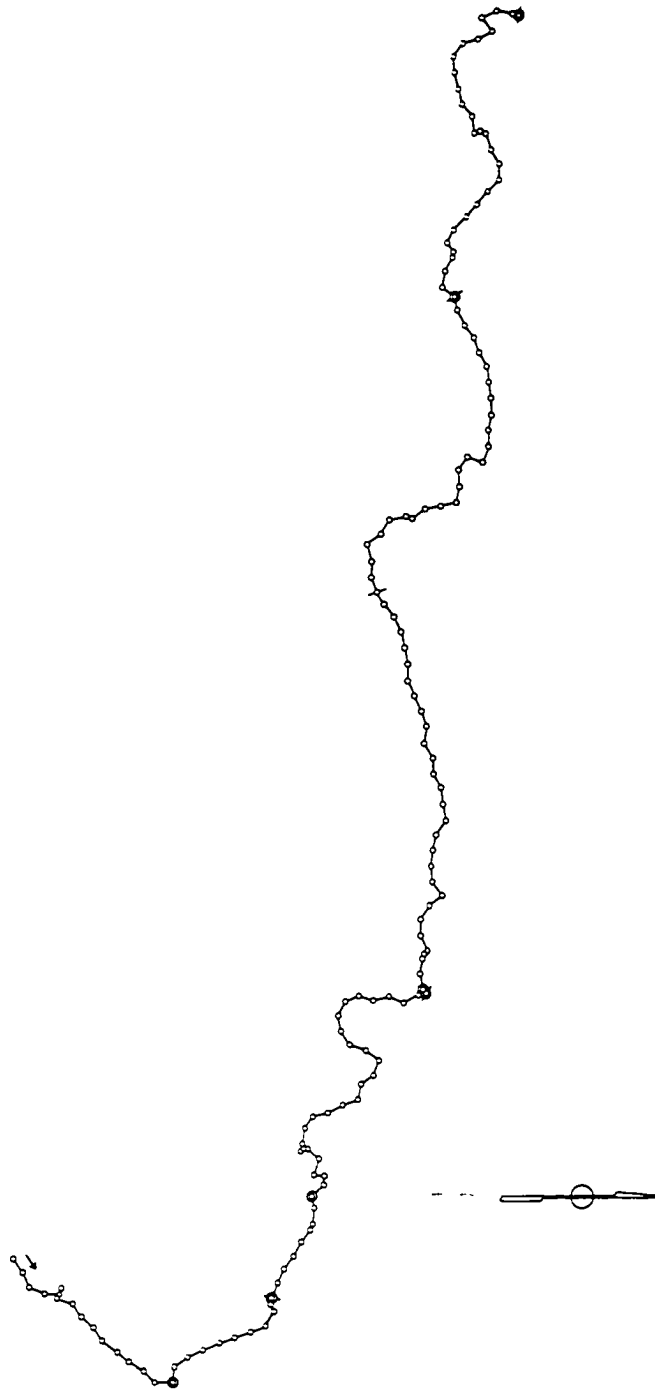
# TURTLE X1

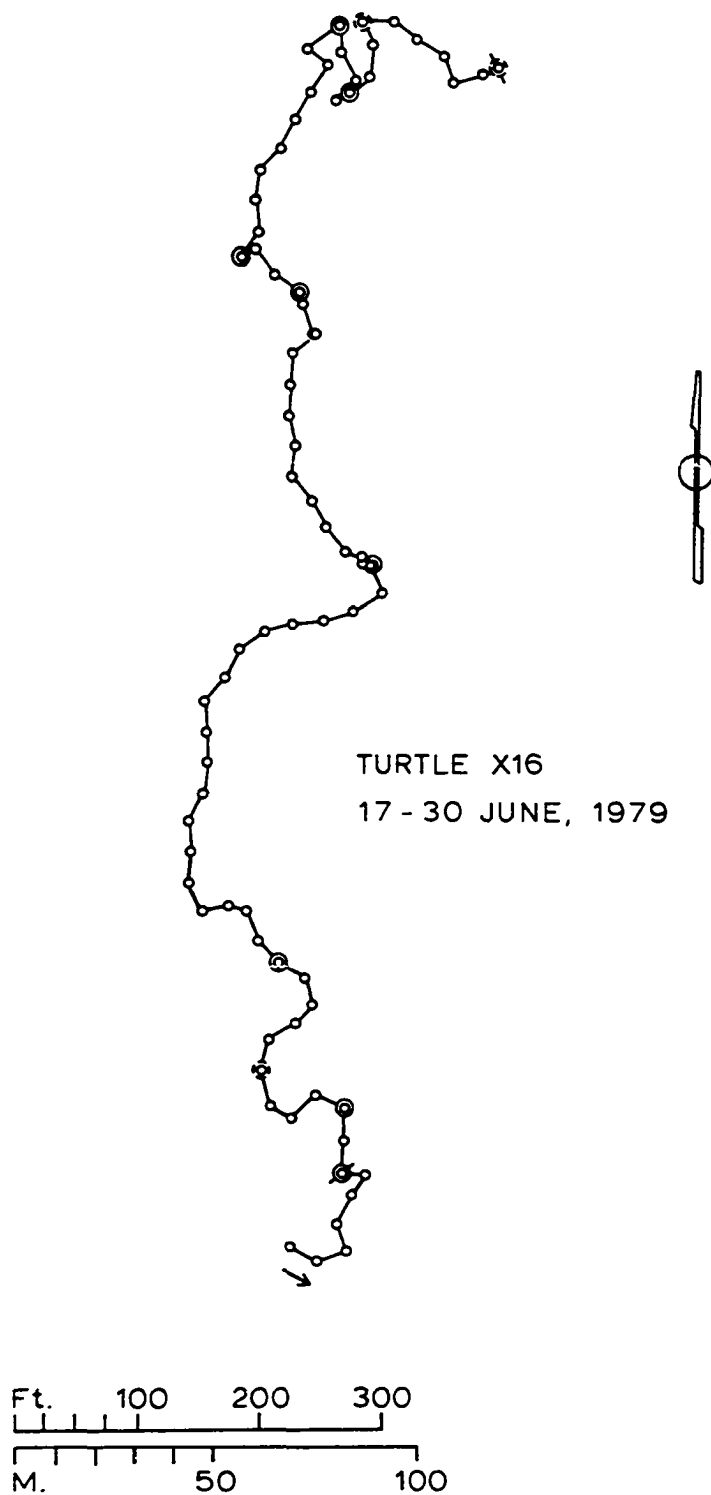


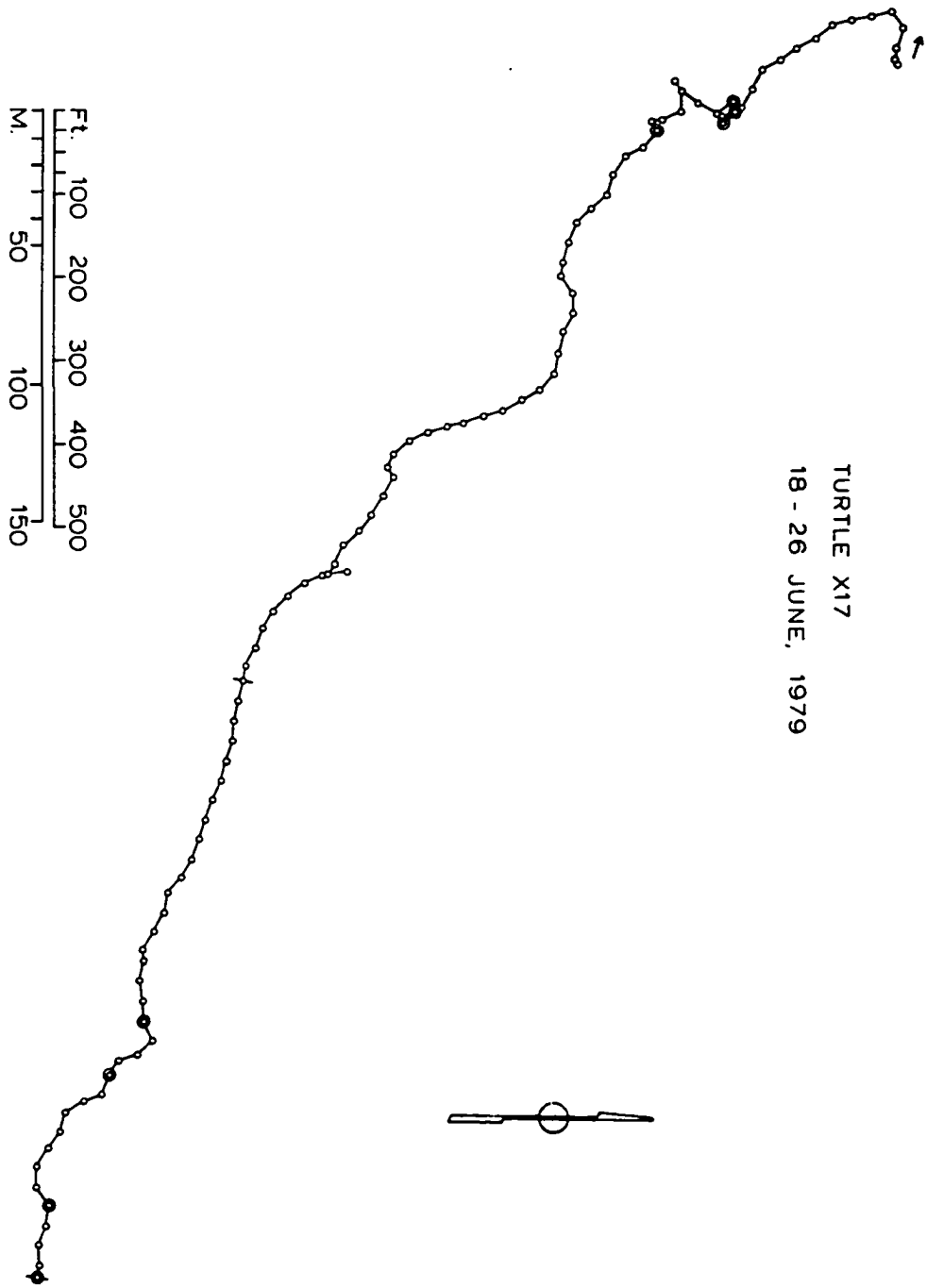


TURTLE X15  
10 - 20 JUNE, 1979

Ft 100 200 300 400 500  
M 50 100 150



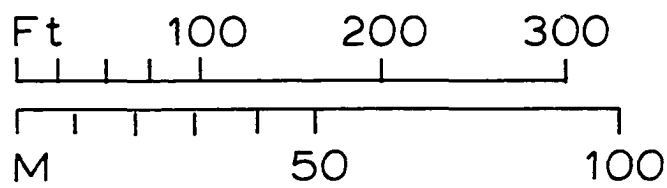
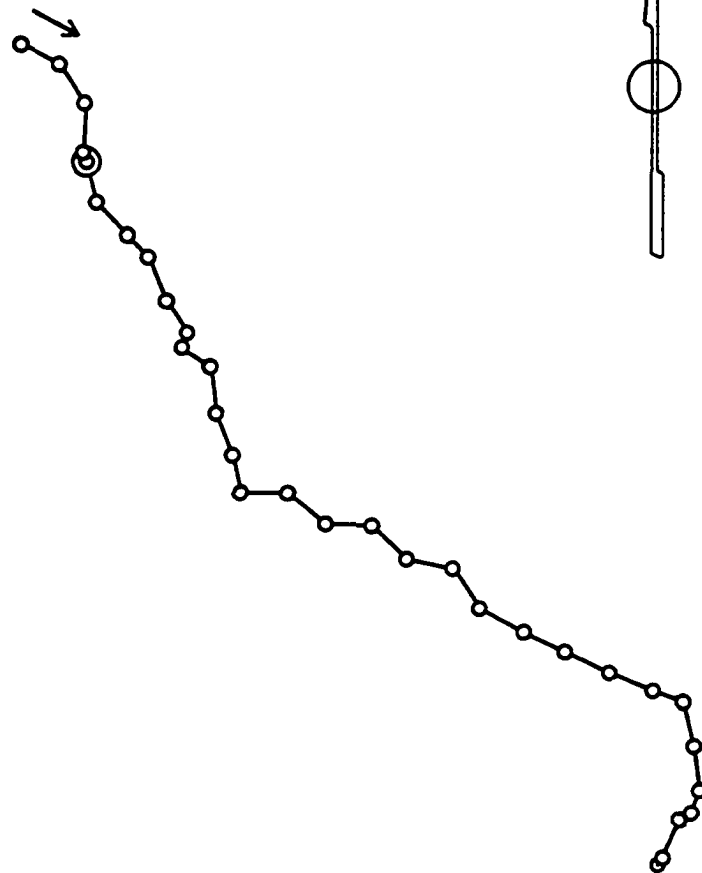




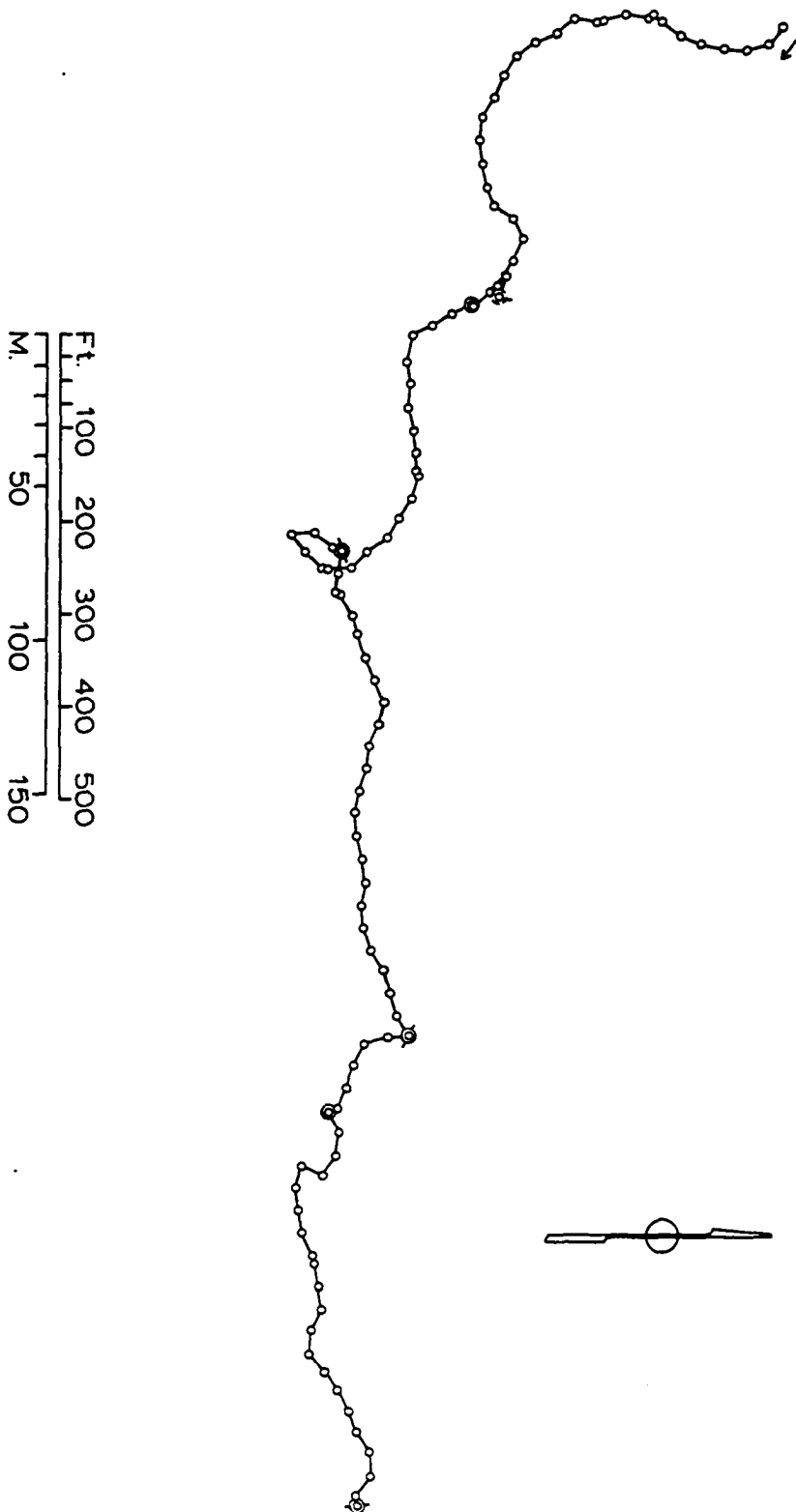
TURTLE X17  
18 - 26 JUNE, 1979



# TURTLE X18



TURTLE X19  
6-13 JULY, 1979



### **CHAPTER III. VOLITIONAL WALKS**

#### **A GENERAL THEORY OF HIERARCHICALLY PARTITIONED, STOCHASTIC ROUTES OF TRAVEL**

### III.A. The Reality Underlying an Organismal Walk

Before applying the mathematics of walk models to the mazes of data just illustrated, it is worthwhile asking just what this approach might represent in behavioral terms. Are walk models only a methodologically convenient way of handling route data, or do they actually reflect some underlying behavioral reality? This question is not trivial since the interpretation of the results will depend on the answer.

The segmented appearance of the routes as shown in the maps is, in fact, completely artificial. The surveyed points are separated by an arbitrarily fixed interval, and they only roughly approximate the continuous thread traces that themselves only approximate the routes actually taken by the turtles. Nonetheless, such artificiality has rarely been seen as an obstacle in attempts to fit a walk model to animal movements.

Studies that make use of a walk approach usually view movements as similar to those of molecules in the Newtonian Gas Model. Although there could be fundamentally discrete events within the movements, corresponding to collisions between particles, these are considered to be infinitesimal in nature and essentially unobservable. On a macroscopic level, the question of whether or not to treat the movements as discrete or continuous is then only a matter of the kind of mathematical analysis to be employed. The paths can be first partitioned completely arbitrarily, as in a Riemann Sum, and then the methods of

integral calculus used to obtain diffusion equations for describing the movements as continuous processes (e.g. Gail and Boone, 1970). Or the paths can be considered to be divided at discrete intervals even at the macroscopic level, treating them as fractals, patterns of discrete elements each of which can be decomposed into smaller elements which have the same sort of pattern as larger ones (Mandelbrot, 1983; Katz and George, 1985). A classic example of a fractal is Brownian Movement. Each step in this random walk can be broken down into still finer steps, each series of which also defines a random walk. As with the treatment of movements as continuous processes, a partition at any given scale can be made arbitrarily, since the essential behavior of the phenomenon does not change from one scale to the next. No new properties are expected to emerge either at coarser or finer scales of analysis. In neither treatment do the steps in a series have real meaning in themselves as behaviorally defined entities.

But do these views do justice to all the complexities of control seen in the routes of living organisms? Do animals behave as simply as inanimate particles, or, if they appear to do so, can the units making up a pattern of movements be treated as arbitrarily as in the approaches described above? In this chapter I argue just the opposite.

(1) Even at a macroscopic level, discrete units of movement often correspond to some real behavioral event.

(2) These units can nonetheless be decomposed into yet finer units which themselves represent actual behavioral events.

(3) Routes composed of such steps can thus have an hierarchical structure with emergent properties; they are not fractals.

While this view of organismal movements would seem to complicate the problem of analyzing routes of travel, perhaps putting them beyond the reach of simple walk or diffusion models, I present it here first of all to indicate that caution is needed in interpreting movement patterns, caution that has frequently not been exercised in previous studies. But I also intend to show that, keeping the above points in mind, walk models can actually offer even greater insight into behavior than previously thought, but as components in a more comprehensive model for routes.

I will develop this view of movements by contrasting it to the more prevalent Newtonian model. That model's basic premise is that the trajectory of a moving object represents an interaction between a deterministic, continuous process and a series of unpredictable, deflectional events. For an inanimate particle, the first half of the interaction is specified by the fundamental laws of motion for particles, plus the existence of any fields of force that modify the particle's intrinsic motion in a predictable way. The second half is determined by a series of collisions between particles, occurring at discrete but unpredictable points in time and space.

The model for organismal movements is similar in having two sources of input, one deterministic, continuous, and intrinsic to the organism and one stochastic, discrete and extrinsic. As shall be shown, however, they operate under very different laws. In particular, the organism's potential for decision-making must be considered. Unlike simple particles, animals exert some degree of control over their movements by actively selecting from a set of alternative choices. To draw attention to this crucial feature, I use the term

"volitional walks" to describe the basic model of organismal movements. My exact meaning for "volition" will be described below, but I disclaim here any intent to imput transcendental properties to living organisms or free-will to the box turtle. I will leave those arguments to metaphysicians.

### **III.B. The Intrinsic Movement Tendencies of the Organism**

Newton's First Law of Motion describes the intrinsic movement tendencies of an inanimate particle: (1) when stationary, it will not spontaneously start to move, and (2) when moving, it will not spontaneously come to a stop or alter its direction or velocity. Departures from these predictions are due only to the operation of external, unbalanced forces. If known, their effects on the subject's motion can also be easily calculated. By Newton's Second Law of Motion, both the subject's intrinsic movement and the action of any external force can be represented by vector quantities and the motion resulting from their interaction given by a simple vector sum.

The situation for an animate object, a living organism, is not so simple. The intrinsic motion visible to an external observer is partly determined by internal factors not accessible to him, by the organism's decisions or apparent "volition". Within the black box that is the organism occur processes that give the appearance of spontaneity to the subject's movements such as would not be found in an inanimate particle. Organisms can start, halt, change course or speed without any seeming influence from external forces.

Nevertheless, it is still possible to formulate rules of organismal movement that are analogous to Newton's, particularly his first law. A basic theorem of the search paradigm is that a straight line, or other geodesic (e.g., an arc of a great circle on a spherical surface) is the best route of travel for an organism encountering unfavorable levels of stimulation. Since "unfavorable" also applies to an absence of positive stimulation, an organism moving in an informational void can also be expected to move geodesically. Under the



optimality view of evolution, natural selection should work to give an organism at least the capability for as rectilinear a motion as possible. When no unbalanced, external forces are at work, such motion would then be expected to be "intrinsic".

The resulting paths that are actually observed, of course, would never be entirely straight. The movements of a complicated, organismal system can never match the perfection of motion possible for a simple Newtonian particle. It would also never be possible for the observer to record the exact path taken by the organism, nor would he ever be able to identify all possible external influences acting on his subject. However, he could conveniently attribute all departures from a geodesic course to the actions of external forces, known or unknown.

A similarly convenient idealization could include an intrinsic uniformity of speed for an organism. Optimality theory again could be invoked to predict a most efficient gait and rate of travel through an informational void. Again, any starts, stops, or changes in speed can be attributed to external forces working on the subject.

The perspective developed so far, however, does not seem to leave much room for anything truly intrinsic to the organism. All movements by the organism are considered purely as responses to environmental stimulation (or its absence). But spontaneity as such is not the crucial feature distinguishing organismal movements from those of a Newtonian particle. The quality of control enters the model as the decision-making of the organism, its selectivity. Whether external features or internal changes in motivational state provide the real impetus for movements, no one outcome is forced on the animal. It

always exhibits some degree of choice.

This characteristic of organismal motion is revealed not so much by its difference from Newton's First Law as by its difference from the Second. The inertia an organism displays is behavioral only. Although a vector of a set length can be used to describe an intrinsic tendency for movement at any point in space, it cannot be added to a vector representing an external force in order to calculate a resultant course of travel. In behavioral terms, the organism can be thought of as stopping dead in its tracks, if only for an instant, to consider each change in environmental circumstance (including those in the internal environment). At that moment, the intrinsic tendency disappears and the next course of travel represents an entirely new decision, perhaps with no relation to the movements just past.

A vector used to describe the projected motion of an organism at a given point in time and space thus represents a choice, a property of the organism. Its direction and magnitude reflect environmental factors, but only as selections from among a set of alternatives. This is the true basis for distinguishing organismal movements from those of an inanimate particle. This voluntary feature of organismal movements is also responsible for yet other differences from the Newtonian system.

### **III.C. Directional Dominance and Orientational Fields**

In theory, the Newtonian universe is a completely determined machine. Given the laws governing interactions between objects, plus an exact map of the current configuration of all objects and forces over space, subsequent states of the universe can be predicted from one instant to the next, ad infinitum. The only room left for chance in this system lies solely in the imperfections of the observer. It is the complexity of the universe, both in its current state and past history, that makes it appear largely unpredictable to anyone possessing only a finite perspective.

Nonetheless, on a local level, certain objects and interactions dominate the scene, giving at least a statistical appearance of regularity to finite situations. If a coordinate system is considered fixed relative to these dominant features, then the overall determinism of the local system can be represented by a field of forces. At each point within the coordinate frame, a vector is drawn showing the sum of all the dominant forces potentially acting at that point upon some hypothetically subordinate, movable subject. Under the Newtonian laws of motion, the direction component of this vector will determine the course of travel for a subject set down at that point (having initially no intrinsic motion), while the length component represents the acceleration the subject will experience. Such a field can be mapped by moving a small test object (or charge) around in space and simply observing its direction and acceleration upon release. If unknown (but unbiased) influences are also at work on the subject, the dominant forces will still be indicated, but by a mean vector at each point within the field.

Given a map of the field at any instant, a subject's trajectory can be plotted through space, continuously from one point to the next. If the dynamics of the dominant factors are also known (providing they do change over time), then a trajectory in time as well as in space can be predicted for the subject. Even where unknown, "random" influences are added to the system, trajectories can still be plotted, but they will now represent the average or expected paths a subject will take, based on many different trials from particular starting points. In this case, there will also be some variance expected about the mean vector at a point, and predictions about any one trial cannot be made with certainty.

When the behavioral universe inhabited by volitional subjects is considered, an analogous view is often taken. Indeed, this view forms the basis of the Loebian tradition of orientational studies. Again, it is possible to argue under the optimality principles of natural selection that an ideal organism will be completely decisive in its choice of action from a given set of environmentally presented alternatives; it is, in other words, deterministic. As in the Newtonian view, however, the complexity of the decision process will prohibit an observer from making precise predictions about a subject's behavior. Nevertheless, certain factors often appear to dominate over others, at least over local regions of time and space.

With respect to orientation, the existence of distance-receptors in organisms appears to provide an analogy to Newtonian action-at-a-distance. Orientational "fields", it is possible to argue, could be described in ways similar to fields of force. A spring migrant headed towards magnetic north, for example, would display behavioral deci-

sions at various release points that would strongly resemble the behavior of a test dipole observed at the same spots.

However, it is a mistake to take this analogy too far. The existence of memory, along with the volitional aspects of movements discussed previously, may greatly complicate the organism's orientational capabilities as compared to those of a simple inanimate object. Orientational fields, for instance, may be generated purely internally by the organism, by its keeping an exact record of all its prior twists and turns along a route. Barlowe's inertial guidance mechanism can, in theory, exactly duplicate the action of an external, compass referent.

Other, even more complicated trajectories can be generated within orientational fields that would be beyond the powers of a simple Newtonian field. It has been suggested, for example, that some organisms travel in Archimedean search spirals (Hodge, 1894) or in radially looping foraging rosettes (Jander, 1975). All that is theoretically required in both cases is an ability to record the cumulative polar angle revolved about a starting point in order to set the radial distance from that point. In the spiral, a simple equation specifying this behavior is

$$r = b(\alpha) + c \quad (b > 0, c \geq 0)$$

where  $r$  is the radial distance, the dependent variable, and  $\alpha$  is the polar angle (Batschelet, 1976). The search rosette can be produced by a variety of polar functions, for example by,

$$r = b \left| \sin \alpha \right|^{c/2} \quad (b > 0, c = 1, 2, 3, \dots)$$

where  $c$ , if odd, equals the number of petals of the rosette, and if even, only half the number;  $a$  equals the maximum radial distance reached by each loop.

These two examples illustrate the role of memory in generating complex trajectories, something not available to a Newtonian particle. They also indicate an organism's potential for utilizing separate sources of orientational information in reaching a decision; in these two examples, the polar angle and the radial distance could be monitored by completely different perceptual mechanisms. In yet other cases, several sets of both directional and distance cues might be integrated. In some instances, the interaction could be performed by an operation analogous to a vector summation although the length components of the vectors will never represent accelerations, as in the Newtonian model, only the relative importance of the information.

In other examples the organism departs even further from the Newtonian case by choosing one source of information over others. The classic example is given by the two-light experiments of von Buddenbrock (1922) and Fraenkel (1927a), which demonstrate telotaxis in hermit crabs and isopods, respectively. Instead of steering courses that integrate information from both light sources, the subjects chose to orient with respect to only one, but sometimes switching from one to the other. The vectors representing movement decisions at each point along such a route thus show the complete dominance of one source over the other, not anything like the vector sum expected in a Newtonian field.

Such orientational dominance, which is simply a consequence of the volitional properties of organismal movements described pre-

viously, will be shown below to be of primary importance in defining any orientational fields that govern an organism's movements. However, the selectivity and potential for switching back and forth between different orientational cues characterizes organismal routes more generally, even where a field as such is difficult to define.

Before taking up orientational fields, I will first describe an organism's ability to orient even in the absence of an absolute frame of reference. By doing so, I show that even correlated and random walks fall within the family of "oriented" processes, and that orientation itself is a universal property of volitional routes of travel.

Atactic movements. The term "taxis" conventionally refers only to movements oriented with respect to fixed frames of reference. Movements that lack such referents can hence be termed "atactic". As in the examples of the Archimedean spiral and foraging rosette given above, control of a course can be a relative function of previous movements. Although such movements are completely deterministic and undeniably oriented, a fixed field of directional preferences cannot be mapped for them. With respect to any single point in space, the predicted course of travel will depend completely on how the organism arrived there. Different routes up to that point will involve different accumulations of the polar angle, and, consequently, will generate movements towards points of different radial distance from the starting point (presumably along the radii, since that would involve no further change in the polar angle).

While the behavior of an atactic organism may be entirely deterministic at any point in space, a vector representing its course decisions cannot be defined at that point. The choice of heading at

any particular point does not result from the influence of a field but from the effects of all previous movements. If the organism is displaced repeatedly from one point to another, but by means of a variable path, the resulting course vectors at the second point will have a completely random distribution. No field of directional preferences is mappable for an atactic system.

Although the two examples I used above require a memory for previous routes of travel, memory in itself is not the defining feature of atactic movements. The tactic systems that will be described below can also employ memory. It is only the absence of a mappable field that distinguishes this form of orientation. This distinction can be more clearly seen by considering the classic correlated walk as an oriented process.

At every point in space, a single projected line of travel can indeed be specified for a correlated or even a random walk. This heading is simply the same one the organism possessed as it arrived at the point in question (see Figure 3.1). This definition follows simply from the rules of movement discussed previously: in the absence of any unbalanced, external forces (as is assumed in the random and correlated walks) an organism can be expected to travel along a straight line. Only the stochastic, deflectional influences of the environment (yet to be discussed) make the path depart from linearity.

This behavior can be characterized by a simple equation:

$$\alpha_1 = \alpha_{1-1} + \delta_1$$

where  $\alpha_{1-1}$  is the azimuth of the immediately preceding movement and  $\delta_1$

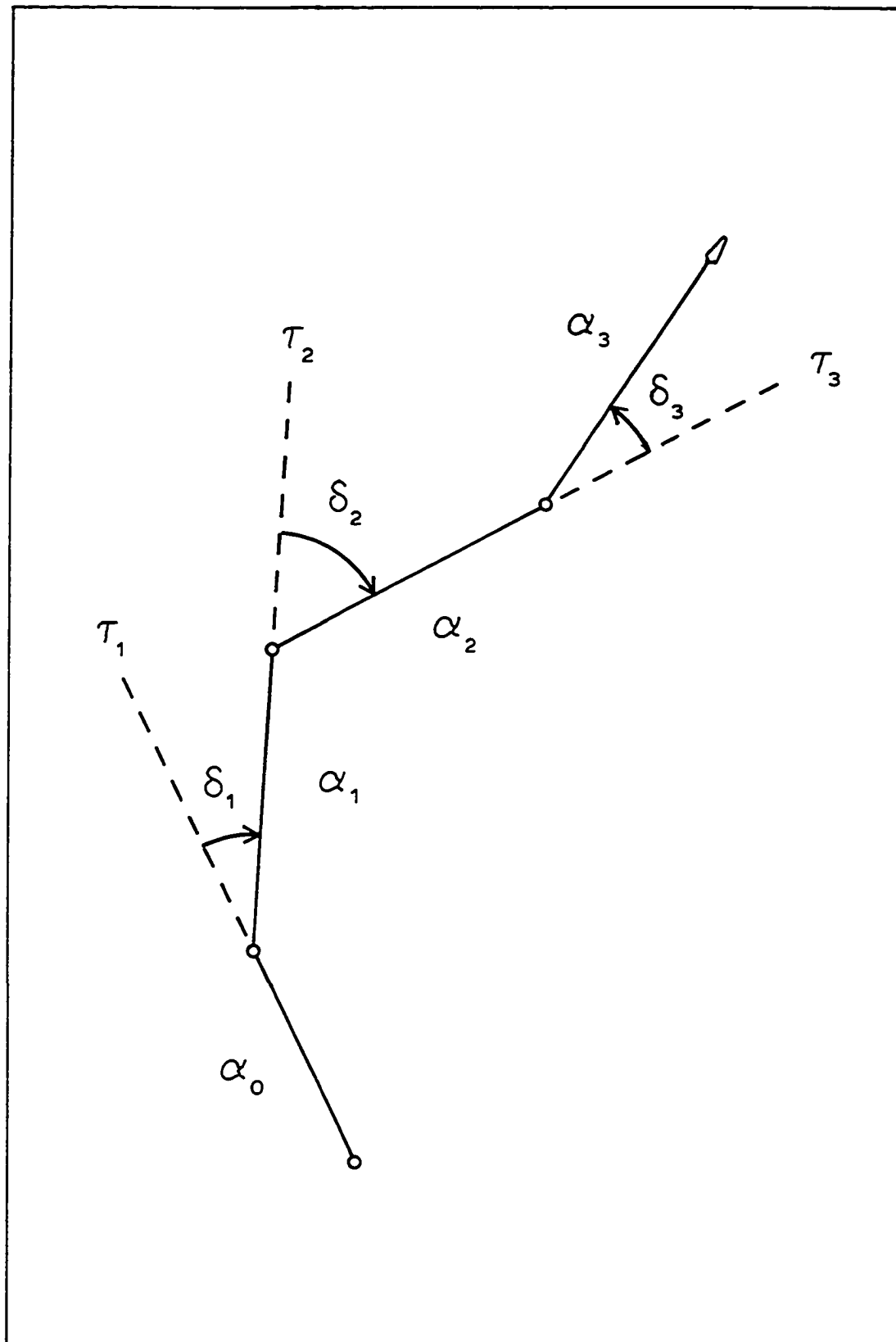


**FIGURE 3.1** The relationship between the directional variables of a correlated walk.

$\alpha_i$  = azimuth of step  $i$

$\tau_i$  = target heading of step  $i$

$\delta_i$  = deflection angle of step  $i$



is the deflection angle experienced at the next instant in the series. The term  $\alpha_{i-1}$  may also be considered to be a target heading.

A general formulation for all oriented behavior is simply,

$$\alpha_i = \tau_i + \delta_i$$

where  $\tau_i$  is the target heading selected by the organism at a particular point. The only way different orientational systems differ is in the way this target is determined.

The inclusion of correlated walks in the set of oriented processes is not all that far fetched. Although this system comes as close to Newtonian expectations as is possible for organismal movements, it should be recalled that even a purely klinokinetic searcher has considerable control over its movements through its regulation of deflections. As will be discussed in Section III.D., deflections in organismal systems are behavioral events, rather than the merely mechanical interactions of Newtonian physics, and hence, are at least under the partial control of the organism.

Also recall from the Introduction that choosing deflections from even a completely uniform distribution can in some cases be adaptive. The random walk is only one extreme of a spectrum of behavior employed by a klinokinetic searcher. Furthermore, a random walk can also represent an extreme case in any oriented process, tactic or atactic. From the general equation of orientation given above, any process can be made random by simply drawing the deflections from a uniform distribution, no matter how the target heading is chosen. The organism might actually be trying to maintain a definite course through space but is prevented from doing so by encountering deflectional events

beyond its control. Or it could itself relax its vigilance over route control in order to take advantage of a particularly concentrated or rapidly renewing resource (as in the case of the pure klinokinetic searcher).

There is yet one other way in which these atactic walks, usually thought of as lacking control over routes, can be related to more traditional kinds of orientational processes: just the addition of a little more memory to these systems can greatly add to the control the organism exerts over its movements, while altering only slightly the generally stochastic features associated with these processes. Indeed, in the higher-order correlated walks theorized by Tchen (1950), the target heading is influenced by the directions of travel several steps back in the sequence, not just by the one immediately past. Behavioral analogues of such processes can be found in the various hypotheses of turn-alternation and turn-compensation mentioned in the Introduction, all of which involve a memory for directions at least two steps back in a sequence.

In a more elaborate theoretical model, Ollason (1983) suggested that a searching animal could gain tactical efficiency by not only avoiding areas previously depleted but also by remembering headings that have been productive in the recent past, especially if its resources display some sort of oriented distribution over space. At any given point, the organism chooses its next course according to a weighted mean of the directions of several steps just past; the weights correspond to the successes (or failures) experienced along the various lines of travel.

Ollason's model not only illustrates the elaborateness possible for atactic systems, but also indicates one final feature of these models: it is not so much the source of the information that is used to guide a route, as it is the way such information is used that determines whether a model is tactic or atactic. Ollason's hypothetical organism could be storing directional information acquired from some fixed frame of reference, for instance the Earth's magnetic field. It is its output in terms of route construction that characterizes the movements as atactic. In choosing its next course of travel based on previous movements, an atactic organism incorporates not only the influences of its previous target headings but those of the deflections as well.

It is this deflectional influence in atactic systems that actually makes the behavior at any point in space unpredictable, at least over several trials and involving different routes leading up to that point. In absence of deflections, the behavior could be quite replicable, especially if the targets were selected with reference to an fixed frame of reference. Looked at in the converse way, it is the predictability of movements at particular points in space even in the presence of deflection that distinguishes tactic movements from atactic, as shall be discussed next.

Tactic movements. A uniquely mappable field of orientational vectors implies the presence of a dominant directional influence at work over an extensive area of space. Stochastic, deflectional events can still occur over smaller regions, but once over, their influence vanishes from all further consideration; their effects are suppressed by the dominant influences represented by the field.

The result is that, at each point in space, there is a specific target heading for the animal's next course of travel, one that does not depend on the nature of the route by which the animal arrived at that point.

An equation representing this sort of behavior is

$$\alpha_i = A_i + \delta_i$$

where  $A_i$  is the direction given by the field at the point where step  $i$  begins.  $A_i$  is constant at that point, unlike the target heading for the correlated walk. The only source of variability comes from the term,  $\delta_i$ , which again represents a deflectional influence occurring at the start of the next movement.

Movements within such fields are termed "taxes" (Fraenkel and Gunn, 1961; Schone, 1984). Consistent with the traditional view that tactic control is fundamentally rotational rather than translational, there are important differences that separate the self-controlled movements of animals within an orientational field from the passively guided particles in Newtonian fields of force.

Unlike the vector quantities associated with each point within a field of force, the quantities within an orientational field are simple directions only, with no lengths associated with them whatsoever. Given the intrinsic ability of an organism to stop each time it makes a new movement decision, there is nothing in an orientation field that corresponds to an acceleration (measured as the length of a force vector). The impulse to move forward from one point to the next comes entirely from within the animal and can therefore be considered separate from the influences that guide it. In this model this im-

pulse will be considered to be uniform over space although realistically it will vary.

Since the field direction at any point in space represents a calculated decision on the part of the organism, it can be oblique to any physical referent it may be using. In fact in some cases no such external referents exist. In Barlowe's model of inertial guidance or in the Mittlestaedts' more general concept of idiothetic course control (Mittlestaedt-Burger, 1972; Mittlestaedt and Mittlestaedt, 1973), the field is generated strictly internally by means of memory for previous courses of travel. While the use of such memory is similar to that in atactic systems, the product of the calculation is a target heading that is independent of the exact details of the prior twists and turns that have been experienced.

The upshot of these differences from the Newtonian model is that orientational fields are not mappable in a way analogous to physical fields, something that has been often overlooked in traditional studies of orientation. If the organism charts its movements by dead reckoning, for instance, then serial placements of it at different locations cannot be considered independent tests of the field, or if they are, as a result of some sort of experimental disruption of the animal's normal abilities, then they will reveal nothing about the true existence of a field. The traditional mapping methods used for inanimate objects simply do not work in such situations.

On the other hand, using the serial dependency in movements could reveal a map every bit as fixed in space as a magnetic field. An appropriate way of mapping an idiothetically generated field, for instance, would be to let the animal do its own traveling but in the

presence of known deflectional circumstances. This is already done in detour studies, but if this method were extended to cover longer sequences of deflections, it would provide, in fact, a general approach to mapping any orientational field, within the laboratory or out where the animal is free to range.

In route analysis, as opposed to traditional orientational analyses, the discovery of the geometric properties of a field is an end in itself. The abstract relationships among the field directions (or among atactic target directions) can be used to define the type of course control used by the animal. An animal, for instance, could use any number of perceptual mechanisms to maintain a given compass bearing (e.g., sun-compass, magnetic-compass, anemotaxis, or kinaesthesia). While the underlying configuration of stimuli differs widely in each of these modes, the important thing for route patterning is that they produce the same sort of output, a field with identical target headings at each point.

This abstract concept of an orientational field thus leads to a parsimonious classification of movements that is especially useful when contextual information (the sort of information needed to define the exact perceptual mechanisms involved) is hard to obtain. Two types of field in particular recur throughout the realm of organismal movements: menotaxis and telotaxis. The rest of this section will further illustrate the concept of orientational fields by means of these two examples, since they are the ones I will actually make use of in analyzing the box turtles' routes of travel.



**Menotaxis.** In the simplest of all possible tactic systems, the field direction is constant for all points in space:

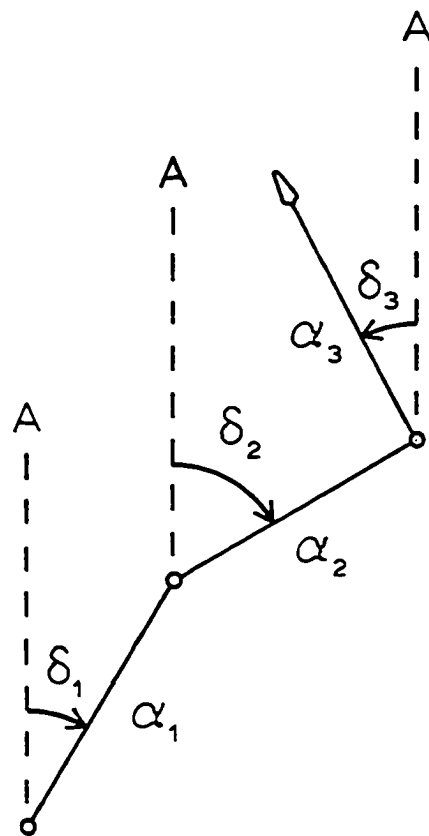
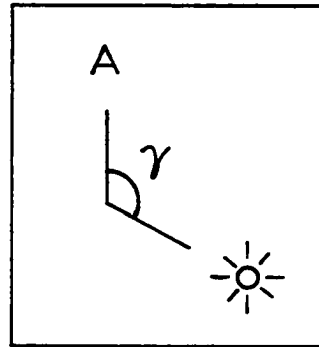
$$\alpha_1 = A + \delta_1$$

In this model the target heading is given by A, a constant azimuth or compass bearing towards which the organism attempts to steer, but which may be oblique to any physical cues to which it refers for guidance (this corresponds to the traditional usage of the term). A field representing this sort of orientation is given in Figure 3.2.

After any deflectional event which takes the organism a step off target, the target heading can be regained on the next step, completely cancelling any effect of the deflection itself. While such behavior usually suggests that a fixed, external referent is consulted at the beginning of each step, it should also be clear that this behavior can result from simply counterturning to subtract the direction of the previous deflection (as in the model of Kleerekoper et al., 1969). The only thing distinguishing this last possibility from similar atactic movements is that the correction must be exact; any error in counterturning will henceforth be built into the target heading, and the effects of such errors will gradually accumulate. The counterturn need not be made immediately, however. In Barlowe's model of inertial guidance, the effects of several deflections can accumulate in the path so long as they are also registered in the organism's memory, allowing for exact compensation to be made at some point along the route.

In addition to referents, both real and imaginary, that have some structural correspondence to a field of parallel lines, a menotactic

**FIGURE 3.2** Relationships between the directional variables of a menotactic walk;  $A$  = a constant azimuthal target. Classically, menotaxis refers to travel oblique to some reference direction (as indicated by the inset). A menotactic walk, however, can be defined simply by the constancy of its target heading, or, in other words, by an orientational field represented by a field of parallel lines.



field can also be generated by reference to spatial features that themselves have a very different sort of geometry. In Tinbergen's concept of pharotaxis, for example (steering a straight course relative to a fixed beacon or beacons; Tinbergen and Kryt, 1933), the lines of reference radiate out from a central point or otherwise change over space as a result of parallax. Nonetheless, the animal is able to calculate in some way the effects of parallax and compensate in order to maintain a constant target heading. In a similar way, sun-compasses and magnetic compasses are defined as cases of menotaxis even though the actual physical field created by the referent again converges on a central point. Here the effects of parallax are so slight as to be ignored by the organism since the reference point is located far away. In all these cases the orientational field is defined as menotactic strictly by the organism's behavior at each point in space, not by the actual physical referents it employs.

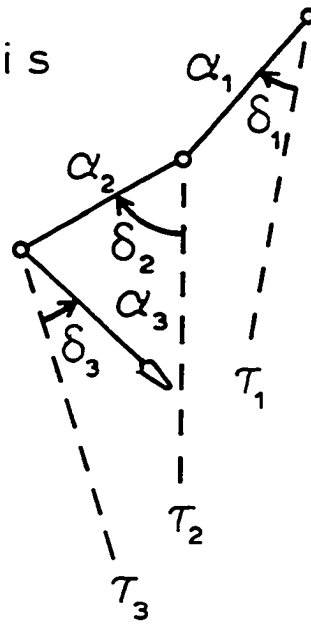
**Telotaxis.** When the effects of parallax are important and not counteracted, a radial orientation field generates telotaxis, which I use here to include centrifugal behavior as well as centripetal. An equation for this behavior is

$$\alpha_1 = (A_1 + t) + \delta_1$$

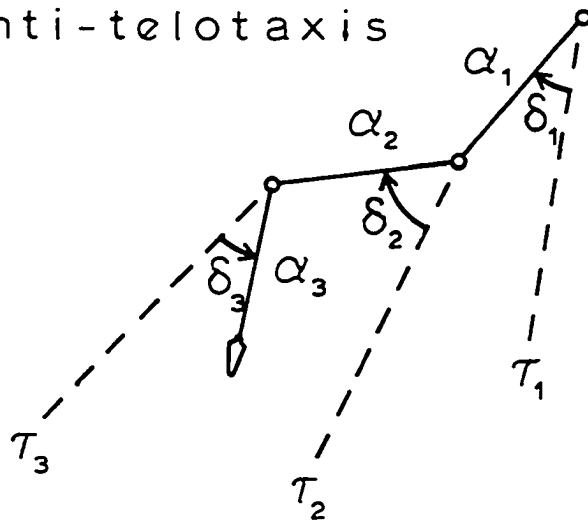
where  $A_1$  represents the direction towards the center of the field and  $t$  is set at either  $0^\circ$  or  $180^\circ$ , depending on whether movements are outwardly or inwardly directed. Figure 3.3 illustrates this type of orientation and makes it clear that, unlike the menotactic field, target headings can differ with location, depending on the organism's direction from the target.

**FIGURE 3.3** Relationships between the directional variables in centripetal (telotactic) and centrifugal (anti-telotactic) walks. Note that the target heading,  $\tau_1$ , is different at the start of each step and that over identical series of deflections the centrifugal walker travels further, roughly  $2 \frac{5}{8}$  vs  $2 \frac{1}{8}$  if the step lengths are of unit length. Further compare these series to that of the menotactic walk shown in Figure 3.2, also confronting the same set of deflections; the menotactic walker travels an intermediate distance,  $2 \frac{3}{8}$ . These differences will be taken up at length in Chapter V.

Telotaxis



Anti-telotaxis



The centripetal case is the general model for goal orientation, at least when the goal is assumed to be fixed in space (moving targets will involve atactic orientations). Along with menotaxis, this type of orientation is widespread among organisms and can be accomplished by a similar range of physiological mechanisms, external and internal referents.

The centrifugal case, on the other hand, has virtually never been considered as part of an animal's repertory, even though it requires no more complicated perceptual abilities than are used in centripetal walks. A centrifugal walk, it should be noted however, is the best means of moving through an area as quickly as possible, when deflections preclude straight-line travel. After each deflection a centrifugal organism chooses its next course of travel in such a way as to maximize its distance from its starting point. A menotactic organism, in contrast, turns more strongly following a deflection, and though exactly compensating for its effects, "wastes" distance through turning a more acute angle than is optimal for maintaining as linear a path as possible. Other tactic movements waste even more distance this way (as is true for a centripetal walk), while some atactic processes come somewhat closer to the centrifugal ideal, as demonstrated in the next chapter.

The examples above raise one final point about the orientational components of the routes: their relative adaptiveness may be determined entirely with respect to deflections. The real nature of animal movements needs to be viewed as an interaction between the elements of control and those that represent all the unforeseen aspects of daily existence, unforeseen by the organism, the observer, or both.

### III.D. Course Deflections as Stochastic and Discrete Behavioral Events

In the gas model, all departures from the predicted lines of travel for a particle, given its intrinsic motion and any external fields of force, are due to collisions with other particles. While the motion of each particle is completely understandable in itself, when bounced around by myriad other particles, all having different velocities and orientations, any one particle's trajectory becomes largely unpredictable to a finite observer. It also takes on a more discrete character than it had when considered in isolation; to a limited observer, these collisions occur over infinitesimally small intervals and appear to represent points of discontinuity in what had previously been a continuous line of travel.

In the gas model, it is collisions, thus, which produce both of the basic features of a walk, its stochasticity and discretely partitioned appearance. The presumed independence of the collisions further implies that the steps observed in a single particle's movements will also be independent, both in direction and length. In the simplest situation, where no field is present, these properties of the particles allow their average trajectories to be modeled by a first-order, unbiased correlated walk. Where it is the behavior en masse that is of interest, these same properties allow diffusion equations to be applied rather than walk models. Diffusion models also have been developed for more complex situations, where fields are present, that would pose difficulties for more detailed treatments making direct use of trajectories.



Even in the absence of any field-like constraints on movements, organismal routes of travel are inherently more complicated than those of inanimate particles. As discussed in the previous sections, the underlying rules of movement for living systems involve decisions, and an organism's selectivity governs deflections away from a target heading as much as maintaining a predictable, smooth trajectory.

But how does this fundamental difference from the Newtonian model affect the possibility for applying discrete and stochastic walk models to organismal movements? How can the ubiquitous orientational capabilities of organisms, both tactic and atactic, be handled by simple walk models that assume both independence between steps and stationarity of probabilities over time and space, both of which would seem to be frequently missing in organismal decisions?

The answer lies in the voluntary switching between control systems that is possible for an organism but not for an inanimate particle. A change in heading from the deterministic path represents a decision on the part of the organism, a behavioral event that lasts until it is replaced by another. There is no physical inertia to worry about; during the course of a given decision, no other control system, such as represented by orientation, need be considered to have any effect. While orientation links the different steps together into a definite pattern, the events that shape the steps themselves can at least be considered both independent of one another and of the orientational system. This behavioral definition of deflections is another major axiom for the theory of volitional walks.

Deflectional decisions, in some cases, will be completely known by the observer and occur at predictable points in space and time. In

such cases, they can be incorporated into the orientational field, which presumably includes all the deterministic features of the routes, whether continuous or discrete. More often, however, the events affecting an animal's course of travel will be completely unpredictable, especially when the observations of the movements are obtained by remote methods such as radio-triangulation or Ariadne's technique. All that might be observed is that a route is punctuated by discrete changes in heading at random intervals. When this situation arises, then both the stochasticity of the routes as well as their discretely partitioned nature can be attributed to the action of unknown but fundamentally independent behavioral events. Any correlation observed between steps can likewise attributed to the action of an orientational system, rather than to any intrinsic relationship between the step-events themselves.

The independence between the discrete and stochastic elements of a route and the continuous and deterministic fields that govern their interactions is represented by the following general equation for animal movements:

$$\vec{s}_i = \begin{bmatrix} \alpha_i \\ s_i \end{bmatrix} = \begin{bmatrix} \tau_i + \delta_i \\ d_i \end{bmatrix}$$

where  $\vec{s}_i$  is a step vector beginning at point  $i$ . The quantities inside the brackets are polar coordinants (direction and length) and indicate the field's contribution (  $\tau_i$  ) to the behavior at each step is directional only; it lacks a defined length component. It is the deflectional event that determines a step's length ( $s_i = d_i$ ). The deflection also contributes a component to the step's orientation (  $\delta_i$  ) equal to that of the field's (refer to Table 4.1 at the

beginning of Chapter IV and at the end of the References for a more extensive key to the symbols).

This equation implies a simple solution to the analysis of organismal routes of travel. If the field direction at any point in space is known, even if only hypothetically, then it can be subtracted from the equation leaving just the stochastic and discrete elements to consider. Conversely, if anything is known beforehand about the deflections, then the model can be used to test hypotheses about the field, as has been done in detour studies. Neither of these possibilities arises in the Newtonian model with its inextricable components of the field and of the collisions, and it is the separability of the deterministic and stochastic elements of volitional walks that provides the real basis for applying walk models to organismal movements.

Even if this separation is accepted in theory, there still remains the question as to how well it can be accomplished in practice. Whereas the step trajectories of gas particles are assumed to be perfectly straight, at least in the absence of a field, the movements of an organism within just a single behavioral event can be quite complicated. The pursuit of a prey item (or, conversely the escape from a predator) can have a sharp onset and offset, as postulated by the model, but the route in between will often be convoluted or broken into yet finer series of discrete steps. These problems will be taken up in Section III.E.

Complicating analysis still further is the likelihood that the series of deflectional events represents a mixture of dissimilar kinds of behaviors, each with a different probability distribution. The

nature of this problem, which poses difficulties with respect to the assumption of independence between step lengths and directions, can be best illustrated by discussing just what sort of features the different classes of deflections might have. The following discussion is addressed particularly to the behavior expected for box turtles. It should also serve to point out the importance of gathering more information on the nature of deflectional events in general than has usually been done in traditional studies of animal movements.

Detours. The classic examples of behavioral deflections, at least for laboratory situations, are those produced by experimental detours as mentioned in the Introduction. The subjects in detour studies are allowed an initial choice of direction and are then confronted with a barricade across their path. Rather than simply rebounding from this obstacle as would a Newtonian particle (in the absence of any other external, biasing forces), the subject displays some degree of voluntary control by moving parallel to the blockade until it is once more free to choose its own course. At that point, the dominant orientational guidance switches back on, whether tactic or atactic.

While such experimental barricades are completely under the control of the observer, and hence should produce completely predictable effects, they have clear counterparts in nature in all the jumble of physical obstacles to straight-line movement an animal encounters in its normal daily travels. Such barricades are especially important to low-built, non-agile crawlers like the box turtle but probably also exist in some form (as habitat barriers for instance) in such animals as birds and fish that move smoothly through their more homogeneous

environments.

When such barricades are fixed in position they are potentially mappable by an observer. In telemetric studies, on the other hand, all the myriad boulders, logs, topographic declivities and ridges that might deflect an animal from its chosen path must usually be treated as stochastic rather than deterministic, at least until maps of repeated movements through an area suggest otherwise. Most often, the effects of detours can be treated as occurring randomly over space and time with the barriers assumed also to have a random orientation. Again if departures from these assumptions are detected in the maps, as for instance where barricades are clustered in space or have some particular alignment, there is the option to include them as part of the field by way of more thorough environmental mapping.

The possibility that two successive detours might have the same orientation, in effect creating one long deflection, presents another problem that in theory also can be handled only by more exact mapping. It might seem splitting hairs to distinguish the separate events making up such a detour but the failure to do so could produce consequences for analysis that are very real. In a purely stochastic walk, such alignments of deflections have a definite chance of occurrence (as they do in the general theory of volitional walks; consider the case not just of two successive detours but of two different kinds of deflections, a detour and a pursuit of a food item, for instance). To ignore the endpoints of such hard-to-distinguish events will result in overestimates of the average step lengths and of the magnitude of the angles turned between steps (there will be too few zero-degree turns), both essential parameters for predicting the features of a walk. This

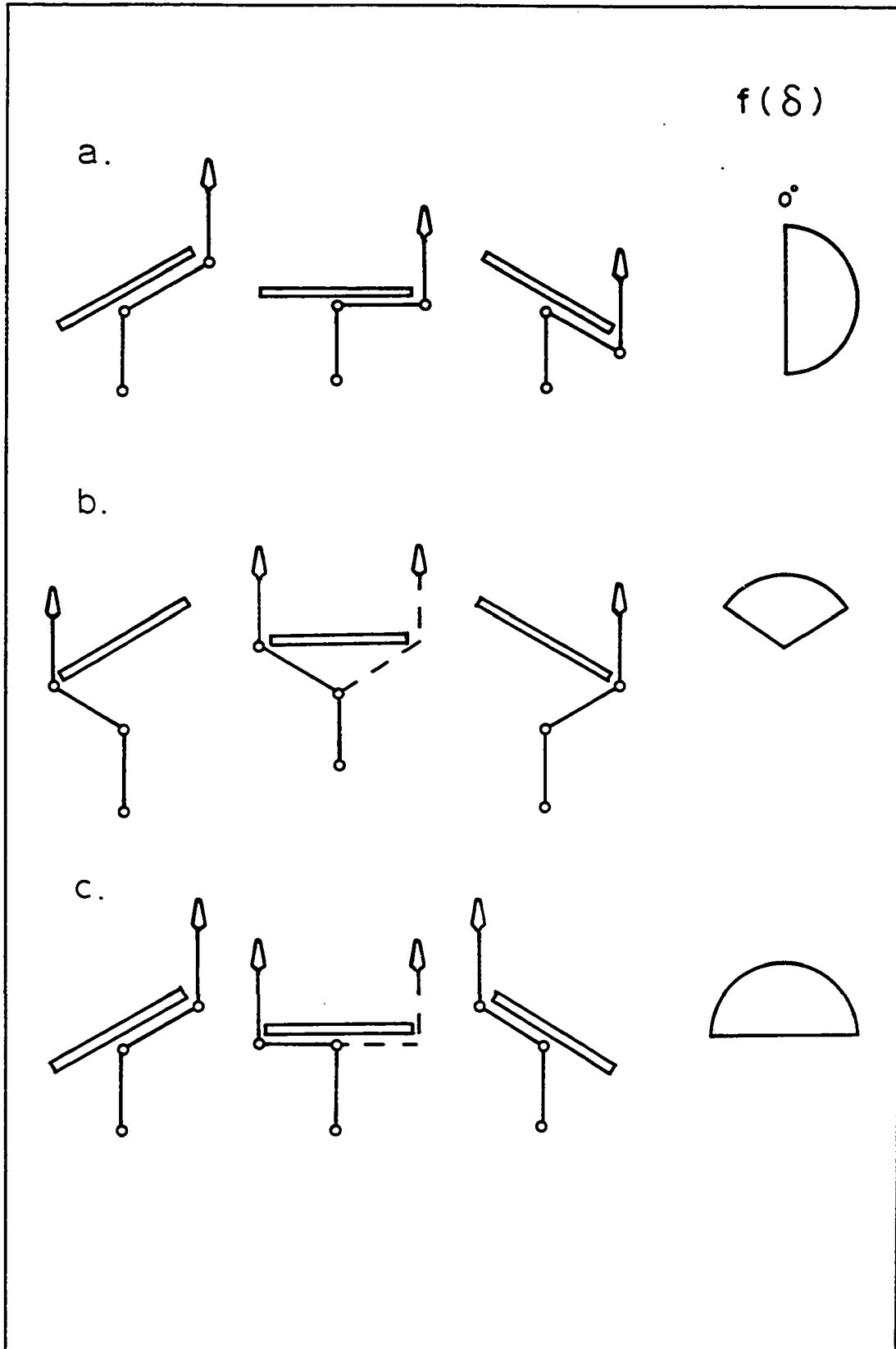
intractable problem should be kept in mind through the discussion of other kinds of deflections, since it logically affects them as well (and it has often been overlooked in studies that define deflections solely with respect to changes in orientation). Approximate ways of getting around this problem are discussed in Chapter V.

Even if all detours could be exactly mapped, as in the laboratory experiments, one final point must be mentioned that has also been previously overlooked: in addition to the volitional features mentioned above, the organism can also display a great deal of self-determination in how it chooses to go around the barriers it naturally encounters in its travels (detour experiments often involve tightly confining corridors that do not permit any options to their subjects). Three possible choices open to an unconfined animal are illustrated in Figure 3.4. In all three cases, an animal can make its point of encounter anywhere along the length of the barricade, not just at one end, as is the rule in detour experiments.

In the first example, the animal responds to a detour by always turning towards one side. Given a random alignment of the barricades, this kind of decision leads to a distribution of deflections that is semi-circularly uniform and centered at  $90^\circ$  relative to straight ahead, towards the preferred direction of turning. If detours are closely spaced this could result in a series of biased turns that could conceivably be of use in a convoluted search for spatially-clustered resources. In most cases, however, such decisions would be inefficient; for a convoluted search there are more reliable ways of producing a series of biased turns, and for a straighter path through a series of obstacles, the other two kinds of detour decisions are the

**FIGURE 3.4** Examples of three different ways to make a detour and the distributions of deflection angles ( $\delta_1$ ) that result from these decisions.

- a. deflections always made towards one side
- b. deflections made towards the closer of the two ends of the barricade (equally likely choices are indicated for the middle example); the range of the deflection distribution will vary as a function of the length of the barrier and the distance from the barrier where the deflection begins (the distribution shown will hold only where all barriers have equal length and the deflection always commences at the same distance)
- c. deflections made towards the side that will produce the shallowest angle upon contact with the barricade (equally likely choices are shown in the middle example)





ones to make.

The most efficient forward progress will be made by an animal that reacts to a barricade before it actually comes even with its nearest projection. As shown in the second example, this allows the animal to choose to follow the either the smallest angular or linear deflection from its chosen path. If such decisions are always made at the same distance from the nearest point of the barricade and again assuming that the barricades all have a random alignment, the resulting distribution of deflections will be a uniform sector of the circle, centered on  $0^{\circ}$ , the straight-ahead direction. The width of the sector will depend on the reaction distance but should never exceed  $180^{\circ}$ .

Many animals, however, probably do not respond to a barricade until actually encountering it and finding no way over or under. This is the principle underlying the use of drift-fences, often employed in trapping reptiles, amphibians, and other crawling species. In this case, the option to go around the closer end of the barricade might be difficult to put in practice: it might be too hard to perceive the ends of the obstacle, especially if it is irregular in outline. The animal can still avoid backtracking and thus "wasting" forward progress by choosing to follow the shallowest angle it encounters at the point of contact. This rule will again result in a uniform semi-circle of deflection angle probabilities, but one that always occupies the entire  $180^{\circ}$  semi-circle about the straight-ahead direction. This behavior is typical for box turtles encountering logs or other barriers.

Still other reactions are also conceivable (the rebounding behavior of a gas molecule for instance), but the examples shown, particularly the last two, seem the most likely. If this is the case, then it follows that a large contribution to the overall distribution of deflection angles will be a uniform arc of the circle, probably no more than  $180^{\circ}$  in extent and most likely centered on  $0^{\circ}$ . Deflections that are found to be more than  $90^{\circ}$  in magnitude must then be due to causes other than simple responses to barricades.

Aversions. The most likely source of obtuse deflections are responses to stimuli that the subject expects to be injurious or otherwise harmful in nature. Here, if anywhere, the organism might be expected to respond by "rebounding" away from the source of the deflection. Examples of such aversive stimuli include predators, dominant conspecifics, competitors, or the edge of an unfavorable habitat.

If active flight is the response, however, then the movements involved probably represent more than a simple deflection within a walk that will be soon resumed. More likely, such responses represent the termination of the previous sequence of behavior and the initiation of an entirely new walk (or run in this case). In any event, flight would probably last over some prolonged distance and the inclusion of such movements within a series of more typically shorter steps also possessing smaller deflection angles would so bias the observed frequency distributions as to make predictions about the walk overall very difficult. For that reason alone, any pronounced aversive reaction should probably be treated as a separate walk.

Less overt reactions to aversive stimuli are, of course, also possible. For example the box turtle's usual response to a potential

predator is to freeze and rely either on its crypticity or its redoubtable shell for defense. Once the hazard is past, it often proceeds as if nothing had happened. Other animals in similar situations might also at least temporarily avoid the path taken by the retreating danger, in which case the aversive response can truly be considered a momentary deflection. In such cases, the directional distribution for aversive deflections will approach the Circular Uniform Theoretical Distribution: all angles of avoidance might be expected to occur if the animal moves directly away from the direction of the aversion and if those directions themselves are distributed randomly with respect to the subject. If the subject also includes some component in its decision representing its former favored heading, the deflection directions will be weighted towards straight ahead. But in any case, such events will probably be far less common than other sorts of deflections and will make only a small contribution to the overall distribution of deflection angles.

Attractions. Much more frequent in the daily lives of animals are their own pursuits of attractive stimuli, whether of food, mates, trespassing conspecifics, and so forth. The walk patterns of organisms are probably designed primarily to maximize the number of such encounters. For instance, the movements of pollinators within a flower patch or those of any other cropping forager can consist solely of short steps between attractants. Even for animals like the box turtle that search widely for sparse resources, attractants should be common, although perhaps less so than detours or deflections resulting from course errors.

Whatever their relative frequency, the theory of search as outlined in the Introduction suggests certain things about the directional distribution of attractive deflections. Because the wake of the organism is the least likely area in which to find new items (since it includes the area just explored or exploited), the organism can be expected to encounter most attractants in the straight-ahead direction. Most organisms additionally show a strong cephalization of sensory structures for the sake of guidance, which again makes detections in the forward direction the most likely.

Since it is further safe to assume that attractant deflections are equally likely to occur to the animal's right or left, the expected distribution of deflection directions is unimodal and symmetric about  $0^\circ$ . Any extension of the distribution into the semi-circle centered in the reverse direction will depend on the orientation of the organism's sensory structures, its efficiency in detecting attractants as it moves through an area, and in the renewal rate of the attractants themselves. Most likely the distribution will be highly platykurtotic, perhaps even sectorially uniform in the forward direction with no tail beyond  $+ \text{ or } - 90^\circ$ .

Sign-alternating turning has, however, also been frequently reported in foraging movements (e.g. Smith, 1974a, b), as have other structured patterns in the harvesting of resources, for example radial loops or Archimedean spirals (Jander, 1975). In these cases, the successive deflections in a series are not independent of one another, the result of which would be a major violation of the assumptions of walk analysis. As discussed previously, a way around this problem is to ascribe such regularity in the movement pattern to the action of

the orientation system of the organism. Atactic models can be particularly appropriate in this regard.

This solution works, however, only so long as the movement pattern is regular enough to make hypotheses about orientational control. Another potential violator of the assumptions of walk analysis cannot be handled the same way. Klinokinesis, also usually connected with foraging movements (although originally associated with aversive stimuli), remains a problem for analysis whether or not it is under the control of the organism or more directly results from the patchy nature of the environment. Changes in the distribution of deflection directions or lengths when the organism moves into or out of a concentration of attractants, no matter how they are accomplished, violates the assumption of stochastic stationarity needed by walk analyses. Unlike concentrations of detours, which can potentially be handled by mapping them as fixed features of the orientational field, concentrations of attractants can be difficult to pin down in either time and space and thus remain irreducibly stochastic elements of the model.

On the other hand, if there is no fixed spatial or temporal regularity to the changes in the deflection parameters and if klinokinesis plays only a fleeting and comparatively small role within any particular walk, then its effects will not present significant problems for walk analyses, which examine the average behavior over several different series of steps. Only where the shifts in parameters are all aligned across the routes to be averaged will there be any noteworthy effect (at least one such instance shows up in the analysis of the box turtle data). For the most part, klinokinesis will play an almost negligible role in route patterning by widely foraging animals

like the box turtle.

"Zero-degree" and "spontaneous" deflections. With the possible exception of the movements of a cropping forager within an extensive patch of concentrated resources, the kinds of deflections so far mentioned surely do not fill up all the space within which a walk occurs. There must be gaps between deflectional events where the animal can be expected to match its orientational target heading as closely as possible. There must also be times when the direction of the orientational target and that of the deflection must coincide. In these cases a "zero-degree" deflection is definable; its length corresponds either to the gap between events or to a definite deflectional event as described before. (For the sake of clarity, I must point out that zero-degree deflections are not the same as zero-degree turns, except within a correlated walk, although two zero-degree deflections strung together will produce a zero-degree turn, as will any other pair of matching deflections.)

Although the most probable angular value of the deflection in such intervals will be zero, the actual chance of hitting that value is infinitesimal. As opposed to the perfection of motion expected of a Newtonian particle, the movements of organisms will involve self-generated course errors, as a result of imperfections in their locomotory or perceptual apparatus. Consequently, there will be a relatively narrow spread of values symmetrically distributed around zero degrees representing "spontaneous" deflections (biased distributions of such errors might also occur, representing defects affecting only one side of the organism's body, but these should not be of normal occurrence). Error detection by the organism might furthermore occur

at discrete intervals, after the animal has passed some threshold of detection. Thus a path can have a segmented appearance even in the complete absence of such concrete deflectional events mentioned previously.

Especially interesting for the theory of volitional walks are cases in which "spontaneous" deflections serve some adaptive value and their initiation is under the control of the organism. Here changes in direction away from the target heading represent trials rather than errors. Examples are classic klino-kinesis, in which the points of turning are decided by the animal and not determined strictly by the environment, and klino-taxis, in which turning trials are used to obtain information about the orientational field (it should be noted that klino-kinesis can also accompany oriented movements, including klino-taxis, where part of the information sought is positional and is related to the distribution of attractants or aversions as well as to the subject's motivational state).

As with pure errors, the angular distribution of "spontaneous" (actually idiothetic) trials can also be expected to be symmetric about zero degrees (departures from this expectation should again be treated as involving orientation rather than deflection). However, the spread should be much greater. In the classic examples of klino-kinesis, where the angular distribution is hypothesized to be circularly uniform, the spread is expected to be a full  $360^{\circ}$ . Among klino-tactic animals, on the other hand, the angular deviation of the trial from the sought-for target will only rarely be larger in magnitude than  $90^{\circ}$ .

Mixtures of deflections. From the preceding discussions, it should be clear that an animal can encounter many different sorts of deflections within the course of a single walk. The sample of deflections will then be a composite representing a variety of behaviors, not the ideally homogeneous one desired for walk analysis. Some of the problems that arise from this mixture of processes in terms of non-independence or non-stationarity of the steps have already been mentioned. At this point I would like to bring up one further problem that deflectional heterogeneity introduces, namely a lack of independence between step length and direction.

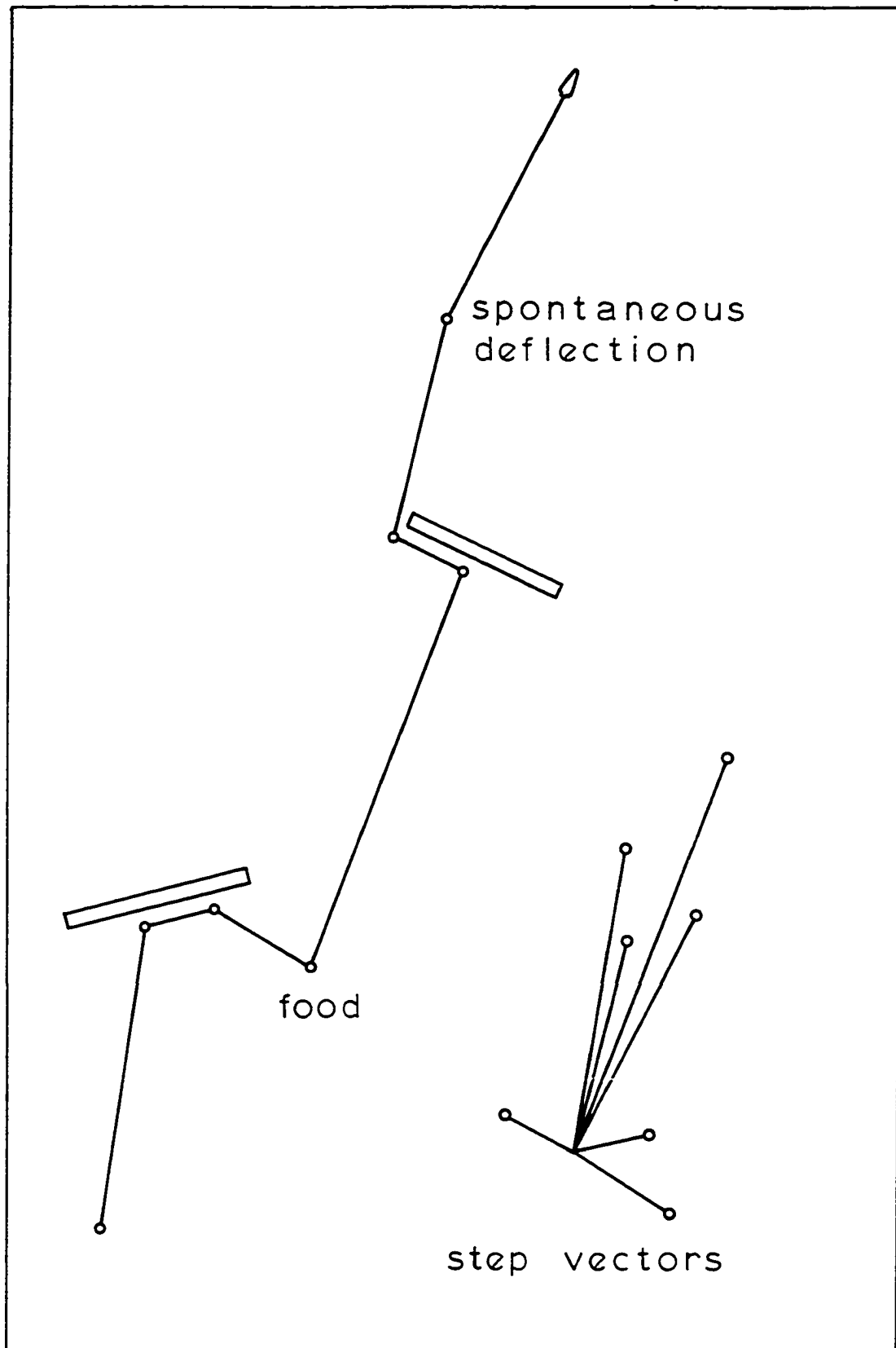
Consider, for instance, the example illustrated in Figure 3.5. This could represent the path expected for an animal that, like the box turtle, is only occasionally deflected by detours or attractive stimuli. Alternatively, the path could be viewed as a case of klinotaxis (or negative klinokinesis within a stimulus gradient, as described by Ulliyot, 1936b).

The vectorial distribution of deflections shows quite clearly that the closer the angle of deflection is to zero degrees, the greater chance it has of being of great length; conversely, the greater the magnitude of the deflection angle the less likely it is to play a major role in the walk. Obviously, any prediction of overall route properties, such as the mean squared distance of travel, must take this correlation into account.

On the other hand, this difficulty affects only analyses in which step length is an essential variable. In the next chapter, I will show that much can be learned by ignoring the information that step length provides, at least at first. If the steps are all treated as



**FIGURE 3.5** A path illustrating a mixture of deflections that produces a correlation between step length and direction.



though they were uniform in terms of distance, then the orientational relationships between the steps, of crucial importance in determining whether or not they represent independent events or still include the residual effects of some form of orientation, can be examined in isolation. If they do prove to be independent of one another, then the addition of the length information can be used to deduce something further about the nature of the deflections (including the control the organism exerts over their selection). In Chapter V, I will also discuss a more approximate way of handling correlation between step variables, one that deals with zero-degree turns, klino-kinesis and other sorts of problems as well.

One more problem to discuss related to the definition of steps and of walks themselves is the likelihood that organismal movements are structured hierarchically. Such structuring would introduce yet another source of dependency between steps, one leading to even more egregious errors than those mentioned above. Without precise recognition of the limits and components of individual walks, no sort of analysis, approximate or otherwise, can hope to succeed.

### III. E. Hierarchies of Route Control.

In the study of actual rather than ideal gases or fluids, the paths of the individual particles are rarely of much concern. It is rather their indirect but measurable consequences that are of interest, especially the aggregate properties of billions of such particles. As mentioned earlier, a major presumption underlying the study of diffusion, pressure, rates of reaction, and so on, is that behavior on the macroscopic level can be simply extrapolated upward from the microscopic level of the particles. In other words, selection of the scale of measurement is determined by its convenience and feasibility for the observer. Looked at from the other way around, an observer chooses to examine diffusion-level phenomena because of their measurability and then extrapolate downwards to propose an explanation in terms of particulate behavior.

From the preceding discussion of deflections and control systems, however, it should be clear that an organism's movement decisions are probably organized according to a hierarchy, one that is intimately connected with scales of measurement. Imbedded within an overall guidance scheme are decisions that take control over shorter distances or intervals of time. Within individual deflections yet smaller course decisions are made. Conversely, the particular orientational field in which the deflection occurs can itself be a component within an even greater scheme of movements.

More than any of the other departures from the gas model, it is the hierarchical nature of decision-making that distinguishes organismal routes of travel from simple walks. While the movements of an inanimate particle reflect all the external forces, both large and

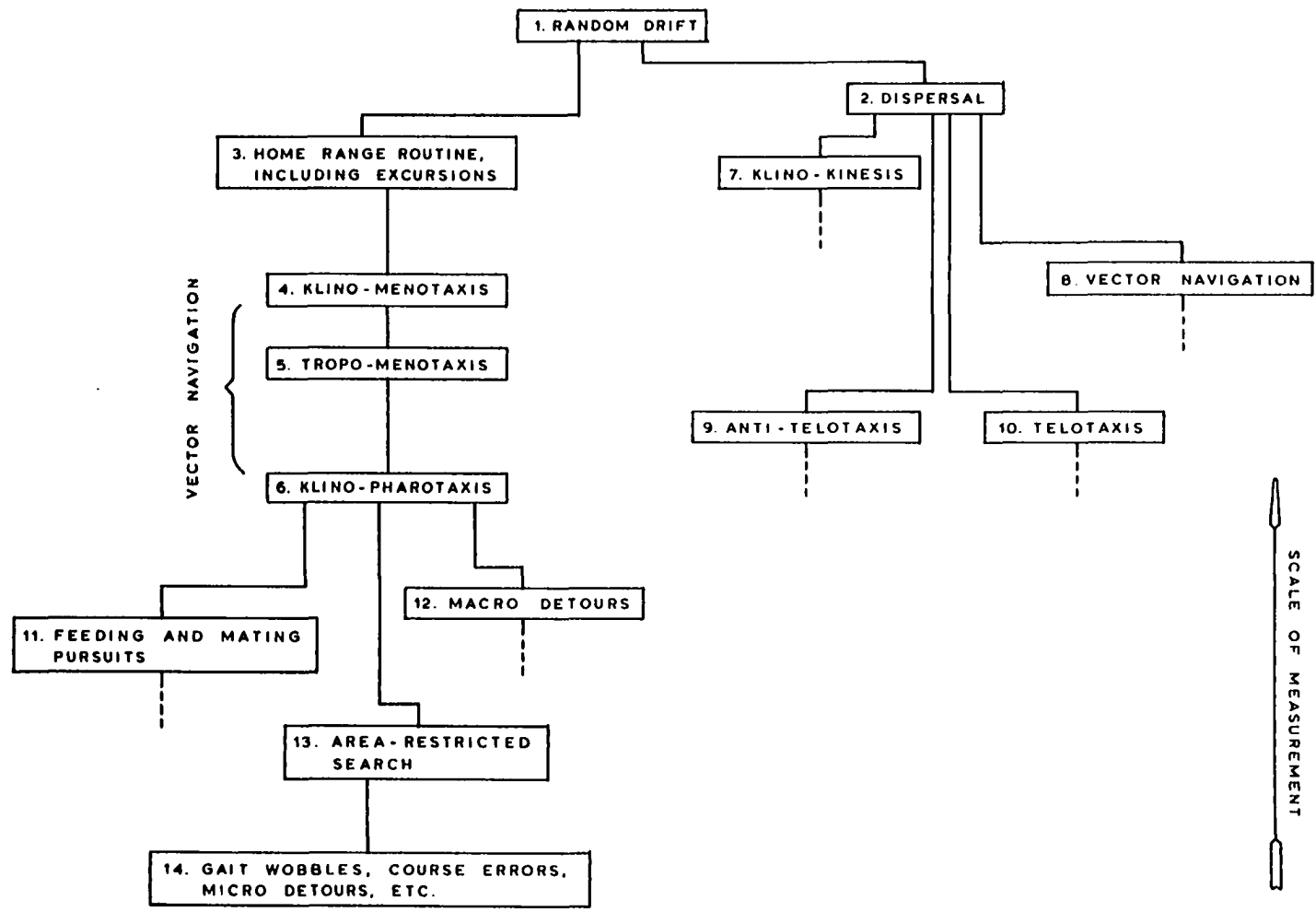
small, at work on it simultaneously, the influences governing an animal's route of travel switch on at different scales of measurement. Extrapolation from one scale to another is thus essentially impossible for organismal movements (although I do not deny that exceptions can occur). The observation that an animal travels randomly at one scale of movement does not imply randomness at either a higher or lower scale of measurement. The same is true for both atactic and tactic forms of oriented movements.

An example of a decision-making hierarchy governing an organism's movements is diagramed in Figure 3.6. Each box represents a particular kind of behavioral process, and each of the lower boxes represents a subroutine within the box immediately above it in the hierarchy. Control begins in the uppermost box, is then switched down through one or more lower ones, and eventually is switched back upwards to where it started. From the scale roughly indicated by the position of each process from the top of the figure, it can also be seen that lower level processes produce movements that are either shorter or more transient than those above it in the hierarchy.

In terms of walks (the output of the model), one run through any particular subroutine produces one "step". At the end of that step, control is passed back to the immediately higher governing process, whereupon it is sent back down to the same box or to a different subroutine at the same level. The boxes at each level are independent of one another and represent the various classes of "deflections" operating within a particular control regime. True "control", of course, could be absent at a particular level, and the string of steps constitute either a correlated or random walk, and thus depend solely

**FIGURE 3.6** An example of a route-control hierarchy. Although this particular model is close to the one I will develop to explain box turtle movement patterns, it is not the only one conceivable. I use it here only to point out a few things about route models in general:

1. While each box represents a walk process, not all need represent "control" processes (e.g., boxes 1 and 14).
2. The control processes themselves need not be all of one type. For example, the home range process (box 3) dictates movement decisions based on spatial position and memory for past events, whereas the processes indicated in boxes 4 - 10 (all forms of classic orientation mechanisms) do not depend on prior history of movements.
3. Steps within any given walk can be heterogeneous, as indicated by the alternate branches stemming from several of the boxes (e.g., boxes 2 and 3 both contribute to the random walk at the highest level). Not all branches need be employed, however, in any particular run.
4. A given kind of process can operate at different points in the hierarchy as well as over different scales of measurement (e.g., telotaxis occurs in boxes 10 and 11, area-restricted processes in boxes 3 and 13).



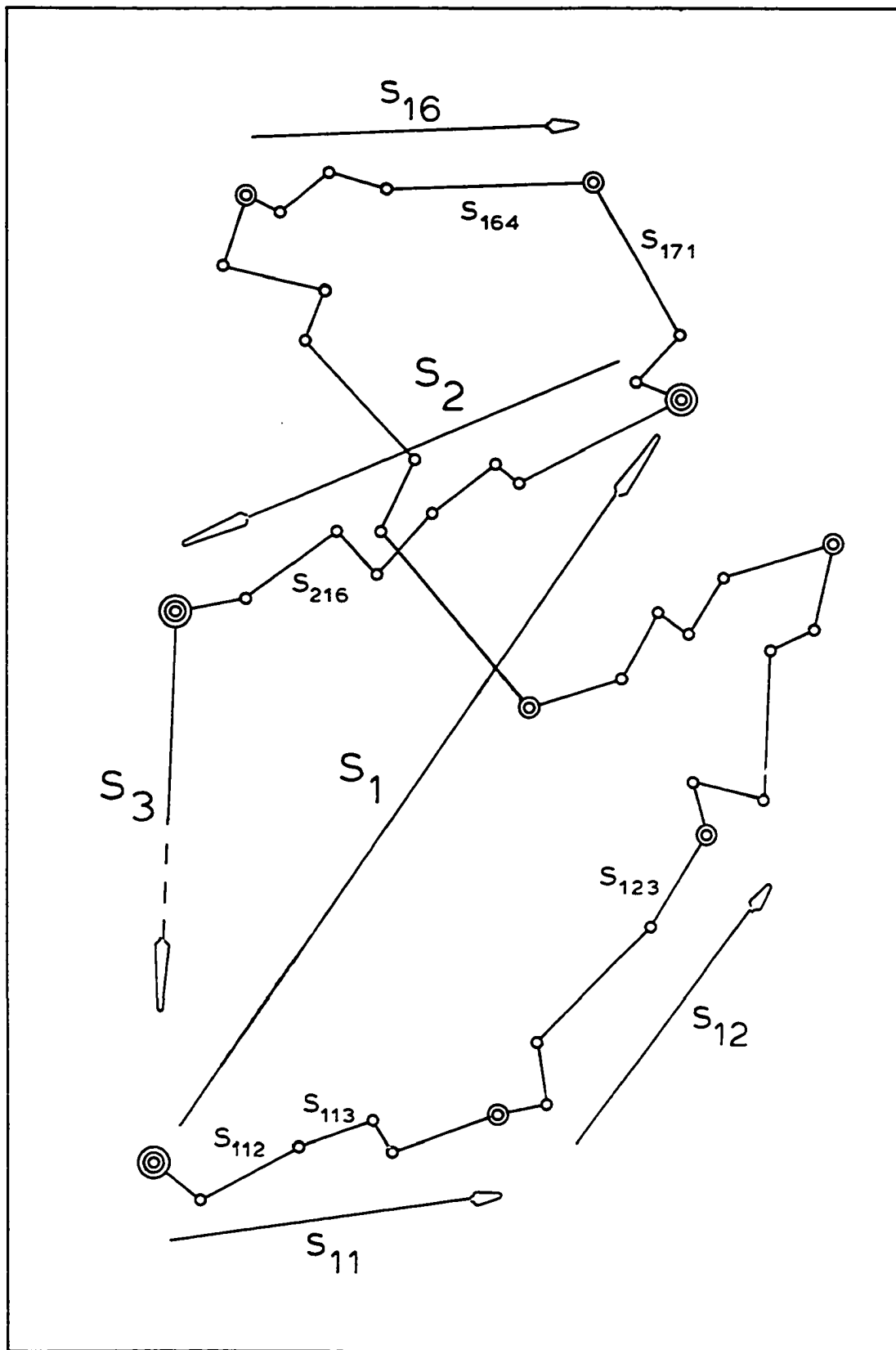
on the nature of the deflections. An example is given by the box at level one, which presumes that after a series of dispersive and residential interludes, the animal's drift is essentially random.

After a step has been completed and control passed back to the next higher box, it may then be passed up to yet another level. This terminates a step at the intermediate level but also terminates an entire walk at the first level mentioned. An organismal route, as distinguished from a simple walk, is thus a composite of many different walks, each step within any one of which may itself be a composite of walks. An example of a route produced in this fashion is given in Figure 3.7, representing three levels of walks or control processes.

Whether or not this example is typical of any animal's ranging pattern (in the Discussion I will present evidence that it is), it clearly illustrates the problems potentially present in extrapolating from one scale of measurement to another. Suppose an investigator is aware of the step changes given by the single dots (movements between food items, for instance), but not at the other levels shown. In attempting to fit a simple walk model to his observations, he would confound walks governed by different sets of parameters (the steps of the higher-level control process). Even if he somehow manages correctly to identify the walk processes at his level of interest, he will still be unable to predict the meanders or spatial constraints of the levels above. For example, the mean-squared-distance curve will level off, something he would not have predicted from knowledge of the lower level steps alone. While he might then accept the existence of higher-level spatial constraints, in the absence of any information about where the endpoints of the larger steps occur, he



**FIGURE 3.7** An example of a route composed of three levels of walks. The highest level steps, indicated by the  $s_i$ 's and endpoints with three concentric circles, represent home range constraints. The second level steps, indicated by the  $s_{ij}$ 's and double-circle endpoints, show a fairly meandering pattern similar to a correlated walk. The lowest level steps, indicated by the  $s_{ijk}$ 's and single-circle endpoints, obey a klinotaxis, where step length and deviation from the target heading show a negative correlation.



will be unable to determine anything else about the details of the more inclusive patterns.

At the other extreme, an observer who only surveys the endpoints of the largest steps shown, indicated by the three concentric circles, would be in even greater ignorance about the nature of the animal's control over its movements. The strongly oriented patterns on the lowest level would be lost from view, as would the looping walks at the intermediate level. In fact any loop that brought the animal exactly back to where it started would be replaced by a "step" of zero length; it would not even be represented in the walk on the level above! While the observer might correctly identify the overall lack of drift as indicating the existence of a home range, he would be unaware of the processes that show its function. Any attempt he might make to explain his findings in terms of lower level behavior would be essentially fruitless.

Comparing these two examples, it seems safer, as a rule, to start at the lowest level of movements possible and to work upwards, replacing low-level sequences with single steps as the processes become understood. This is the approach to route analysis I advocate, especially when the steps at the lowest level are selected arbitrarily by the observer, in terms of either a fixed distance or unit of time. While there is no possibility of deciphering processes below the level of the smallest step in the survey, there is at least some hope that the endpoints of the steps belonging to the next level up can be discovered. Finding those endpoints further guarantees that the endpoints of the steps at all higher levels will also be represented on the maps (if still not identified as such). Thus in Figure 3.7, the

termination of a walk always occurs at the termination of some lower-level step. This information at least provides the chance that higher-level patterns will also become discernable.

This approach, of course, still presumes that, at any particular level, walk analysis can be used to characterize the movement process. It remains to be shown, however, that walk models can be adapted to the complexity organisms show in their control over their routes of travel. The next chapter attempts to do just that, presenting a general method for testing hypotheses about a walk process, although one that depends on at least the tentative specification of a control system. To the extent this method succeeds so does the overall theory of movements I have presented.

## **CHAPTER IV. MATHEMATICAL ANALYSIS OF VECTOR SEQUENCES**

TABLE 4.1 SYMBOLS\*

I. Theoretical Quantities

A. Variables

$\tau_i$	the target heading for a step beginning at point i
A	an azimuthal target that is constant over all steps
$\vec{d}_i$	a deflection vector occurring at point i
$d_i =  \vec{d}_i $	the length component of a deflection vector
$\delta_i$	the directional component of a deflection vector

B. Population parameters

$\vec{\mu}_\delta$	the mean vector of the directional components of deflections
$\mu_\delta$	the directional component of the mean vector of deflection directions
$\rho_\delta$	the length component (concentration parameter) of the mean vector of deflection directions

II. Measurable Quantities

A. Variables

$\vec{s}_i$	a step vector beginning at point i
$s_i =  \vec{s}_i $	the length of a step vector
$\alpha_i$	the azimuth of a step vector
$\theta_{ij}$	the angular difference (turn angle) between the azimuths of steps i and j
$\theta_k$	a turn angle of order k, where k is the number of steps that separate points i and j (i.e., $k = j - i$ )

\* This choice of symbols represents a compromise between the literature of stochastic walks and orientational statistics

**TABLE 4.1 CONTINUED**

$\vec{D}_n = \sum \vec{s}_i$	the net vector of travel over n step vectors
$D_n =  \vec{D}_n $	the net distance of travel over n steps
$R_n =  \sum \alpha_i $	the length of the azimuthal resultant over n steps (a quantity similar to $D_n$ but where the step lengths are treated as having unit values)

**B. Sample statistics**

$m_\alpha$	the mean angle for a sample of step azimuths
$r_\alpha = R_n / n$	the concentration parameter for a sample of step azimuths
$m_{\theta k}$	the mean angle for a sample of $k^{\text{th}}$ order turns
$r_{\theta k}$	the concentration parameter for a sample of $k^{\text{th}}$ order turns
$\overline{c_{\theta k}} = m(\cos \theta_k)$	the mean cosine for a sample of $k^{\text{th}}$ order turns
$m(D_n^2)$	the mean squared distance of travel over n steps (also denoted by "MSD")
$m(R_n^2)$	the mean squared resultant over n steps
$m(s^2)$	the mean squared step length

#### IV.A. Transformation of an Observed Series of Steps into a Pure Sequence of Deflections

Despite the many potential complexities in the routes traveled by organisms, simple walk analyses are still of use in untangling patterns of movement. According to the theory presented in the previous chapter, any relationship between steps is due to the action of a deterministic control system, the operation of which is presumably known to the observer, at least as an hypothesis. If the components of a route representing the control can be subtracted, then the residual, stochastic elements can be handled by methods such as the mean-squared distance analysis described in the Introduction. This process serves not only to clarify the nature of the less well understood deflectional components, but also provides a test of the control hypothesis itself: if a walk model fits the purified deflections, then there is no reason to suspect any form of control other than that already assumed.

As illustrated in Figure 4.1, any step,  $i$ , in a particular walk will have the following form:

$$\vec{s}_i = \tau_i \otimes \vec{d}_i$$

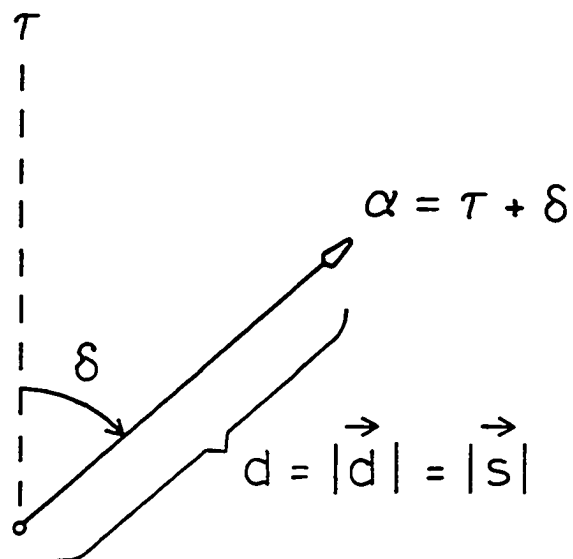
The term representing orientational control is  $\tau_i$ , a purely directional quantity. It represents either the turning response relative to a previous series of steps in an atactic system, or the field direction in a tactic system. As shown, it may be different for each



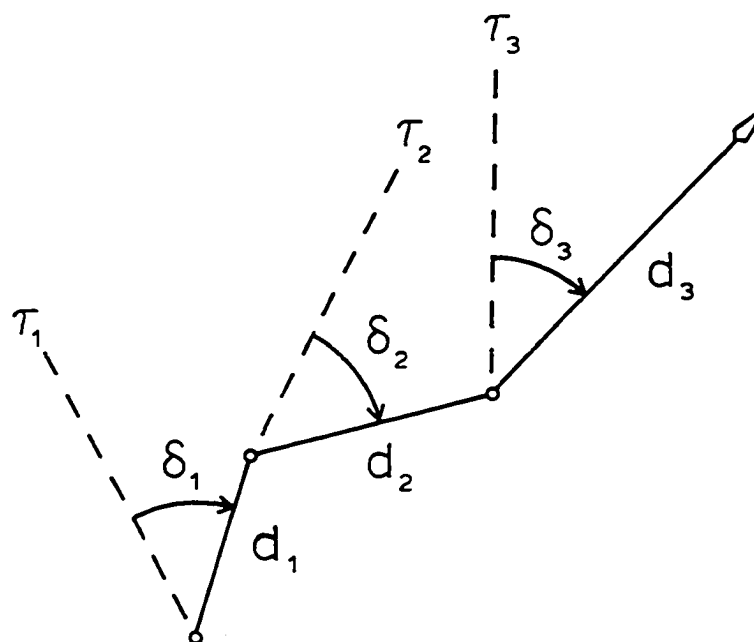
**FIGURE 4.1** The relationships between steps, targets, and deflections in a generalized walk.

- a. The length component,  $s$ , of a step is equivalent to the length component,  $d$ , of the deflection vector. The azimuthal component of the step,  $\alpha$ , is equivalent to the sum of the target heading,  $\tau$ , and the directional component,  $\theta$ , of the deflection.
- b. The sequential relationships among a series of steps represent an interaction between target headings and deflections. In this example the series shows an alternation of turns between steps although the deflection angles are all to the right; the zig-zagging is due in part to the differences in target heading from step to step.

a.



b.



step in the series.

The term representing the deflection,  $\vec{d}_i$ , on the other hand, is a vector, possessing both a length and a direction. To show the interaction between these two different sorts of terms, I introduce a rotational operator, signified by  $\phi$ , which indicates the deflectional term alters the chosen heading by a certain degree and also determines the step's length.

Considering only the directional quantities,

$$\alpha_i = \delta_i + \tau_i$$

If  $\tau_i$  is known for all  $i$ , then the steps of the walk representing a particular control regime can be transformed into a more tractable series by simple directional subtraction:

$$\alpha_i - \tau_i = \delta_i$$

In terms of the step vectors this transformation can be thought of as a counter-rotation:

$$\begin{aligned} (-\tau_i) \phi \vec{s}_i &= (-\tau_i) \phi \tau_i \phi \vec{d}_i \\ &= \vec{d}_i \end{aligned}$$

The quantities left after this operation should be solely the deflection vectors. By hypothesis they should now be independent of one another and have a common zero direction. If they further all have the same mean, variance and other distributional parameters and if the step lengths and directions are also uncorrelated, then the mean squared sums of these vectors can be predicted from the step statistics by means of one of the equations mentioned in the Intro-

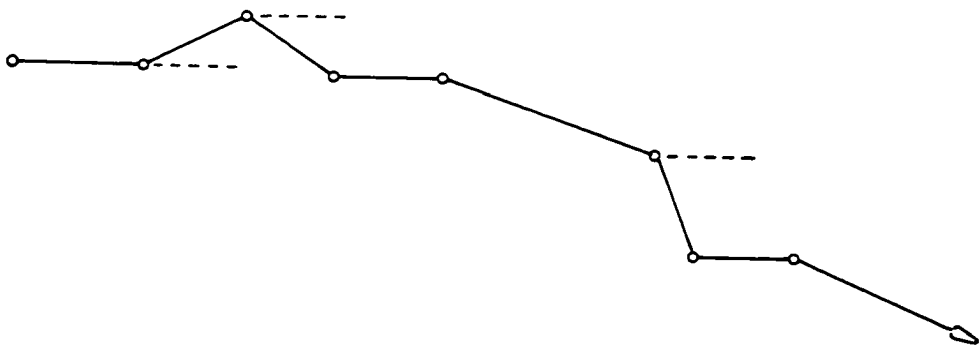
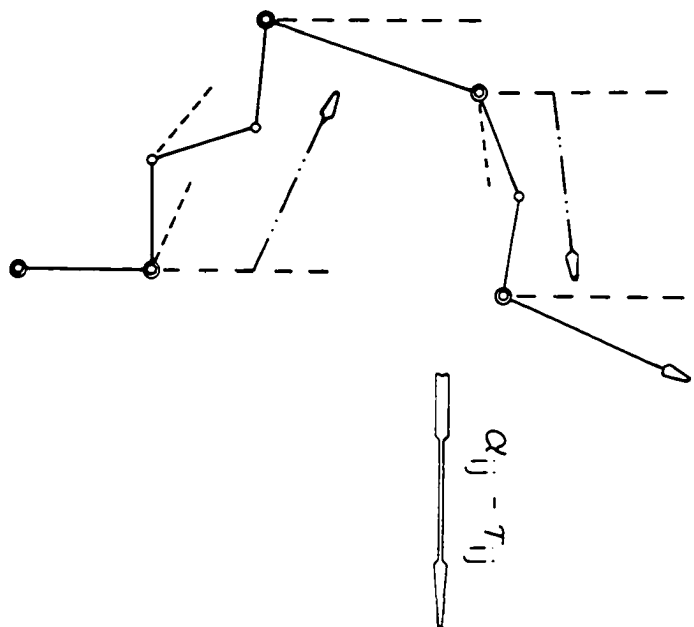
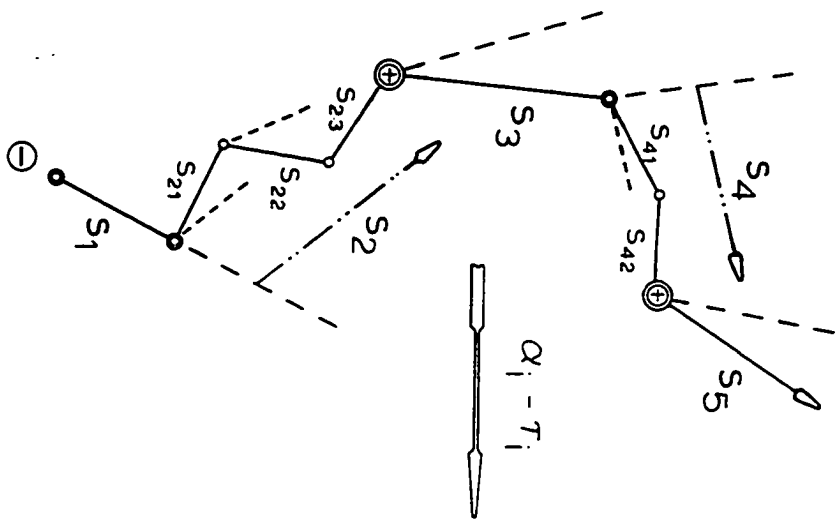
duction. Observing how well the data fit the expectations provides a test of the overall assumptions of the particular model.

That this approach also works for hierarchically structured routes is demonstrated in Figure 4.2. Instead of just one homogeneous series of steps, several walks are shown, constituting two different levels in a hierarchy. Again, each walk is governed by a single target regime with known effects. If these targets are known for all levels above the most basic steps, then the directional components that they contribute to the steps can be subtracted, leaving again just the series of stochastic units. Conversely, if one or more of the target headings are unknown (indicated in the second azimuthal equation as higher-order deflections), then the series of lower steps will be assuredly heterogeneous and the methods of walk analysis will not apply (except to show the movements are more complicated than assumed).

Proceeding under the assumption that the series of steps in question does represent a purified series of deflections, all belonging to a single population, the standard and well-studied equations of the correlated walk could be used to predict the squares of the vector sums for the series over any number of steps (only where the original process is a first-order correlated walk will the these sums represent the actual physical displacement of the organism, its mean squared distance of travel).

In order to use these equations, however, another transformation must first be done to the directional components of the deflections. The steps treated by correlated walk analysis do not actually correspond to actual deflection vectors. In a true correlated walk, the

**FIGURE 4.2** The route shown on the left is governed primarily by anti-telotaxis (directed away from the circled minus sign). The steps obeying this process are indicated by the  $s_i$ 's. Two of these steps,  $s_2$  and  $s_4$ , are further subdivided into telotactic series (directed towards the circled positive signs). In order to obtain a series of just the deflections, first the highest-order target headings must be subtracted from all the steps (on both levels), then the lower-order targets. Assuming that the deflections all represent a single population, the methods of stochastic walk analysis are now applicable to the series shown on the right.



deflection directions are equivalent to the angles turned between the steps, not the azimuths of the steps themselves (the length components, however, are identical to those of the true deflections). To create a series of steps that the equations can work with, the deflection headings must be summed cumulatively. As shown in Figure 4.3, these sums (plus some arbitrary initial heading) produce the directions of the steps relative to a fixed frame of reference, in other words, azimuths.

Since,

$$\tau_1 = \alpha_{1-1}$$

consequently,

$$\alpha_1 = \alpha_{1-1} + \delta_1$$

By induction,

$$\alpha_n = \alpha_1 + \sum_{i=1}^{n-1} \delta_i$$

As with any other homogeneous series of steps within a single target regime, the deflections may be regained by subtracting the target heading,

$$\alpha_1 - \alpha_{1-1} = \delta_1$$

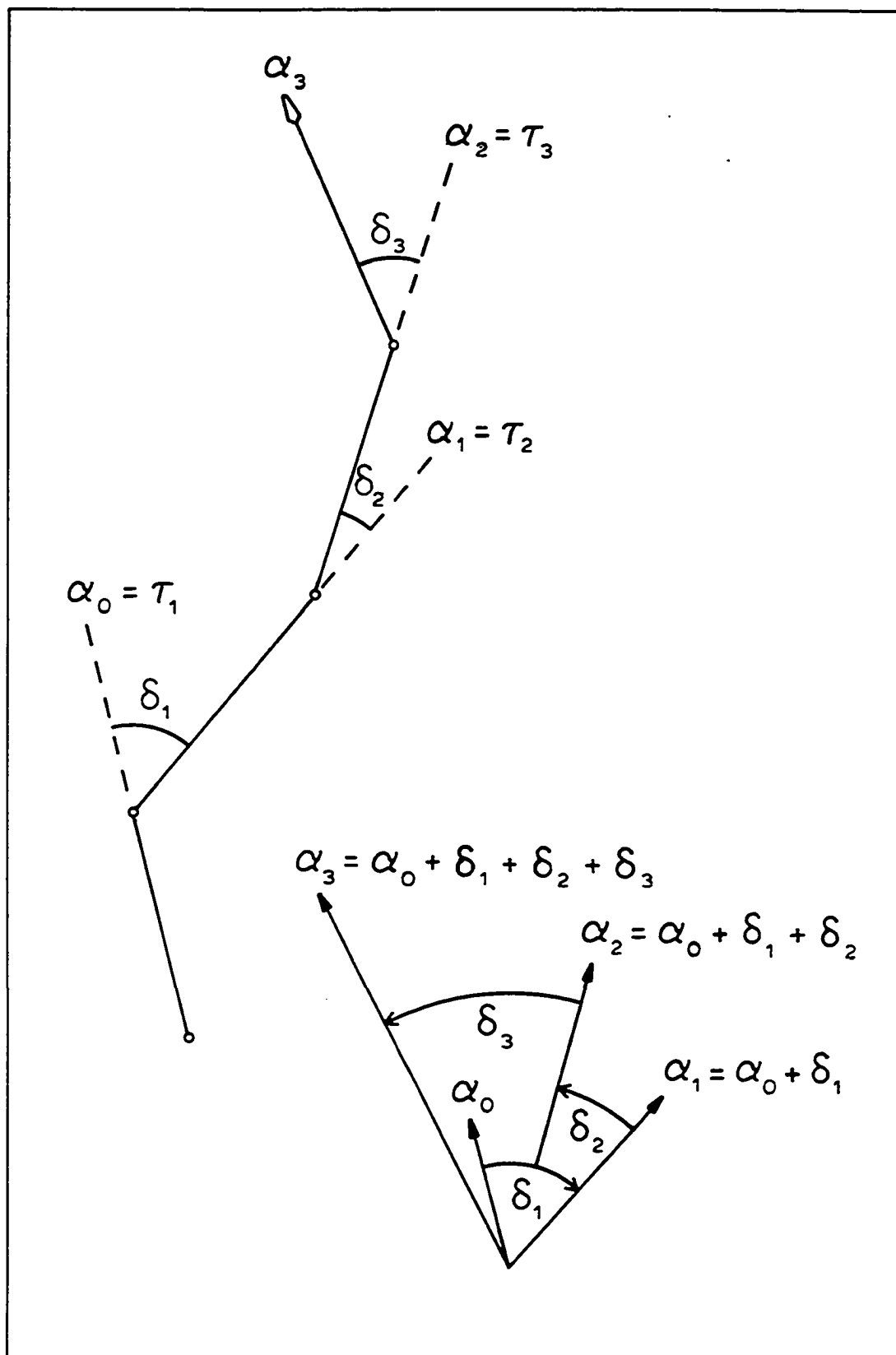
or,

$$\delta_1 = \theta_{1j}$$

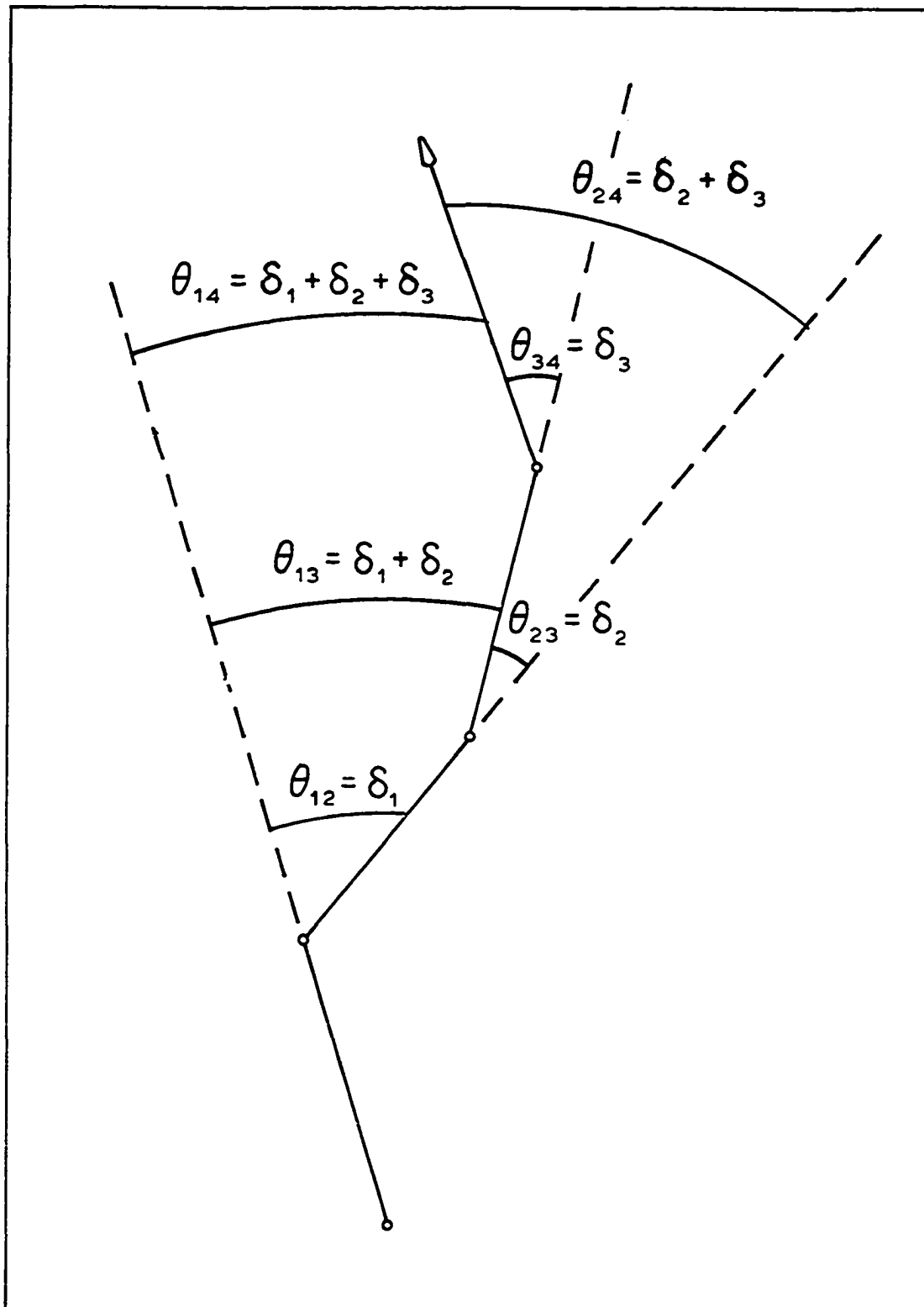
where  $\theta_{1j}$  stands for the angle turned between immediately adjacent steps  $i$  and  $j$  (higher-order turns, indicated in Figure 4.4, also

**FIGURE 4.3** The relationships between deflection angles,  $\delta_1$ , and step azimuths,  $\alpha_1$ , in a first-order correlated walk.





**FIGURE 4.4** An illustration of the relationships between turn angles,  $\theta_{ij}$ , and deflection directions,  $\delta_i$ , in a first-order correlated walk.



play an essential role in calculating the mean squared distances of travel).

In a correlated or any other kind of walk, the deflection distances are the same as the step lengths. Using the separate distributions of the deflection lengths and directions (in these series now equivalent to the turn angles), the expected squares of the vector sums over a particular number of steps can be easily calculated (Kareiva and Shigesada, 1983).

Rather than adopt that approach here, however, I will develop what I believe is a simpler one, a method that makes use of the series of deflection vectors directly. This approach has several advantages.

(1) The deflection variables, both lengths and directions, can be treated together by means of simple vectorial statistics (treating the directional components as turn angles, in comparison, makes them seem to have less physical connection to the steps themselves).

(2) The form of the MSD equation I develop below is simpler than that for the correlated walk, a parabola instead of an asymptotically linear curve.

(3) The deflection series has a direct analogue in the untransformed steps of a menotactic series, a common type of movement among organisms and one that can be used to approximate many others. Even if the target headings have not been correctly identified for each step, the MSD curve for menotaxis can still provide a reasonably good fit.

Because of the significance this approach has relative to meno-

taxis, I will use the term "menotactic walk" to refer to any series of independent and stationary deflections. This approach to analyzing a series of movements can hence be termed "menotactic walk analysis".

#### IV. B. The Basic Features of a Menotactic Walk

The connection just mentioned between a series of independent deflections and actual menotaxis can best be understood by an illustration (Figure 4.5.) Menotaxis has traditionally referred to the maintenance by an animal of a constant heading, usually at an oblique angle to some fixed reference direction (Kuhn, 1919). It is often now used simply to refer to compass-orientation, any active maintenance of a particular azimuthal target whether by idiothetic or allothetic information. It may be thus expressed by

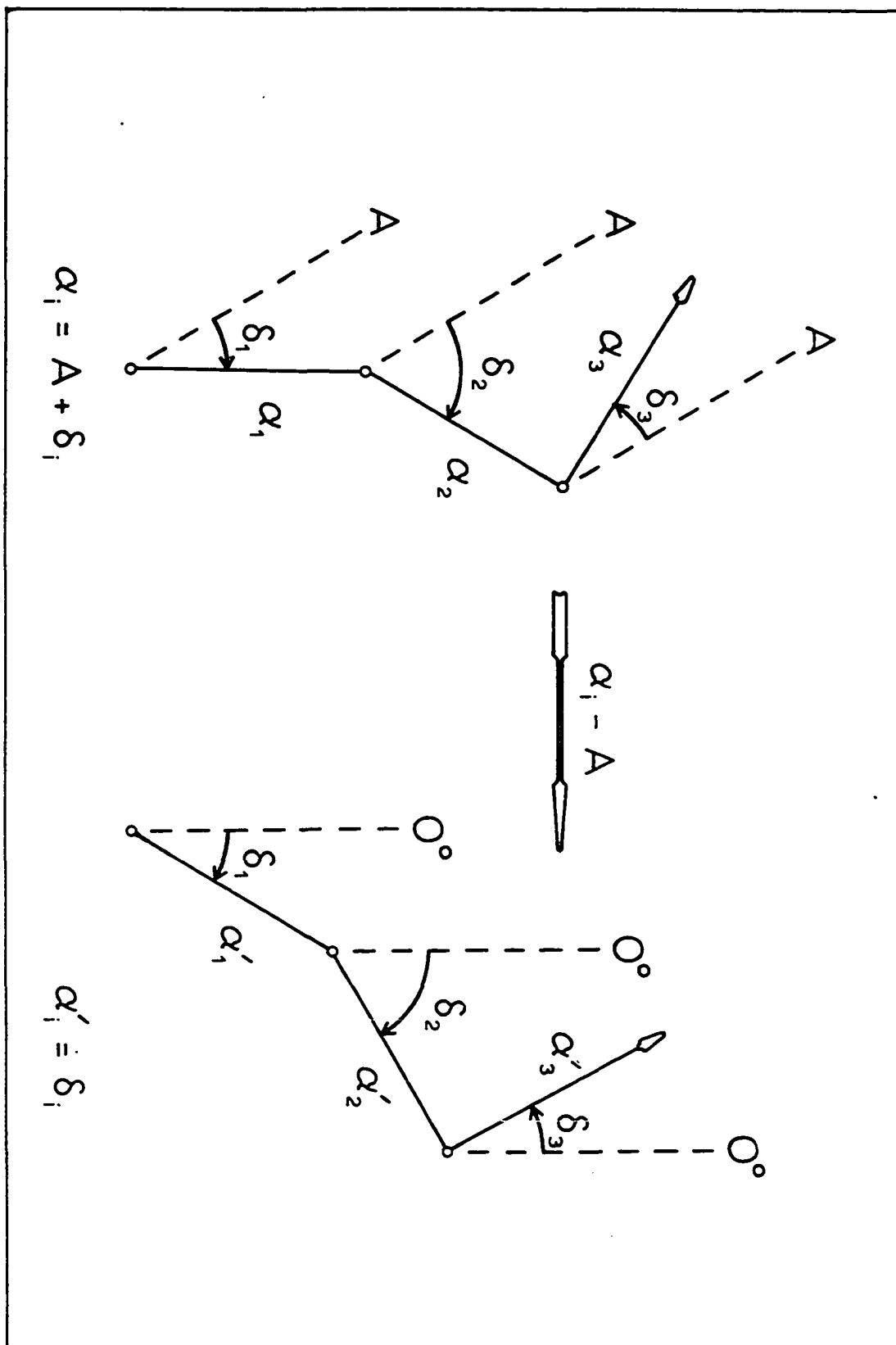
$$s_i = A \phi \vec{d}_i$$

where A is constant over all steps in a series.

A series of steps with the target headings subtracted as described in the previous section, leaving only the pure series of deflections, can be treated identically to the special case of menotaxis in which the target azimuth is  $0^\circ$ . In actual practice, the identity of the target makes no essential difference to the analysis. The equations that I will use to characterize a menotactic walk do not even make use of the mean direction of the steps. Furthermore, it is not possible to distinguish whether the mean direction of the steps actually corresponds to a target heading or to a mean deflectional tendency; the two possible contributions to an observed mean have the same practical consequences for movements.

The mean heading of the steps could, in fact, have no behavioral meaning whatsoever; if the distribution of deflection angles is skewed or multimodal (or, correspondingly, if there are two or more possible target headings at every point in space) then the resulting mean will

**FIGURE 4.5** Transformation of the steps in a menotactic walk into a pure series of deflections. Note that for this type of walk (and this one alone) the transformation does not change the angular relationships among the steps. Conversely, any pure series of deflections may be thought of as a menotactic walk with  $A = 0^\circ$ .





simply be a statistical artifact. On the other hand, since the mean direction of the individual steps will also be the resultant heading for the entire series (on the average, if there is no correlation between step lengths and directions), then natural selection will most likely have given the animal some true behavioral control over its choice.

Whatever the actual nature of the mean heading, the fact that it is a constant is the sole defining feature of menotaxis and a precondition for applying menotactic analysis to any series of purified deflections. If the mean heading varies from step to step, then more information about the control system must be obtained before this sort of analysis can proceed.

In the simplest form of menotaxis, the other parameters of the distribution of the steps will also be stationary, but unlike the variance in the mean heading, departures from this ideal will not necessarily affect the outcome of the analysis, as will be discussed below. Menotaxis can even be defined where a correlation exists between step length and direction. This latitude in the definition of menotaxis allows it to be thought of as occurring where klinotaxis and klinokinesis are also at work. Whatever else is going on, the constancy of the mean heading for the steps labels the process as menotactic.

Proceeding under the assumption that the step distributions are at least stationary, the simplest predictions that can be made about a menotactic walk concern the expected net (unsquared) distance traveled by an animal over a given number of steps. In terms of step vectors, this distance for any number or steps,  $n$ , can be calculated as a

simple vector sum,

$$\vec{D}_n = \sum_1^n \vec{d}_i$$

or in terms of the Cartesian coordinates of the step endpoints,

$$\vec{D}_n = \begin{bmatrix} x_n \\ y_n \end{bmatrix} = \begin{bmatrix} \sum x_i \\ \sum y_i \end{bmatrix}$$

Since,

$$x_i = d_i \cos \delta_i$$

and

$$y_i = d_i \sin \delta_i$$

consequently,

$$\vec{D}_n = \begin{bmatrix} \sum d_i \cos \delta_i \\ \sum d_i \sin \delta_i \end{bmatrix}$$

The length of  $\vec{D}_n$  is easily computed by the Pythagorean distance formula,

$$D_n = \left[ (\sum d_i \cos \delta_i)^2 + (\sum d_i \sin \delta_i)^2 \right]^{0.5}$$

Its direction is given by,

$$\begin{aligned} \Delta_n &= \tan^{-1} (y_n / x_n) \\ &= \tan^{-1} (\sum d_i \sin \delta_i) / (\sum d_i \cos \delta_i) \end{aligned}$$

For the expected distance of travel over a number of different series, all having the same parameters for their step distributions, the corresponding equations are:

$$\begin{aligned} E(\vec{D}_n) &= \begin{bmatrix} E(x) \\ E(y) \end{bmatrix} = \begin{bmatrix} n E(d_1 \cos \delta_1) \\ n E(d_1 \sin \delta_1) \end{bmatrix} & 4.1 \\ E(D_n) &= n \left[ E(d_1 \cos \delta_1)^2 + E(d_1 \sin \delta_1)^2 \right]^{0.5} \\ E(\Delta_n) &= \tan^{-1} E(d_1 \sin \delta_1) / E(d_1 \cos \delta_1) \end{aligned}$$

It should be emphasized that the expected values represent average behavior across different series, not necessarily within any one of them. As long as any variations in the parameters of the steps (other than their mean headings, which must be constant) are not correlated across the series, then the observed relationship of net distance and step number will still be linear. Otherwise the plot will undulate upwards and downwards depending on whether the steps in a particular part of the paths are all longer or shorter than the average or the angles are more or less concentrated about the mean.

This curve illustrates the defining features of menotaxis still further. A purely random walk will also have a stationary distribution of step parameters, along with independence of step lengths and directions. In contrast to a menotactic walk, however, it has no definable mean direction; at any particular point in space all directions of travel for the next step are equally likely. It follows then that,

$$E(x) = E(y) = 0$$

and

$$E(\vec{D}_n) = 0$$

In other words, the expected net distance of travel from a point of origin will always be equal to zero for a random walk; a plot of net distance against step number will be a straight line but will have no slope. In true menotaxis, where a constant and mean heading is present by definition, the plotted line will always have a positive slope.

On the other hand, there is another process not usually considered to represent menotaxis that can also produce such a curve: Ull-yot's example of negative klinokinesis. In his model, an organism moves through a directional field without actually being able to sense the axes of the field; the directional components of the steps, hence, show no mean heading. Progress along a preferred axis can nonetheless be quite steady, provided the organism curtails travel in the wrong directions; the crucial factor is a strong directional correlation to the step lengths. Referring back to equation 4.1, it is the non-uniform (and stationary) distribution of step vectors about the target direction that ensures a constant and positive value for the covariance term (the expected product of the components), not the presence of a mean heading per se. Given the fundamental similarity in terms of results, this kind of orientation will here be considered as a special case of menotaxis. Another way of looking at menotaxis, then, is to define it operationally by a constant mean heading for the distribution of the step vectors, not just for their directional components in isolation.

This example also suggests a way to examine the importance of directional correlation among the step lengths: determine whether or not the slope of the plot of net distance against step length is greater than expected under the hypothesis of independence between the step components. This procedure is useful to follow even when a mean heading is known to exist for the directional components. In that situation, the findings of a greater slope than expected would indicate the action of a klinotactic mechanism, which possibly adds to the efficiency of the walk or serves as the actual means whereby menotaxis is effected.

Under the assumption of independence between step length and direction, equation 4.1 can be much simplified:

$$E(\vec{D}_n) = \begin{bmatrix} n E(d) E(\cos \delta_1) \\ n E(d) E(\sin \delta_1) \end{bmatrix}$$

and

$$\begin{aligned} E(D_n) &= n E(d) \left[ E(\cos \delta_1)^2 + E(\sin \delta_1)^2 \right]^{0.5} \\ &= n E(d) \rho \end{aligned}$$

where  $\rho$  is the parameter of concentration for the distribution of step directions (see Batschelet, 1981).

In Ulliyot's klinokinesis  $\rho$  would be equal to zero, as would the predicted net forward progress of the organism (over a number of trials from a given starting point). Nonetheless, the function would plot as a straight line with positive slope, indicating the actual ability of the organism to make headway along one particular direction of travel. For klino-menotaxis, the predicted line under the hypothesis of independence will also have a positive slope, but the obser-

ved line will have one greater still. (Another way of looking for the same effects, of course, is simply to compare the expected covariance between the step components with its empirically-determined counterpart.)

Whether or not the components of the steps are found to be correlated, an examination of the directions by themselves has great value in itself. By replacing the step lengths in the above equation by dummy variables of unit length, it can be seen whether or not the directional components have the assumed property of independence. If they do not, the plot will not be linear and the hypothesis of a constant orientational target must be re-assessed.

Following the above suggestion,

$$E(R_n) = n \rho$$

where  $R_n$ , the length of the azimuthal resultant (Table 4.1), is one of the standard statistics in orientational analysis. Tests described in Mardia (1972) can be used to compare an observed value of  $R_n$  to that calculated from the sample of individual step directions under the assumption of their independence. The null hypothesis is that the two figures should be equal. If the steps are not, in fact, independent of one another, then the value of  $R_n$  observed will be either larger or smaller than expected.

As in the case of linear measurements, such tests of directional hypotheses are most exact when the underlying distribution is known; a circular analogue of the Normal Distribution is the Von Mises Distribution, for which a number of parametric tests have been developed. Unfortunately, the various kinds of organismal deflections described

in the previous chapter of the hold out little hope that the composite distribution has anything like the wrapped, bell-shaped form of the Von Mises distribution. Furthermore, although it seems likely that the distribution of purified deflection angles will have a mean falling on zero degrees, this result is by no means certain, as was also discussed.

On the other hand, I will show in the next section that the distribution of the angles turned between deflections will always have a mean of zero degrees and almost always a bell-shaped form. These properties of the turn angles make them much better suited for analysis of the strictly orientational properties of the steps than are the step directions themselves. I will also show that they have a number of other useful features, not the least of which is that they provide a basis for analysis of the mean squared distances of travel, both for correlated and menotactic walks.

#### IV. C. The Nature of the Turn Angles in a Menotactic Walk

As shown in Figure 4.6, the angles turned between the steps in a true menotactic series do not have the same behavioral meaning as the turns so often studied in the search paradigm (still more remote are the turns between the purified deflections here treated as menotactic steps). Instead of representing the deflection angles themselves, as they do in the correlated walk, they measure the differences between successive deflection angles (represented now by the step azimuths). Consequently, they possess qualities not shared by the underlying deflections, qualities that will be seen to increase their value in terms of analysis but decrease it in terms of behavioral interpretation.

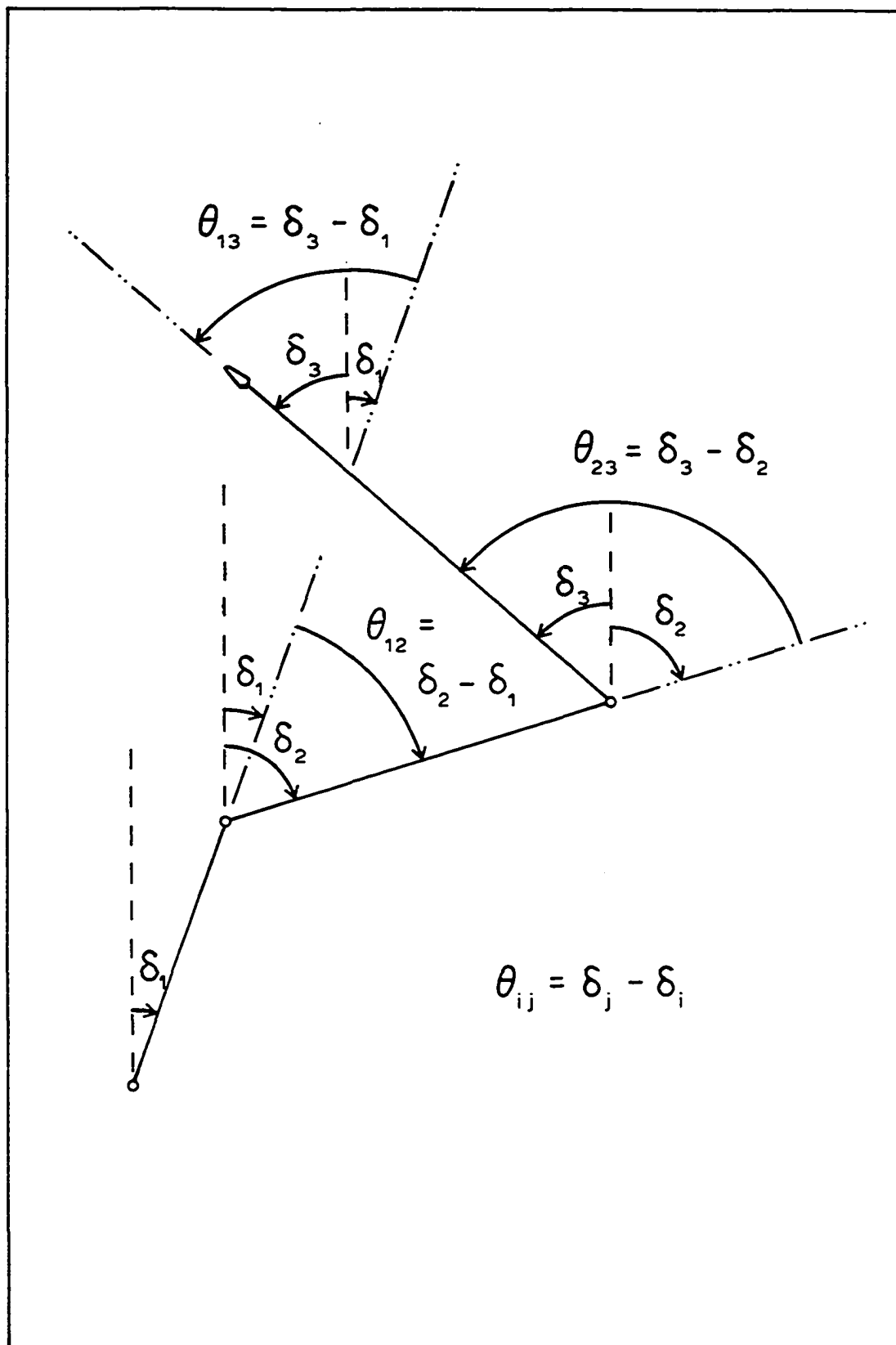
Unlike the distribution of deflection angles, which can take on any shape and mean direction, the distribution of angular differences between the steps in a menotactic walk will always be symmetric about a mean direction of  $0^\circ$  provided only that the distribution of deflections is stationary, an assumption that will be held throughout the discussion that follows. Given that assumption and the axiom of independence between steps, the symmetry of turns follows simply from the fact that the probability of any two deflectional values occurring in succession is the same no matter which value comes first,

$$\theta_{ij} = \alpha_j - \alpha_i = \delta_i - \delta_{i-1}$$

In terms of the relative angles between the deflections, the sequence  $\delta_i \delta_j$  will produce a turn equal in magnitude but opposite in sign to the reverse sequence,  $\delta_j \delta_i$ . Since this is true for all possible



**FIGURE 4.6** The relationship between the deflection directions,  $\delta_i$  , and turn angles,  $\theta_{ij}$  , in a menotactic walk. Note that this relationship is independent of the target heading and holds true for all orders of turns, that is, for any steps  $i$  and  $j$ .



pairs of different deflections, the distribution of turns will be symmetric about zero degrees no matter what the distribution is of the  $\delta_i$  themselves.

This symmetry about the x-axis ( $0^\circ - 180^\circ$ ) further implies that the mean vector for this distribution only depends on the x components (cosines) of the turns:

$$E(\sin \theta) = E(y) = 0$$

Consequently,

$$\rho_\theta = E(\cos \theta) = E(x) \tag{4.2}$$

where  $\rho_\theta$  is the length of the mean vector for the turns. Its direction,  $\mu_\theta$ , is given by,

$$\mu_\theta = \tan^{-1} 0 / E(\cos \theta) = \begin{matrix} 0 & | & E(\cos \theta) > 0 \\ 180 & | & E(\cos \theta) < 0 \end{matrix}$$

Intuitively, the mean direction for the distribution can be seen to be equal to  $0^\circ$  rather than  $180^\circ$ . Since all possible deflections have some probability of following themselves in sequence, producing zero-degree turns, but not all deflections have angles opposite in value that are equally likely to occur (unless the distribution of deflections is uniform, in which case the walk is random, not menotactic), this weights the distribution towards the  $0^\circ$  pole.

To demonstrate this point more rigorously, all that needs to be shown is that  $E(\cos \theta)$  in Equation 4.2 is always positive. This conclusion follows from an argument relating the length of the mean vector of deflection angles,  $\rho_\delta$ , to the corresponding value,  $\rho_\theta$ , for the turns between them. Since,

$$\theta_{ij} = \delta_j - \delta_i$$

it follows for all i and j that,

$$\rho_\theta = E(\cos \theta) = E(\cos(\delta_j - \delta_i))$$

By simple trigonometry,

$$\begin{aligned}\rho_\theta &= E(\cos \delta_j \cos \delta_i + \sin \delta_j \sin \delta_i) \\ &= E(\cos \delta_j \cos \delta_i) + E(\sin \delta_j \sin \delta_i)\end{aligned}$$

Since the deflections are all independent by definition, and, for stationary distributions, all have the same expected value from step to step, it follows that,

$$\begin{aligned}\rho_\theta &= E(\cos \theta_j) E(\cos \theta_i) + E(\sin \theta_j) E(\sin \theta_i) \\ &= E(\cos \delta)^2 + E(\sin \delta)^2\end{aligned}$$

This equation can be further simplified first by considering that the distribution of turns between steps will be unaffected by adding a constant to the direction of each step. If this constant is set equal to  $-\mu_\theta$ , the effect on the distribution of deflections will be to rotate it so that its new mean direction will be equal to zero (this is done solely to simplify the calculations; even without doing this procedure the results will be the same). Under this condition,

$$E(\sin \delta) = 0$$

and consequently

$$\rho_\delta = E(\cos \delta)$$

The equation for  $\rho_\theta$  may now be rewritten:

$$\begin{aligned}\rho_\theta &= E(\cos \delta)^2 + 0 \\ &= \rho_\delta^2\end{aligned}\tag{4.3}$$

Since  $\rho_\delta$  must always be positive, it follows that  $\mu_\theta$  must be always be equal to zero (at least for stationary series of deflections), as was desired to be proven.

Along with the symmetry and mean direction of zero degrees, the relationship between  $\rho_\delta$  and  $\rho_\theta$  has been shown to be an invariant property of stationary menotactic walks; it does not depend in any way on the form of the deflections, as illustrated by a few examples shown in Figure 4.7. As is clear in both the equation and in these examples, the distribution of turns will always be more spread out than the corresponding distribution of deflection angles. The values of  $\rho_\delta$  and  $\rho_\theta$  always fall between 0 and 1, consequently  $\rho_\theta$  will always be smaller than  $\rho_\delta$  (the cases where  $\rho_\delta$  is equal to either 0 or 1 do not qualify as menotaxis).

Related to this effect, the distribution of turns tends to be smoother and more circular normal (having a bell-shaped form wrapped around a circle) than the distribution of deflection angles, at least where that distribution is not circular normal to begin with, an unlikely event in light of the discussion presented in Chapter III. While the exact form of the turn distribution will vary in a complex way depending on the distribution of  $\delta_1$ , it can be calculated by means of a simple algorithm:

1. Determine the probabilities of all possible pairings of azimuths by the multiplication rule for independent events.

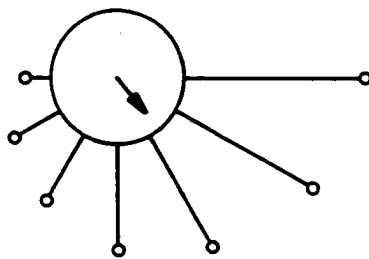
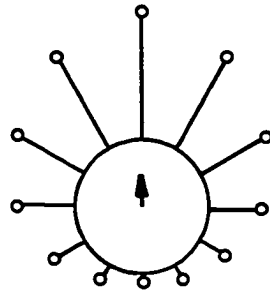
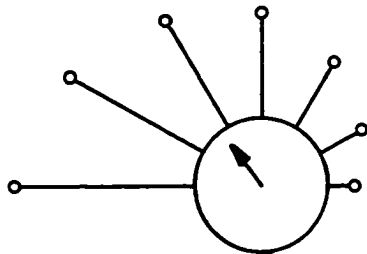
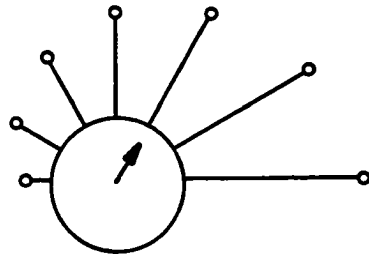
2. Determine the probabilities for the turn angles by adding the probabilities for all pairs of azimuths whose differences have a given sign and magnitude, e.g.,

$$\begin{aligned}
 p( \theta_{1j} = 180 ) &= p( \alpha_1 = 0 ) \times p( \alpha_j = 180 ) + \\
 &\quad p( \alpha_1 = 1 ) \times p( \alpha_j = 181 ) + \\
 &\quad \dots p( \alpha_1 = 359 ) \times p( \alpha_j = 179 )
 \end{aligned}$$

Several examples produced by this method are illustrated in Figure 4.7.

An important consequence of these findings is that parametric tests based on the Von Mises Distribution can be used to determine the validity of the hypothesis of a menotactic walk (real or transformed) and hence the underlying assumptions of independence and stationarity among the deflections (the step directions). Although most of these tests are robust enough to handle departures from the strict form of the Von Mises Distribution, especially if the observed frequencies are unimodal and symmetric (Batschelet, 1965), they become more appropriate the closer the fit is of the observed to the theoretical probabilities. In almost all cases it will be the distribution of the turns rather than the distribution of the actual deflections that is the more appropriate choice to use in hypothesis testing. The fact that the mean direction of the turns is always known under the hypothesis also allows for the use of the most powerful tests available. As will be discussed in Chapter V, one highly useful test for menotaxis is Stephen's Test of the Concentration Parameter when the Mean Direction is Known. As implied by its name, this test makes use of all the fixed relationships between the distributions of deflection

**FIGURE 4.7** An example of a distribution of turn angles,  $\theta_{1j}$ , produced by three different distributions of deflection directions,  $\delta_1$ , under menotaxis. Note also the lack of behavioral meaning in the mean directions for the deflections and their complete irrelevance in determining the mean direction for the turns.  $\rho_\delta = 0.65109$  in all three cases;  $\rho_\theta = 0.42391$ ,  $\mu_\theta = 0^\circ$ .

$\delta$  $\theta$ 



angles and the turns between them.

The invariant features of the turns, which make them so attractive for statistical analysis, however, also make them relatively meaningless in terms of behavioral interpretation. Whereas the distribution of the step directions holds much information in all its complexity of form and possibly non-zero mean direction, the wrapped bell-shaped form and fixed mean heading of  $0^\circ$  found in the turn angles reveals little. Furthermore, although I have shown that the expected distribution of turns (under menotaxis) can be quite easily constructed from the distribution of the step directions, the converse is not true (the estimation of  $\rho_\theta$  from  $\rho_\theta^{0.5}$  being an important exception). As indicated by the examples shown in Figure 4.7, a given turn distribution can be generated from two or more different deflection distributions.

These points have been overlooked in previous investigations. In many studies of animal movements, the only information that is collected are samples of turns, perhaps as the result of the ease of observing sequences that are only two steps in length or the hunch that turn angles may be more appropriately pooled than the step azimuths (see the Introduction for a more thorough discussion). While these ideas can be quite correct (but only if the movements obey either a correlated or menotactic walk), the conclusions about behavior drawn on the basis of such samples can be quite erroneous, depending on whether the underlying movement process has been correctly identified as a correlated walk. This model, however, is usually assumed without any proof, even if it is questioned at all!

The unimodal, symmetric, zero-centered, and wrapped bell-shaped features of turn distributions have, for instance, have all elicited speculations as to their behavioral significance (see Pyke et al., 1977, for a review). Any such interpretations, however, would be valid only if the turns actually correspond to deflection angles, which will be the case only if the movements represent the rudimentary orientational control of a first-order correlated walk (something I would find surprising in species such as Siniff and Jessen's foxes, racoons and hares, or even Pyke's bumblebees). If the movements are actually governed by menotaxis (or some other form of tactic orientation), then any lateral biases or other irregularities in the deflections can go completely undetected as effects within the distribution of turns.

Indeed, the wrapped bell-shaped form of the reported distributions of turns suggests to me that tactic orientation applies rather than a simple correlated walk, at least if we are dealing with single deflectional events rather than the summed effects of several smaller ones (I will show in Chapter V that sums of deflections have similar distributions to those of differences, at least when the distribution of single events is symmetric about  $0^{\circ}$  to begin with). Whereas this form of distribution is an almost necessary feature of the turns produced under tactic orientation, it is an unlikely one for the distribution of deflections themselves. As I discussed in the last chapter, the deflections more than likely have a complex, composite distribution with little tailing into the semicircle centered on  $180^{\circ}$ .

Only one explanation for a circular normal distribution of deflections has in fact been proposed. Pyke (1978a) presented a complex

model for bumblebee foraging that produced such distributions as the result of an interplay between the reward experienced at a particular flower, the angle scanned upon departure for the next choice, and the distribution of nearest neighbor distances. While this klinokinetic model might perhaps be appropriate for a cropping forager, it does not seem general enough to account for all the situations in which circular normal distributions of turns have been discovered. It might not even be a good model for the movements of bees. Recently Soltz (1986) tested Pyke's hypothesis for foraging bumblebees and found none of the klinokinesis predicted by the model but still found a distribution of turn angles that was roughly circular normal.

Even where the distribution of deflections has this form rather than the one I theorized, it can still be quite misleading to derive behavioral models from information obtained solely from the turn angles unless, once again, the underlying movement process corresponds to a simple correlated walk. For example, Siniff and Jessen (1969) were perhaps correct to interpret the bipolar turning distribution they found in snowshoe hares as representing a tendency for their subjects to occasionally move directly away from a previous target heading (presumably in response to aversive stimuli). However, as shown in Figure 4.7, some  $180^{\circ}$  turns arise as the result of the animal turning only  $90^{\circ}$  to the left of a menotactic target following a turn of  $90^{\circ}$  to the right (or vice versa). Probabilities discovered in the frequency distribution of the turns would confound these very different kinds of movements and there would be no way to explain the animal's behavior accurately given this information alone.

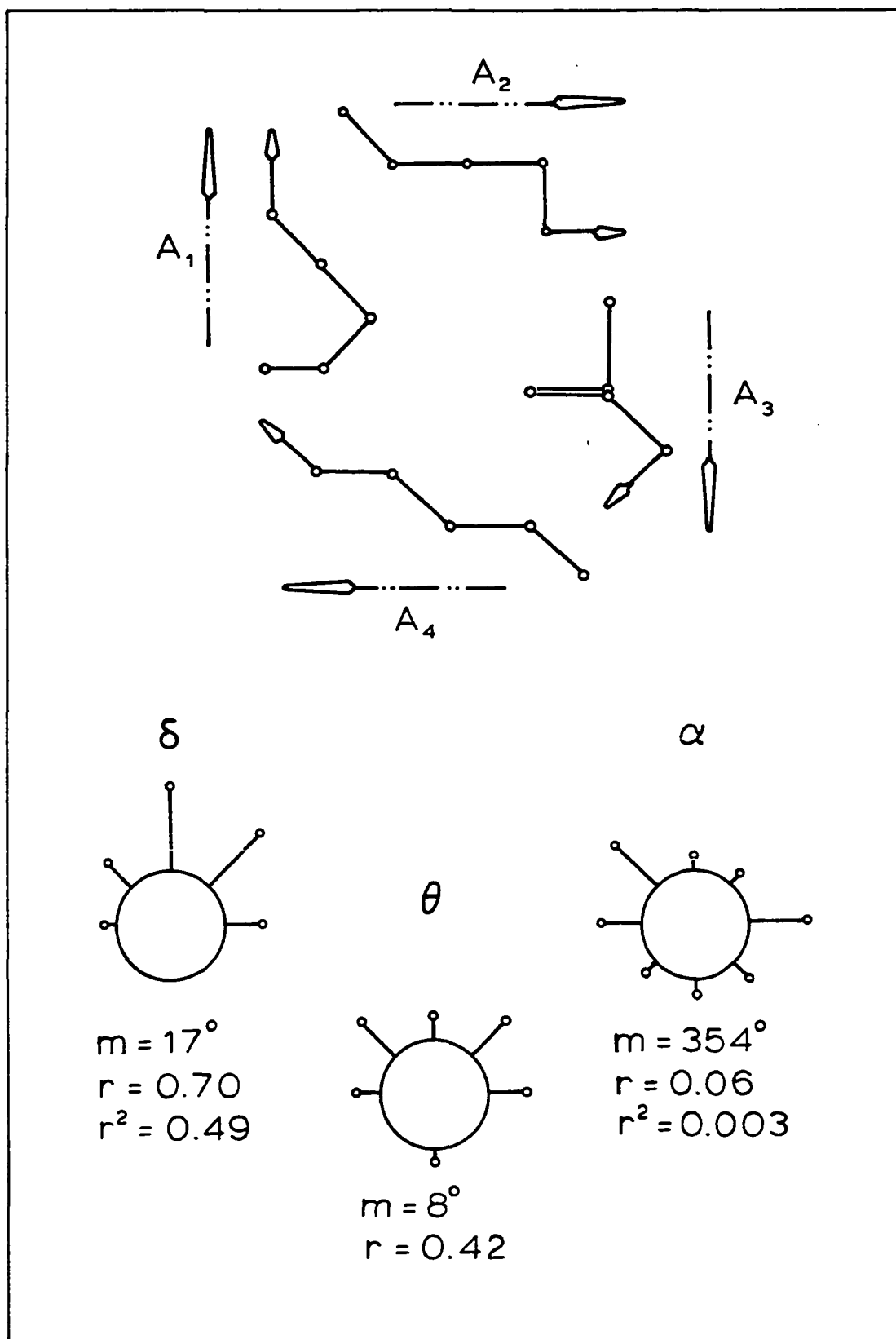
The message is simply that turn angles in themselves do not contain much information, unless, of course, they represent true deflection angles. Although I will show in the next section that they do contain sufficient information to predict the mean squared distance of travel even for a menotactic walk, all that finding indicates is that less information is needed to test the menotactic hypothesis than is present within the distribution of deflections. While such limited information is often economical to collect, a complete understanding of an animal's decision processes still requires the actual distribution of deflections. Wherever possible, this information should be gathered first, then any subset of the information regarding the distribution of turn angles can be produced by means of the algorithm given above.

#### IV. D. The Mean Squared Distances of Travel in a Menotactic Walk

Although calculations of the expected squared distances of travel are more complicated and less directly meaningful in terms of behavior than the procedures described in the two preceeding sections, they have two distinct advantages.

(1) These equations do not require as much information as the one for the unsquared distances; they only require samples of turn angles (either deflection angles themselves or their differences) and step lengths. This feature is especially useful where several series of steps are studied (obtained as sections taken from one route or many), each representing the same truly menotactic process but possessing unknown and possibly different target headings (see Figure 4.8). While pooling of the step azimuths would potentially lead to a mixed distribution, with little relationship to the actual distribution of deflections, pooling of the angles turned between the steps would be completely permissible; the target headings factor out in any event when taking the difference between the headings of successive steps. This information can then be used to estimate  $\rho_\delta$ , the parameter of concentration for the true deflections, and from it to calculate the expected net distances of travel across the series. Or the information from the turn angles can be used more directly, and hence more precisely, to predict the mean squared distance of travel across the series. This permits a test of the hypothesis that the series all represent the same menotactic process.

**FIGURE 4.8** Consequences of pooling series of steps with different target headings. Despite the fact that this example illustrates a menotactic process, the sample of azimuths,  $\alpha$ , does not resemble that of the actual deflection directions,  $\delta$ . The relationship between the deflections and turn angles, on the other hand, is unaffected,  $\rho_{\delta^2} \approx \rho_{\theta}$



(2) Calculations of the expected squared distance of travel allow direct comparisons to be made between true menotactic, correlated, and random walks, whereas the simple net distance equations cannot distinguish between the last two. Although a correlated walker will have the same expected rate of travel as a random walker away from a point of origin over a number of different series (that is, zero, since neither shows any preferred direction of travel), the correlated walker will obviously travel much further in each series. A menotactic walker will travel farther still, as a result of its correction for deflections, even when its preference for a particular heading is itself ignored (less information is thus needed for these equations than for the unsquared distances of travel).

The initial steps in the derivation of these equations actually apply to any series of vectors, no matter what their governing process. For any pair of vectors, the dot product of vector algebra states:

$$\begin{aligned}\vec{v}_i \cdot \vec{v}_j &= |\vec{v}_i| |\vec{v}_j| \cos \theta_{ij} \\ &= v_i v_j \cos \theta_{ij}\end{aligned}$$

Since the dot product obeys the associative law, then for any sequence of vectors,

$$\begin{aligned}\vec{D}_n \cdot \vec{D}_n &= (\sum \vec{s}_i) \cdot (\sum \vec{s}_j) \\ &= \sum \sum \vec{s}_i \cdot \vec{s}_j \\ &= \sum \sum s_i s_j \cos \theta_{ij}\end{aligned}$$



Considering further that

$$\vec{v}_1 \cdot \vec{v}_1 = v_1^2 \cos 0 = v_1^2$$

it follows that

$$\begin{aligned} \vec{D}_n \cdot \vec{D}_n &= D_n^2 = \sum_{i \neq j} s_i s_j \cos \theta_{ij} + \sum_{i \neq j} s_i s_j \cos \theta_{ij} \\ &= \sum_{i=1}^n s_i^2 + \sum_{i \neq j} s_i s_j \cos \theta_{ij} \end{aligned}$$

The last term on the right can be further decomposed:

$$\sum_{i \neq j} s_i s_j \cos \theta_{ij} = \sum_{i < j} s_i s_j \cos \theta_{ij} + \sum_{j < i} s_i s_j \cos \theta_{ij}$$

By redefining the subscripts so that  $i < j$  for all steps, the above equation may be rewritten as

$$\sum_{i \neq j} s_i s_j \cos \theta_{ij} = \sum_{i < j} s_i s_j \cos \theta_{ij} + \sum_{i < j} s_j s_i \cos \theta_{ji}$$

In other words, the first term on the right considers all combinations in the forward direction along the sequence, while the second considers the combinations in the reverse order.

Since

$$\theta_{ij} = -\theta_{ji}$$

and

$$\cos \theta = \cos (-\theta)$$

it follows that the two terms are equal:

$$\sum_{i < j} s_i s_j \cos \theta_{ij} = \sum_{i < j} s_j s_i \cos \theta_{ji}$$

Therefore,

$$D_n^2 = \sum_1^n s_i^2 + 2 \sum_{i < j} s_i s_j \cos \theta_{ij} \quad 4.5$$

This much is true for any series of vectors, and hence for any type of walk. This relationship becomes predictive, however, only where expectations can be taken on both sides. In particular, the steps must be both independent of one another and have stationary distributions. Where these properties are obtained, as in only the random, correlated, and menotactic walk (assuming no complications due to klinokinesis), then

$$\begin{aligned} E(D_n^2) &= E(\sum s_i^2) + 2 E(\sum s_i s_j \cos \theta_{ij}) \\ &= n E(s^2) + 2 \sum E(s_i s_j \cos \theta_{ij}) \end{aligned}$$

If additionally the step lengths are independent of the turn angles (as they will be if there is no directional correlation to the lengths of the deflections), then

$$\begin{aligned} E(D_n^2) &= n E(s^2) + 2 \sum E(s)^2 E(\cos \theta_{ij}) \\ &= n E(s^2) + 2 E(s)^2 \sum E(\cos \theta_{ij}) \end{aligned} \quad 4.6$$

Now focus on the sum of the expected values of the cosines, the crucial feature distinguishing menotactic from correlated walks. First, it should be noted that the angles considered in this sum include not only the first-order turns (those between immediately adjacent steps in the series) but also all possible higher-order turns. Since each k-th order turn can itself be seen to be a sum of k first-order turns, i.e.,

$$\theta_{k=j-1} = \theta_{12} + \theta_{23} + \theta_{34} + \dots + \theta_{j-1,j} = \sum_{i=1}^{j-1} \theta_{i,i+1}$$

(for examples, see Figures 4.4 and 4.6), and since all first-order turns have the same distribution under the assumptions listed above, it follows that all turns of the k-th order must also belong to a single population. Furthermore, since there will be (n - k) turns of the k-th order in a series of n steps, Equation 4.6 may be rewritten as

$$E(D_n^2) = n E(s^2) + 2 E(s)^2 \sum_{k=0}^{n-1} (n - k) E(\cos \theta_k) \quad 4.7$$

which is the basic equation reached by Gail and Boone (1970) for the correlated walk. It should be noted, however, that this equation still pertains to the menotactic walk, as well.

This equation can be simplified still further when the distribution of turns is symmetrically distributed about zero degrees, which it must be for menotaxis and can also be expected for most kinds of organismal correlated walks (for reasons discussed in Section III.D). For correlated walks possessing non-symmetric or biased distributions, on the other hand, the simplifications I describe below will not work and the much more complicated approach of Kareiva and Shigesada (1983) must be followed. There is no need to go into their equations here, however, since the main purpose is to arrive at an equation just for menotaxis.

Assuming symmetry then, the sums of turns should also have this general form of distribution (see Mardia, 1972, for a general discussion of angular convolutions); consequently so will all higher-order turns. Moreover, simple relationships can be calculated between the expected cosines of all orders of turns.

Taking the case of the correlated walk first, any higher order turn can be expressed by

$$\theta_k = \theta_1 + \theta_{k-1}$$

where  $\theta_1$  and  $\theta_{k-1}$  are independent of one another (by definition, each turn in a correlated walk represents an independent deflection, unlike the case in the menotactic walk in which turns can share deflections; see Section IV.C.). The expected cosine of  $\theta_k$  then becomes

$$\begin{aligned} E(\cos \theta_k) &= \lambda_{\theta k} = E(\cos(\theta_1 + \theta_{k-1})) \\ &= E(\cos \theta_1 \cos \theta_{k-1} - \sin \theta_1 \sin \theta_{k-1}) \\ &= E(\cos \theta_1) E(\cos \theta_{k-1}) - E(\sin \theta_1) E(\sin \theta_{k-1}) \end{aligned}$$

Since for distributions symmetric about  $0^\circ$ , the expected sines are equal to zero,

$$\begin{aligned} \lambda_{\theta k} &= \rho_{\theta k} = E(\cos \theta_1) E(\cos \theta_{k-1}) - 0 \\ &= \rho_{\theta 1} E(\cos \theta_{k-1}) \end{aligned}$$

For second-order turns,  $k - 1 = 1$ , and

$$\rho_{\theta 2} = \rho_{\theta 1} E(\cos \theta_1) = \rho_{\theta 1}^2$$

Similarly, since all other  $(k - 1)$  order turns can be broken down into a first-order turn plus some  $(k - 2)$  order turn, it follows by induction that

$$\begin{aligned} \rho_{\theta k} &= \rho_{\theta 1}^2 E(\cos \theta_{k-2}) \\ &= \rho_{\theta 1}^3 E(\cos \theta_{k-3}) \\ &= \prod_{k=1}^k \rho_{\theta 1} \\ &= \rho_{\theta 1}^k \end{aligned}$$

4.8

Consequently, for an unbiased correlated walk Equation 4.7 can now be simplified to

$$E(D_n^2) = n E(s^2) + 2 E(s)^2 \sum (n-k) \rho_{\theta 1}^k \quad 4.9$$

which is the equation described by R. L. Hall (1977). For further simplification of the sum of turns, consult his paper.

Returning now to the menotactic walk, it can be shown that the relationship between the various orders of turns follows an even simpler form. Recalling that any higher-order turn can be expressed as a sum of first-order turns and that in menotaxis each turn represents the difference between two deflections, then

$$\begin{aligned} \theta_k &= \theta_{12} + \theta_{23} + \theta_{34} + \dots + \theta_{j-1,j} \\ &= (\delta_2 - \delta_1) + (\delta_3 - \delta_2) + (\delta_4 - \delta_3) + \dots + (\delta_n - \delta_{n-1}) \\ &= \delta_n - \delta_1 \end{aligned}$$

Since the above expression represents the difference between two independent deflections, also assumed to have the same distribution, it follows from arguments given in Section IV.C. that all orders of turns have the same distribution:

$$\rho_{\theta k} = \rho_{\theta 1} \quad 4.10$$

for all k.

For menotactic walks Equation 4.7 thus simplifies to

$$\begin{aligned} E(D_n^2) &= n E(s^2) + 2 E(s)^2 \sum (n-k) \rho_{\theta 1} \\ &= n E(s^2) + 2 E(s)^2 (n^2 - n) \rho_{\theta 1} \\ &= n E(s^2) - E(s)^2 \rho_{\theta 1} + n^2 E(s)^2 \rho_{\theta 1} \quad 4.11 \end{aligned}$$

or, in terms of the deflections themselves rather than the turns,

$$E(D_n^2) = n \left[ E(s^2) - E(s)^2 \rho_\delta^2 \right] + n^2 E(s)^2 \rho_\delta^2 \quad 4.12$$

which characterizes a menotactic walk just as exactly as does the prediction for the unsquared distances of travel.

Mardia (1972) arrived at a simpler version by way of a much more complicated approach, but one which treats only the directional information

$$E(D_n^2) = n (1 - \rho_\delta^2) + n^2 \rho_\delta^2 \quad 4.13$$

As was true for the simple net distances of travel, both these equations are useful, my more inclusive one (4.12) to check the assumption of independence between step lengths and directions, and the more restrictive one (4.13) to examine the relationships strictly within the directional components.

A more important use, however, is to make comparisons among the menotactic, correlated, and random walks; this objective is one that cannot be duplicated through use of the simple net distances of travel. For this purpose, we need only to consider the simpler directional form of the equations, since the major differences between these walks occur only with regard to their angular properties, not their step lengths (it should be noted, however, that the correlated and random walks also have counterparts to Equation 4.12, involving the length components of the steps).

The first point to make is that the three processes differ markedly with respect to the form of the curves produced by their respective functions for the mean squared resultants. The curve for the

random walk is well known to be a simple straight line with slope equal to one. This can be shown easily with Equation 4.7 by setting  $\rho_\delta$  equal to zero and  $s$  equal to one (and using the term  $R$  in place of  $D$ ):

$$E(R_n^2) = n \quad 4.14$$

Since Equation 4.7 applies equally to menotactic as to correlated walks, the random walk can be considered to be a degenerative case of either one. Actually the random walk can be derived at an earlier stage, from Equation 4.6, which indicates that it is a limiting case of any kind of movement process in which step lengths are independent of their directions. At the other extreme, when  $E(\cos \quad)$  equals one, there are no deflections present, and all movement processes produce indistinguishable curves:

$$E(R_n^2) = n + 2(n^2 - n) = 2n^2 - n \quad 4.15.)$$

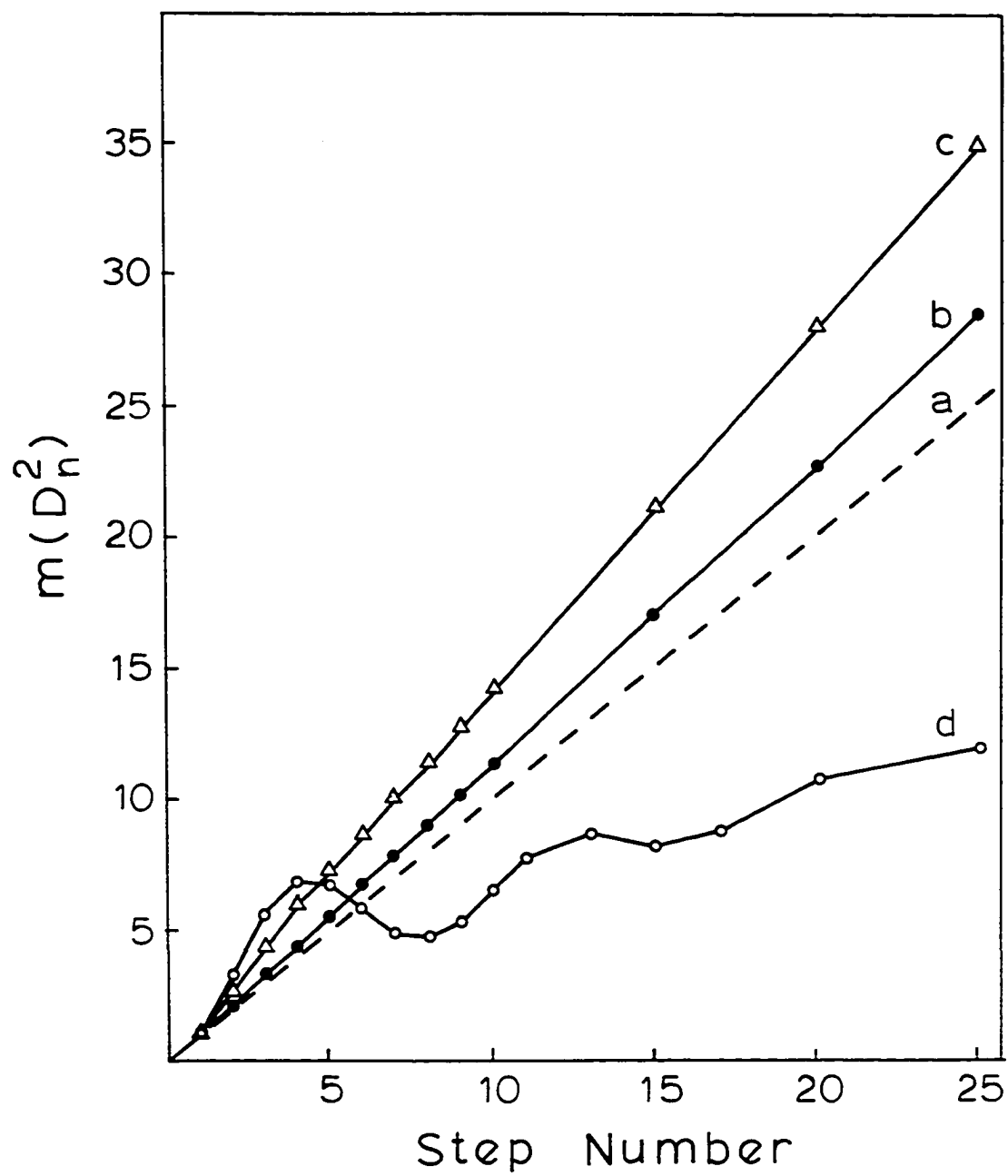
In comparison to the simple random walk, the correlated walk possesses a much more complicated MSD function yet nonetheless resembles the purely random process in that its curve becomes linear asymptotically. This phenomenon is well explained by Hall (1977) for unbiased walks, and from Figures 1.1 and 4.9, appears to apply just as well to biased ones.

The curve for menotaxis, in strong contrast, is a parabola; the terms inside the brackets of Equation 4.13 are constants independent of the value of  $n$ . This quadratic increase is reasonable given that unsquared distances of travel increase linearly. Note though that the expected squared distances of travel are not simply the same as the

**FIGURE 4.9** Behavior of a side-biased correlated walk ( $\mu_\delta = 45^\circ$ ) given different values for the concentration parameter of deflections,  $\rho_\delta$ . Note that all walks appear to become linear asymptotically, just as in the case of the unbiased correlated walk, but that especially for high values of  $\rho_\delta$  there is a marked oscillation (unlike the case for the unbiased walk). The greatest distances of travel seem to be achieved by walks with intermediate values of  $\rho_\delta$ .

- a.  $\rho_\delta = 0$  (random walk)
- b.  $\rho_\delta = 0.1$
- c.  $\rho_\delta = 0.5$
- d.  $\rho_\delta = 0.9$





squares of the expected net distances:

$$E( R_n^2 ) = E( R_n )^2 + \text{var}( R_n ) \quad 4.16$$

Also observe that the variance of  $R_n$ , a value theoretically useful in regression calculations for the unsquared distances of travel, is a function of  $n$ :

$$\begin{aligned} \text{var}( R_n ) &= E( R_n^2 ) - E( R_n )^2 \\ &= n( 1 - \rho_\delta^2 ) + n^2 \rho_\delta^2 - n^2 \rho_\delta^2 \\ &= n( 1 - \rho_\delta^2 ) \end{aligned} \quad 4.17$$

The fact that the curves for both the random and correlated walks either start out or become linear indicates their general failure to keep making steady progress away from a point of origin. After having traveled even a great number of steps from a starting point, there is always some definite probability that a correlated or random walker has accumulated enough deflections to be headed directly back towards where it came from (note that this is a separate phenomenon from their simply lacking the same initial heading, the feature responsible for their expected unsquared distances of travel always equalling zero). In a menotactic walker, on the other hand, deflections do not accumulate and there is virtually no chance of its reversing its course for more than one step (and even that only provided  $180^\circ$  deflections do, in fact, occur).

That even correlated and random walkers can make some headway on the average is demonstrated by the fact that their expected squared distances of displacement are at least monotonically increasing throughout their domain. Just how much progress each type of walk

makes relative to the others can be assessed by the MSD curves. Surprisingly the advantage is not always in the favor of menotaxis!

Consider an organism that desires to move most rapidly through a region and suppose also that it "knows" what distribution of deflection angles it can expect to encounter. Which mechanism should it choose then, either an unbiased correlated walk (biased walks will always be a poorer choice in this situation) or a menotactic walk? The answer depends both on the value of  $\rho_\delta$ , the concentration parameter for the deflection angles, and the number of steps required to leave the area. Compare the following two equations in terms of  $\rho_\delta$  rather than  $\rho_\theta$ , 4.18 representing the behavior expected for a correlated walker, and 4.19 the behavior of a menotactic walker:

$$E(R_n^2) = n + 2 \sum (n - k) \rho_\delta^k \quad 4.18$$

$$E(R_n^2) = n + 2 \sum (n - k) \rho_\delta^2 \quad 4.19$$

For the first two steps, the following is always true (for all  $\rho_\delta < 1$ ):

$$\begin{aligned} \sum_1^{n-1} (n - k) \rho_\delta^k &> \sum_1^{n-1} (n - k) \rho_\delta^2 \\ (2 - 1) \rho_\delta^1 &> (2 - 1) \rho_\delta^2 \\ 1 &> \rho_\delta \end{aligned}$$

The correlated walker always travels farther!

For steps three, four, five, and six it is also possible to determine whether there is some value of  $\rho_\delta$  that allows the menotactic walker to catch up to the correlated walker. All that is needed is to look for a possible point of intersection of the two curves, or to find a solution for

$$\sum (n - k) \rho_{\delta}^k = \sum (n - k) \rho_{\delta}^2$$

$$0 = n^2 - n - \sum (n - k) \rho_{\delta}^{k-2}$$

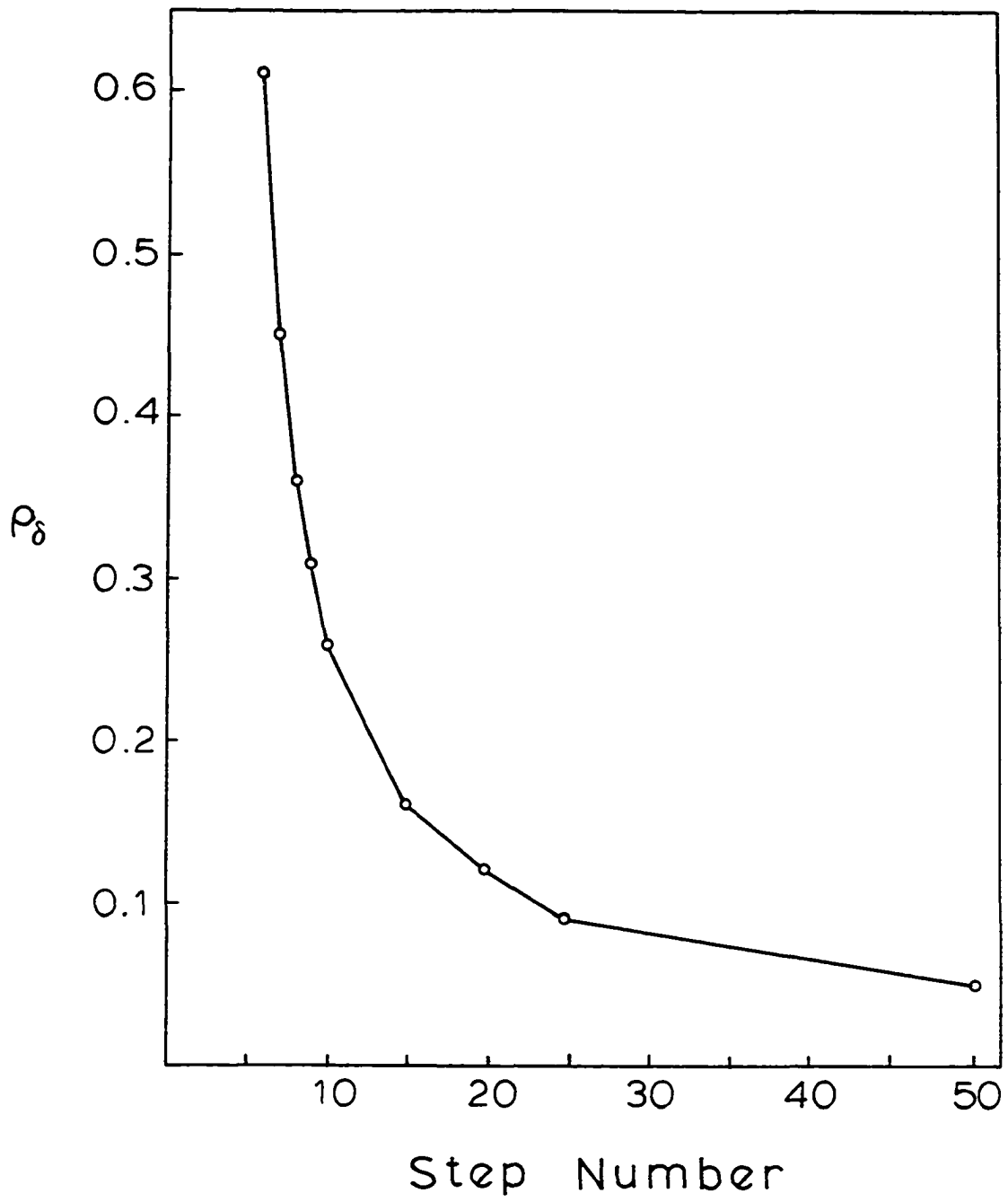
For these step numbers, no more than a quartic equation needs to be solved. If a point of intersection cannot be found within these steps, however, then algebraic methods will be of no avail, since they would require the solution of a quintic equation and higher.

As with the first two steps, no values exist that satisfy the equations for steps three, four, and five; hence it can be concluded that the correlated walker always has the advantage to that point in the sequence. For step six, however (fortunately!), a point of intersection does occur, at a value of  $\rho_{\delta}$  equal to 0.6097. Again, for values of  $\rho_{\delta}$  lower than that the correlated walker will still travel further, but for values that are greater, the menotactic walker travels further.

Although I cannot show it in as formal a fashion, it seems reasonable that at higher numbers of steps still lower values of  $\rho_{\delta}$  will be required for a menotactic walker to catch up. These values can be approximated by iterative methods (see Figure 4.10 for examples). On the other hand, there is perhaps never a step number at which a menotactic walker will always have the advantage. There might always exist some value of  $\rho_{\delta}$  for which the correlated walker will travel further (but I am only guessing, the mathematical proof being beyond my capability).

But how can this be explained in behavioral terms? It seems paradoxical that an animal with no ability to compensate for deflection can ever hope to travel farther than one that can. Afterall, one

**FIGURE 4.10** Values of  $\rho_g$  at which a menotactic walker surpasses a correlated walker after a given number of steps.



of the main reasons why orientational control presumably exists is to keep the course as straight as possible (especially when the target direction itself has no particular importance).

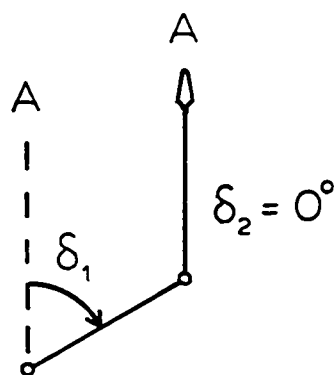
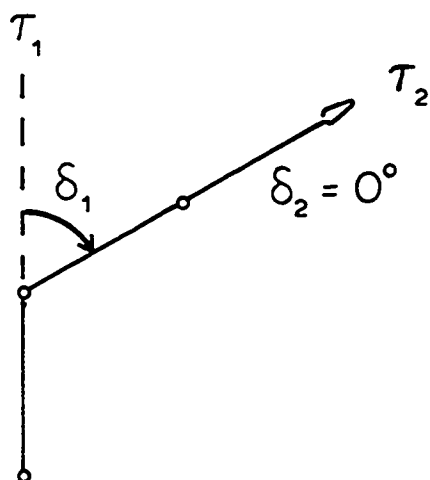
The answer involves the nature of that control. As illustrated in Figure 4.11, the counterturning following a deflection can shorten the path in comparison to that traveled if it made no adjustments whatsoever. Over only a few steps from a starting point, this effect is much more important than the accumulation of "error" that eventually causes the trail of even the least deflected correlated walker to become convoluted. The more the animal has to counterturn in order to compensate for a deflection, the greater the number of steps over which the correlated walker will have the advantage. A telotactic walker, for example, will have to counterturn even more than a menotactic organism and can be expected to have to travel a still larger number of steps in order to catch up to the correlated walker. By similar logic, a telotactic animal on the average can be expected never to catch up to a menotactic animal. Neither organism shows any effect of "error" accumulation but the telotactic organism must turn greater angles to compensate for even a constant magnitude of deflection (see Figure 4.12).

But the complete answer is not as simple as that. The most efficient walk of all is accomplished by anti-telotaxis. As with any other form of tactic orientation, the elimination of "error" due to deflection is achieved by counterturning, but here the compensations "waste" no forward progress whatsoever! The anti-telotactic animal always adjusts its course to travel most directly away from its point of origin. In doing so it turns less than would be expected for a

**FIGURE 4.11** Demonstration that active counter-turning following a deflection shortens the path in comparison to a course that involves no compensation. Observe that the correlated walk also has an initial step without a definable deflection, something that adds to its advantage relative to the menotactic walk over the first few steps.



## Correlated Walk

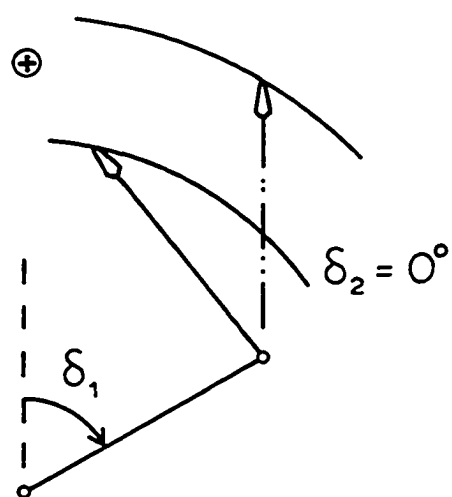


## Menotactic Walk

**FIGURE 4.12** Demonstration of the effects of counterturning in a telotactic walk.

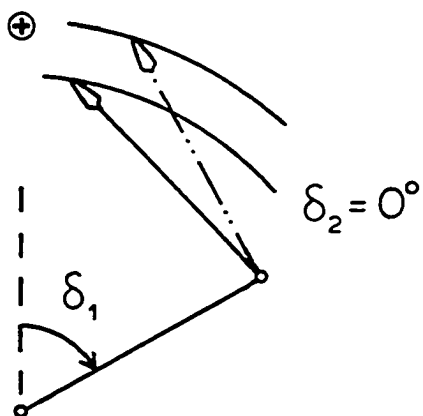
- a. Comparison of a telotactic walk (solid lines) to a menotactic walk (second step indicated by a broken line). Given identical deflections or the same statistical expectation for deflection, the menotactic walker will always travel farther.
- b. Comparison of telotactic walks directed towards targets ( + ) at different distances from the start. The closer the target is the greater the counterturning necessary to bring the course back on target following a deflection, and hence the less the forward travel. At greater and greater distances, the effects of parallax diminish towards zero and the behavior of the walk approaches that of menotaxis.

a.



$\oplus$

b.

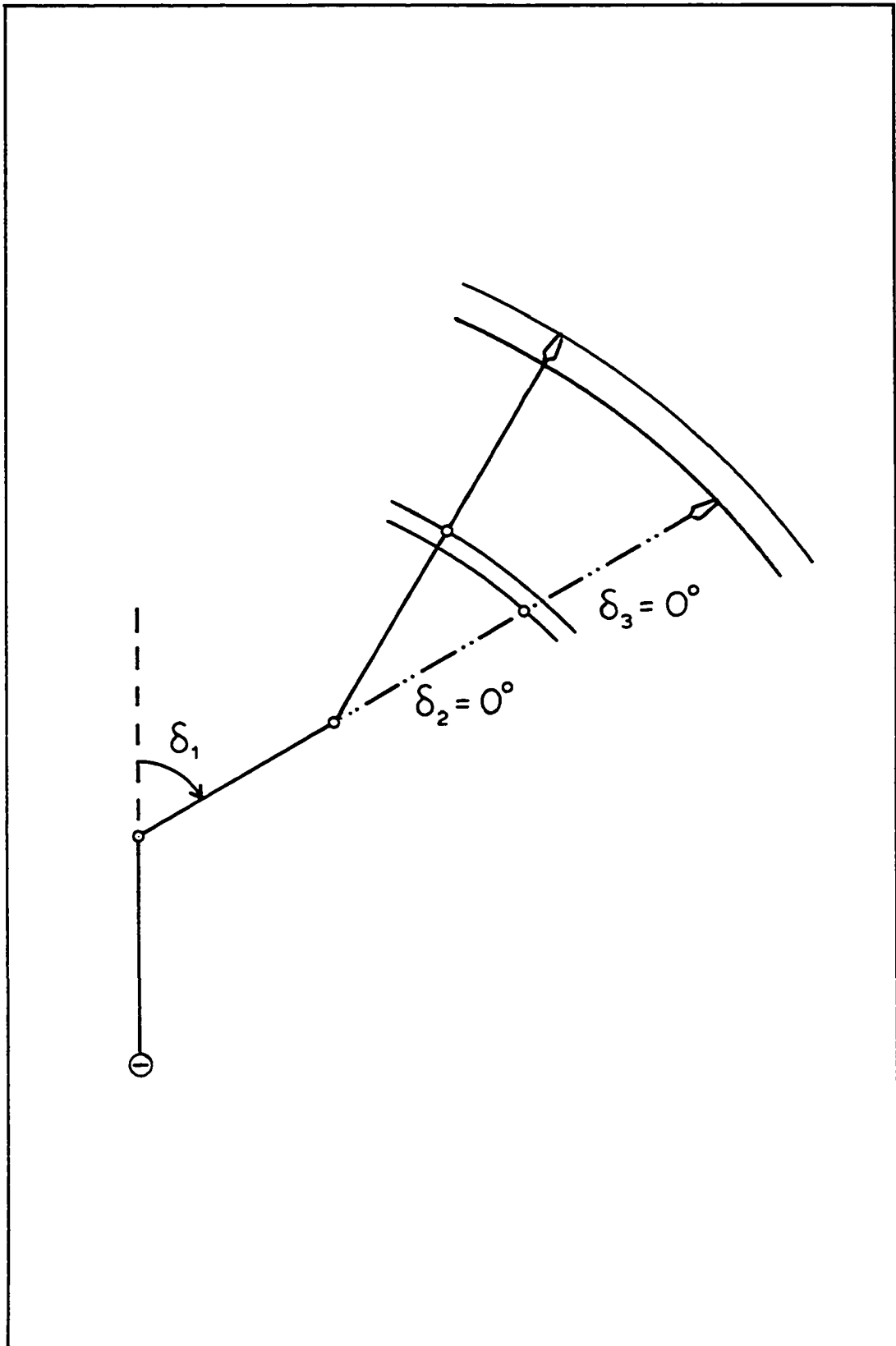


menotactic walker for a given degree of deflection but more than for a correlated walker.

That it nonetheless travels further than a correlated walker for all steps beyond the second (see Figure 4.13) means that the advantages of avoiding convolution now outweigh the costs of counterturning at an earlier point within the sequence than was true for menotaxis. On the other hand, an anti-telotactic walker does not hold a true course; note that its expected unsquared distance of travel will always be equal to zero (although at great distances, where parallax relative to the target point becomes vanishingly small, its behavior will be indistinguishable from a menotactic walker). Even though its values for  $\rho_{\theta k}$  must consequently decline with increasing step number (reaching an asymptotic value of  $\rho_{\delta}^2$ ), producing a form of convolution, the initially high values of  $\rho_{\theta k}$  relative to  $\rho_{\delta}^2$  mean that a menotactic walker on the average can also never hope to catch up to the anti-telotactic walker.

The interactions among turns can thus be quite complicated, even when we examine only the absolute distances of travel (rather than the distance traveled along any particular heading). One message to obtain from these examples is that naive use of the concentration parameter of first-order turns as an "index of directionality" can be misleading, especially in its common application in making comparisons between either individuals or species (e.g., Levin et al., 1971; Pyke, 1978a). Although this term presumably refers just to the general straightness of a path, not its actual heading (perhaps "index of deflectionality" or of "deflection-resistance" or of "path-length" would be a better term), a comparison of two animals using just this

**FIGURE 4.13** Comparison of anti-telotaxis and a correlated walk given the same series of deflections (note that the initial step of an anti-telotactic walker starting at the center of the field is deflection-free, as is that of the correlated walker). Measured from the common starting point, the anti-telotactic walker travels further after the first deflection. This advantage widens with each successive step even without any further deflection from course.



information might give an impression exactly the opposite of what was desired.

Consider, for example, the situation described above where a menotactic and a correlated walker are both confronted with the same set of deflections. Although the correlated walker would have the higher "index of directionality", it would travel the straighter path only over a short number of steps, after which the advantage would pass to the menotactic walker. Furthermore, even if the true deflections were known, the fact that  $\rho_\delta$  is the same for both animals would reveal nothing about the actual differences that exist in the relative straightness or length of their paths.

Even when the orienting mechanisms are the same for both animals, a comparison of the turning tendencies alone might not mean very much. Two menotactic animals, for example, might display only a slight difference in their actual deflectionality (measured by  $\rho_\delta$ ), but the observed turning tendencies would differ by proportionately more, since they reflect the squares of the deflectionalities,

$$\rho_\theta = \rho_\delta^2$$

Conversely, although there could appear to be a large difference between the two in terms of the squared distances they can be expected to travel, in terms of the unsquared distances there would be a much smaller proportional difference.

The message is, once again, that it is the deflections themselves that hold the essential information, not the turns (except for the restricted cases in which they correspond to the deflections). The usefulness of the turns lies solely in the predictions that can be

derived from them (and the step lengths) about the walks as wholes, predictions that can be used to test hypotheses about both the nature of the orientational control and of the deflections.

However, even the knowledge of the exact relationships between turns and mean squared distances for menotactic, correlated, and random walks does not ensure that departures from the predictions can be detected. The problems of hypothesis testing, as opposed to describing the relationships that should exist in theory, are the subject of the next chapter.



**CHAPTER V. APPLICATION OF MENOTACTIC WALK ANALYSIS TO MOVEMENT DATA  
OBTAINED BY TELEMETRY**

#### **V. A. The Limitations of Movement Data Collected by Telemetric Methods**

In the Introduction I described how methods of analysis have not kept pace with methods for recording the details of animal movement patterns. In particular, methods such as radio-telemetry are now routinely being used to gather enormous amounts of sequential information on animals' routes of travel, whereas most forms of analysis still cannot deal with data that have any sort of sequential dependencies.

This situation is now reversed. The theory and mathematical derivations presented in the two preceding chapters should be adequate to test virtually any hypothesis concerning the sequential organization of the routes, but to actually do so requires far more information on the behavior of the subjects than even continuous and detailed tracking of their movements can provide. The theory of movements now requires more than ever that behavioral and ecological contexts be available in order to define the various deflections, targets, walks, and different levels in the route hierarchy. The problem is that even when the subject is directly observed in conjunction with the route surveys, it still will not be possible in all cases to define the behavioral states corresponding to each separate movement. In fact, as mentioned in Chapter III, it may not even be possible to distinguish between separate trajectories (as when two deflections occur in sequence with the same orientation).

When the movements are recorded by telemetric means, such as Ariadne's method or remote radio-triangulation, these problems are compounded. Not only will accessory behavioral and ecological information be more difficult to obtain, but the recording methods themselves divide the routes up into arbitrary units that only roughly approximate the animal's paths. Since any arbitrary partition is sure to cut across the real deflections and walks, either spreading their influence over several artificial steps or series or compressing it into just a small portion of them, how can methods based on the presumed independence and stationarity of the units have any hope of untangling what is going on?

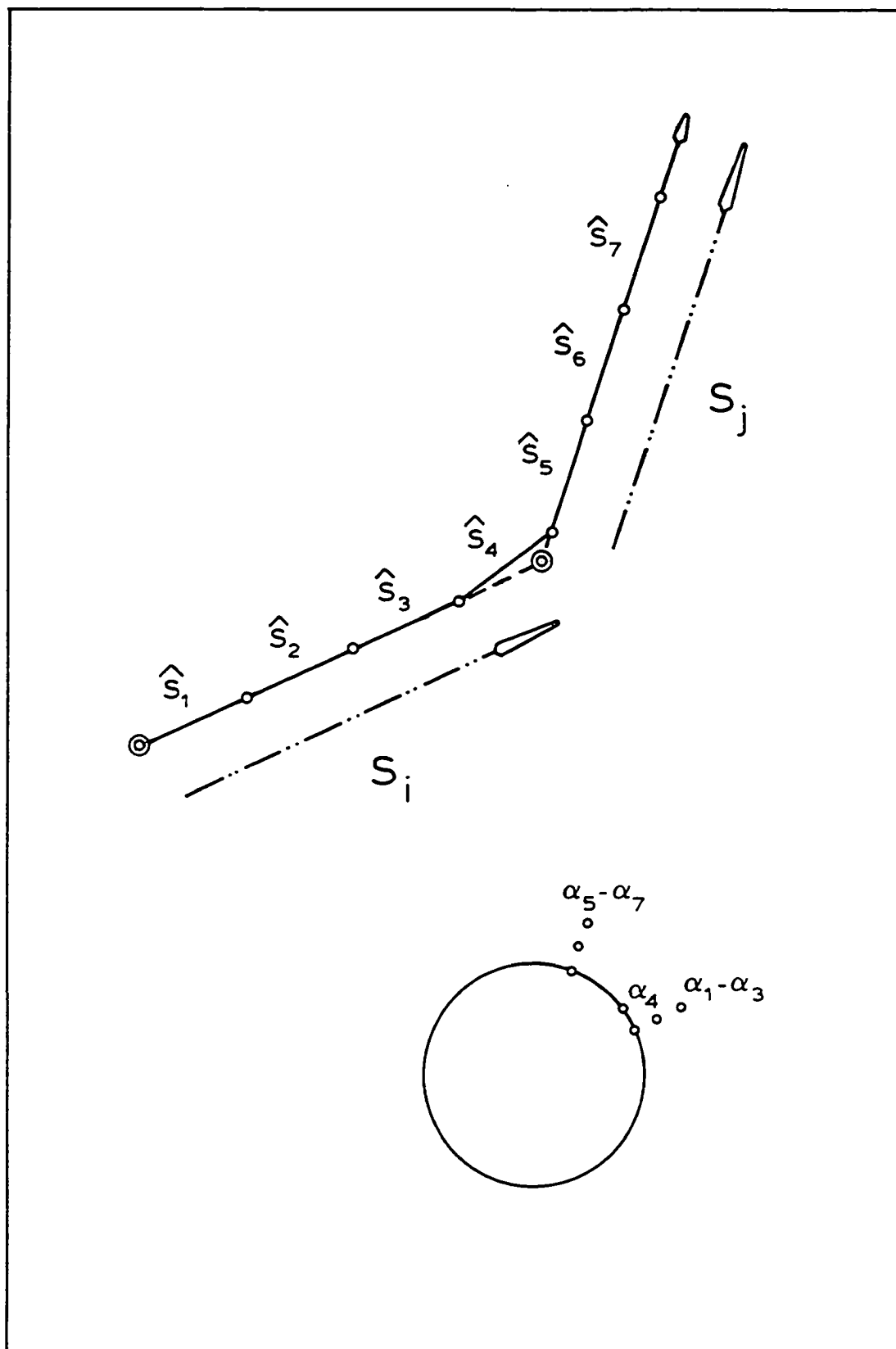
This chapter attempts to provide at least some rough solutions to these problems. It does so, however, at the cost of making certain restrictive, if not entirely unreasonable assumptions about the nature of the routes. Most important, I assume that the underlying processes either correspond to or can at least be approximated by either menotactic or correlated walks. When these assumptions hold true, then even arbitrary partitions can still possess the desired features for analysis. If they do not, then the nature of the failure to match the assumptions can still guide the search for additional information.

## V. B. The Properties of the Steps in an Artificial Partition

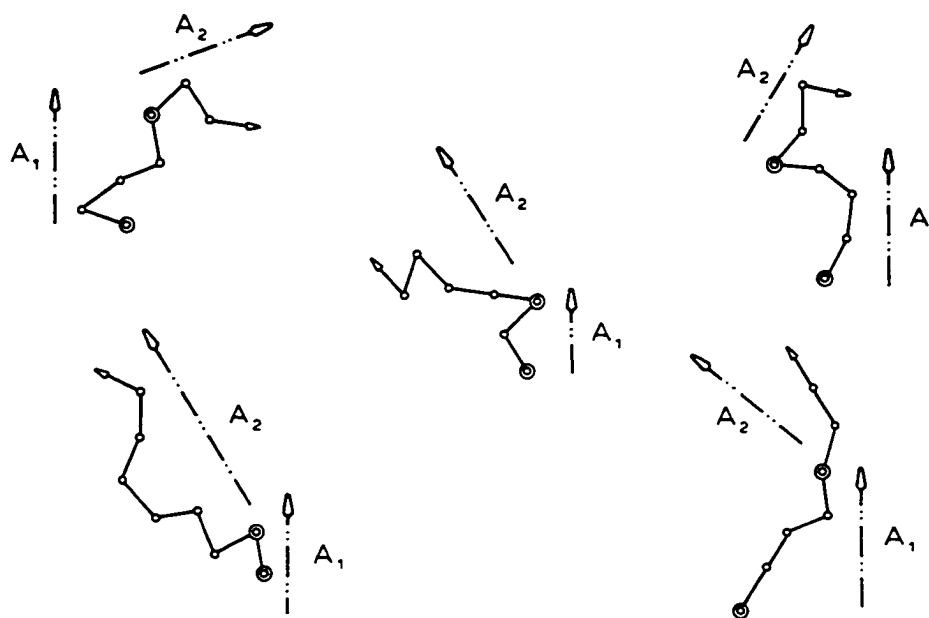
Given that some degree of artificiality is unavoidable in any partitioning of a route into discrete units done by the observer, what are the actual problems that arise with respect to menotactic analysis? Consider an untransformed series of steps that has been at least tentatively identified as a true menotactic walk, one whose steps have the desired properties of independence and stationarity. The effect of choosing an arbitrary partition will be to slice across the true steps, separating parts of single deflections into two or more observed "steps". If the partition is made too finely, as shown in Figure 5.1, the causative events between "steps" will overlap; the "steps" will no longer be independent of one another as is required for analysis. The observed linkage between "steps" would thus indicate some form of orientation in addition to that hypothesized for the walk as a whole, which in fact there is. The problem arises in confounding the control at level of the deflections with that of the next level up in the hierarchy. This same confusion results when the endpoints of separate walks are not recognized; even if the steps at a lower level have been correctly identified, the pooling of two or more walks (the steps in a higher-order series) to form a single series will also confound different levels in the hierarchy and make the observed series of "steps" non-stationary.

Either way, discontinuities are introduced into the series, the effects of which are illustrated in Figure 5.2. Basically, the value for  $\rho_{\delta}$  will be greatly underestimated, especially relative to the value for  $\rho_{\theta}$ , which might be scarcely affected. In terms of analysis, this situation will result in lower predicted values of  $\rho_{\theta}$ .

**FIGURE 5.1** An example of serial correlation introduced into a sample of artificially chosen steps ( $s_i$ ) either by making them too short relative to the natural steps ( $s_i$ ) or by confounding different levels in the actual hierarchy. Either way, there is a failure to distinguish series  $s_1 - s_3$ ,  $s_4$ , and  $s_5 - s_7$ , as indicated in the distribution of azimuths. Note that step  $s_4$  is influenced by the directions of both  $s_i$  and  $s_j$ .



**FIGURE 5.2** The effects of discontinuities on estimates of  $\rho_\theta$  and  $E(D_n^2)$ . The sequences shown are simulated menotaxes, each with one change in target. The observed value of  $r_\theta$  is intermediate between the predictions given by the true deflections,  $r_\delta$ , and the observed azimuths,  $r_\alpha$ . The mean squared distances of travel are quite close to the predictions for menotaxis and far from the line predicted for the correlated walk, both based on the observed value of  $r_\theta$ .



### Angles

$$\delta$$

$$r^2 = 0.446$$

$$\theta$$

$$r = 0.35$$

$$\alpha$$

$$r^2 = 0.277$$

### Distances

Corr. Walk

$$E(D_7^2) = 12.9$$

Observed

$$m(D_7^2) = 20.7$$

Meno. Walk

$$E(D_7^2) = 21.7$$



based on the sample of azimuths, or in higher estimates of the mean squared distances of travel, based on the sample of turns. Both these departures from the predictions would tend to suggest the operation of a correlated walk or some other atactic process rather than the menotaxis or other tactic process that might actually be governing the true series of steps.

Interestingly, reasonably accurate estimation of the mean net distance of travel over a number of steps is still possible. On the average, any given number of "steps" will contain the same number of discontinuities, provided the process at the higher level is also stationary. In this situation the observed value of  $r_a$ , although unrepresentative of the lowest level deflections, will provide information about the combined effects of the two orders of deflections. So long as (1) the process actually is menotactic over at least the higher level, and (2) all observed series have the same target heading, then the relationship,

$$E(D_n) = n \rho_\delta$$

will still hold true. The main effect of the discontinuities here is to increase the scatter of the observed values about their means.

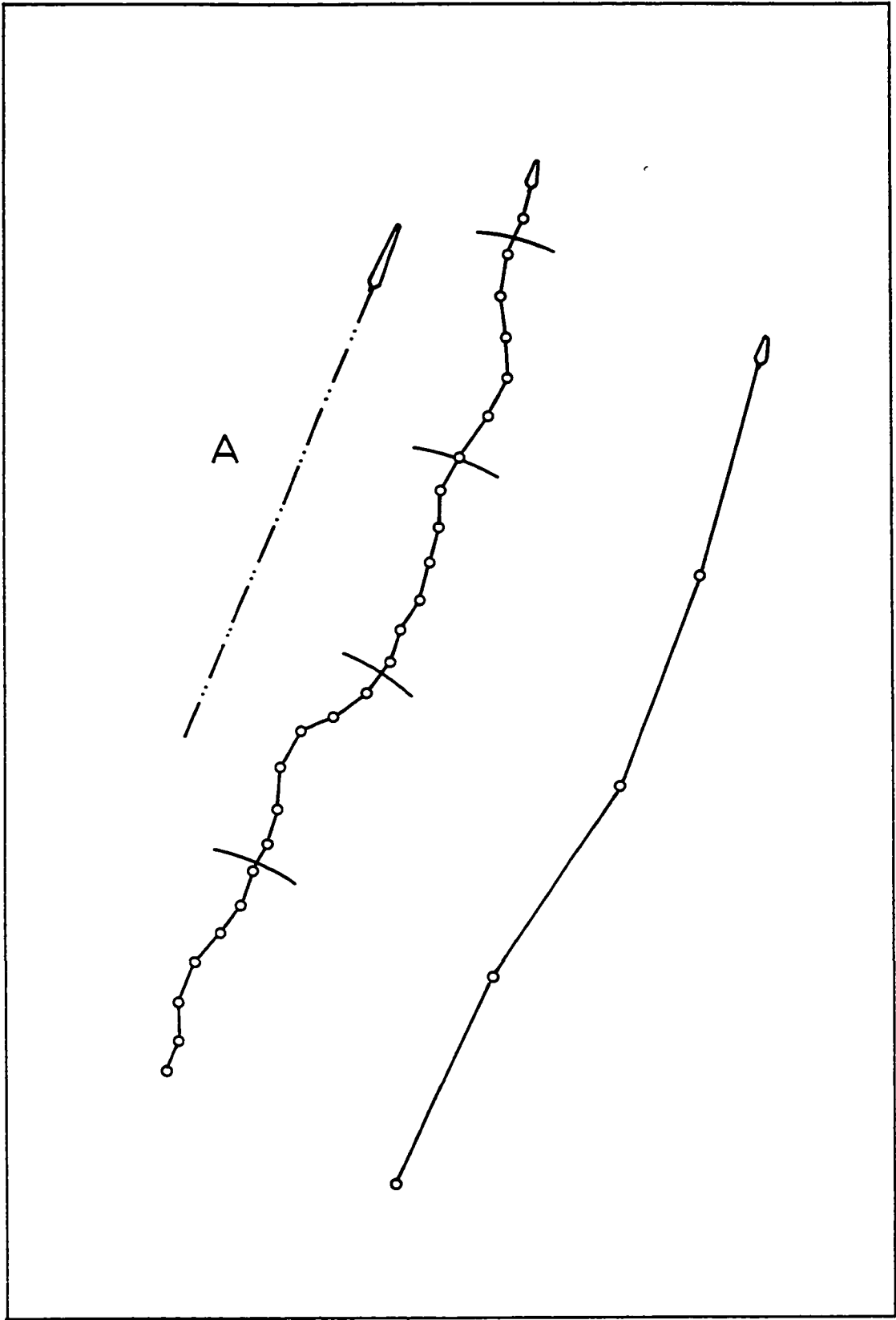
On the other hand, the provision that each series have the same target heading will only rarely be met (as in repeated releases of a homing-pigeon from the same site). In most studies of free-ranging animals, changes in target will usually be frequent, and even if the process is menotactic, the average net distance of travel over several arbitrarily chosen sequences and steps will be unpredictable.

It is just in this very situation that the less restrictive analyses based on turn angles could be most effective. As explained in the previous chapter, information derived from distribution of turns permits analysis of the absolute distances of travel, not just the distances in a particular direction. Such information can thus be used to characterize not only menotactic processes in which the target headings are different (and even unknown) from series to series, but also such "non-directional" processes such as the random, correlated, and telotactic walks. For this reason, the rest of this chapter will be devoted to these methods.

First a way must be found to avoid the problems introduced by the presence of discontinuities within the series. In contrast with the situation indicated in Figure 5.2, if a partition is chosen such that each "step" represents the sum of several true steps, instead of only a fraction of a single one, then any carry-over of deflectional influences across the "step's" termini will be minimal (see Figure 5.3). Furthermore, either each "step" will now represent a sum of several independent deflections, if the process is menotactic, or the turns between them will, if the process corresponds to a correlated walk. In other words, the arbitrarily determined "deflections" should be independent of one another, just as in the true deflections.

The "deflections", in addition, will all have roughly the same distribution if each one represents a sum of the same average number of true deflections. For both menotactic and correlated walks, this result can be achieved by partitioning the observed movements into "steps" of uniform length. In these two processes there is a one-to-one relationship between the number of true steps and the absolute

**FIGURE 5.3** The smoothing effect on menotactic series of creating larger artificial steps from the sum of many smaller true steps. Notice that the original series is homogeneous, that all steps have the same target heading.



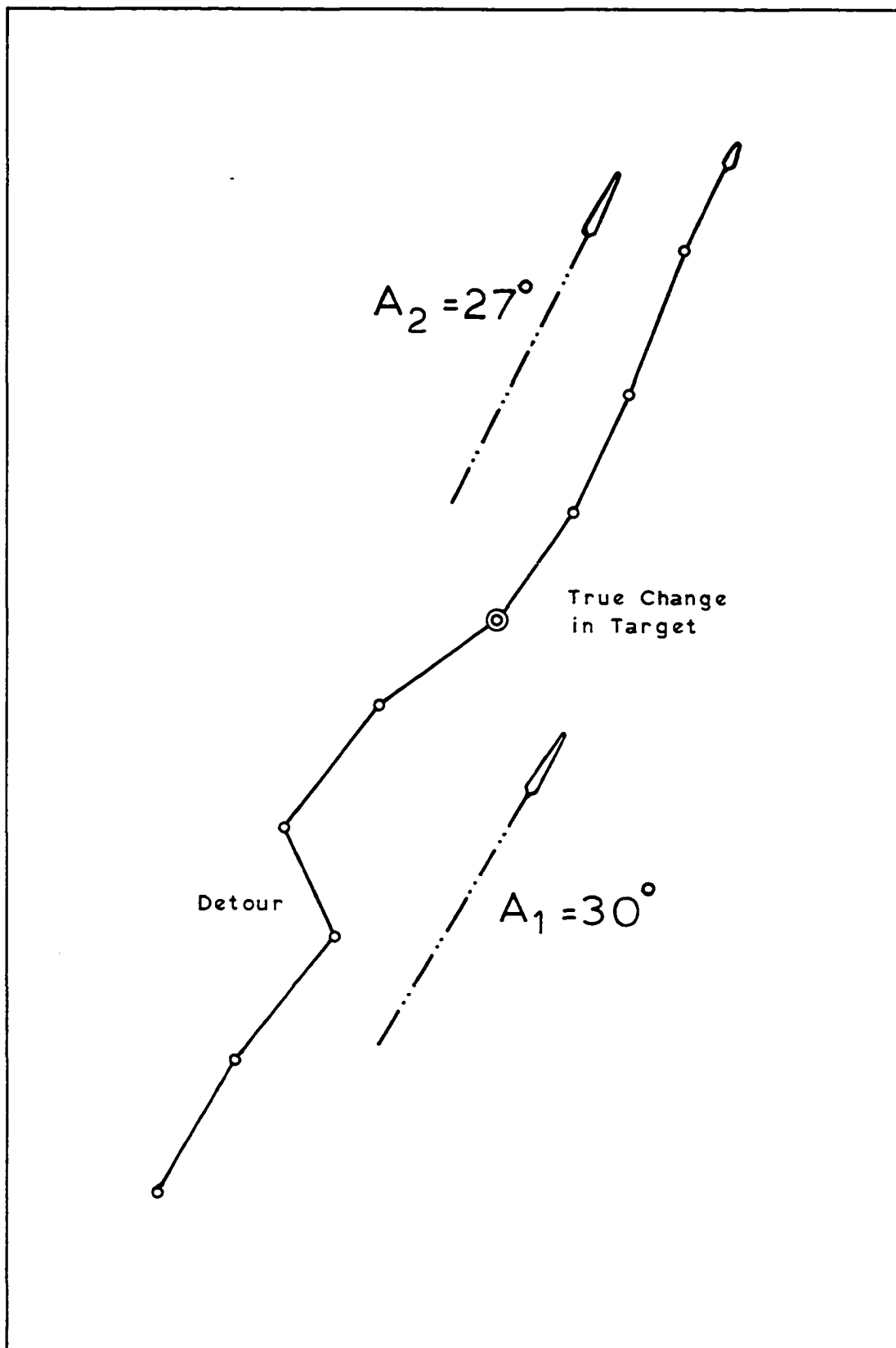
distances of travel, expressed either by the equation for the average net distances of travel or of the squared distances.

Conversely, any other method of partitioning, such as one based on uniform intervals of time (used in most radio-tracking studies), cannot be as sure to obtain stationarity among the "steps". Of course each "step" would represent the same average number of deflections in equi-temporal divisions if the animal always moved at a uniform rate of speed or in some other way encountered the same average number of deflections per unit time, but such behavior is probably rare.

One particular method of partitioning is especially suspect: dividing the routes on the basis of turning magnitude (Figure 5.4). This method guarantees that zero-degree turns will never be observed and, in general, tends to inflate the influence of large magnitude deflections at the expense of smaller ones. A series produced in this manner can never be expected to fit the menotactic or correlated models even if the actual process matches precisely one of the theoretical ones.

In contrast, partitions of uniform length have no problems with respect to deflections of any magnitude. Even zero-degree deflections will contribute their share to the overall sum making up a given "step", and, of course, it will be possible to observe zero-degree turns between the "steps" themselves. Furthermore, the effects of any correlation between the actual step lengths and their directions, such as was suggested in Section III. D. for composite distributions of deflections, will tend to average out when several steps are summed. A similar smoothing out will also apply to short-term cases of non-stationarity in the deflections due to klino-kinesis or klinotaxis.

**FIGURE 5.4** An illustration of the problems encountered in partitioning routes according to absolute changes in direction. Large deflections within an homogeneous series can be wrongly identified as changes in target heading, whereas small but true changes will go undetected.



On the other hand, while steps of uniform length are even more likely to fit a menotactic or correlated walk than the original steps, their use can prevent any chance of detecting violations of the assumptions of stationarity and independence, but then so can any other arbitrary partitioning scheme.

Unless more information is available about the nature of the true deflections than is usual in telemetric studies, a uniform partition -- either made during the original survey or later extracted from the maps -- seems the safest choice. But how large should the "steps" be? Is there any theoretical optimum "step" length that will most efficiently capture the details of the route processes?

There might actually be no one answer to these questions; a range of different sized partitions usually offers the best solution. Examining the effects of changes in the scale of the partition can reveal a good deal about the nature of the routes, more, in fact, than may be possible through use of any one partition by itself.

Such information proves its worth in distinguishing between tactic and atactic processes other than the menotactic and correlated walks. Consider, for example, a MSD curve that at a particular scale of measurement lies between those of the two standard models. Such a curve could theoretically represent either form of orientational control. When the scale of the partition is increased, however, it should at least become clear whether the process is tactic or atactic. As defined in Chapter III, an atactic orientation cannot absolutely remove the effects of previous deflections; over the course of a sequence, "errors" will thus accumulate. If larger and larger steps are used to examine a particular set of such sequences, the effects of



the course errors will become more and more prominent. Consequently, the MSD curves will tend to converge first on the predicted line for a correlated walk and ultimately (if the scale of measurement can ever be made so large) on the straight line representing a random walk.

This stands in contrast to a tactic process where the effects of deflections never accumulate. In fact, the effects of control become more and more prominent with increases in the scale of measurement as the influence of small-scale deflections are averaged out. The MSD curves become ever more sharply increasing in their rate of change, even if never catching up with the parabolic expectations for a menotactic walk.

These findings, of course, depend on the homogeneity of the sequences under observation. If the routes are instead hierarchical in nature, involving periodic changes in orientational targets, then increases in the scale of measurement will lead to unpredictable changes in the nature of the observed results. At the lowest scale, the sequences will represent mixtures of different processes, but the effects of the one on the lowest level should predominate, since the changes in targets representing the action of the higher-level processes should usually be few compared to the number of deflections at the lowest level. Conversely, at greater scales of measurement, the effects of processes at a higher level will become increasingly dominant as the minor wobbles lower down tend to average out.

In terms of the analysis, the results could shift from a curve that indicates tactic orientation to one that represents a random walk to one that represents still another form of tactic control. At the same time, as a result of discontinuities, the observed behavior at

any one of the different scales of measurement might never reflect accurately any of the various processes going on.

Nonetheless, there could be regions within a hierarchical series in which only one form of control is operating, due to the possibility of complete switching of control between levels, as described in Chapter III. The next section takes up the problem of how to subdivide such a route into "walks" as well as "steps", how to obtain several series of steps that are sufficiently homogeneous for menotactic analysis.

### V. C. Single Sequence Tests for Artificially Determined Walks

The decision as to where to divide up a series of arbitrarily partitioned "steps" into "walks" is a matter of trial and error, just as it was for the determination of the "steps" themselves. There is, on the one hand, a requirement for at least a minimum number of steps per walk, and on the other, for a minimum number of walks per route. Both these constraints further interact with the choice of "step" length: the longer the "steps" the fewer there will be to form the "walks" and, consequently, the fewer the "walks" there will be to form the set of walks. All these considerations indicate that no one partition will always be optimum; the choice will depend on the scale of measurement, the absolute length of the route, and the methods of analysis being employed.

To resolve these problems requires discussion of tests for determining how well a single sequence of steps fits either a correlated or menotactic walk. In the present context, the main purpose of these tests is simply to identify sections of a route that contain obvious discontinuities. Where directional information alone is of interest, they are furthermore equally useful as the MSD analyses, if not more so.

The basis for these tests lies in the relationships between turn angles, both first- and higher-order, as discussed in Sections IV. C. and IV. D. In Chapter IV., however, the turns were assumed to be obtained by simple random sampling and hence independent of one another. In sampling turns from a sequence, on the other hand, that provision will often be violated, depending on the nature of the walk and of the sampling process. Before I can describe the tests of the

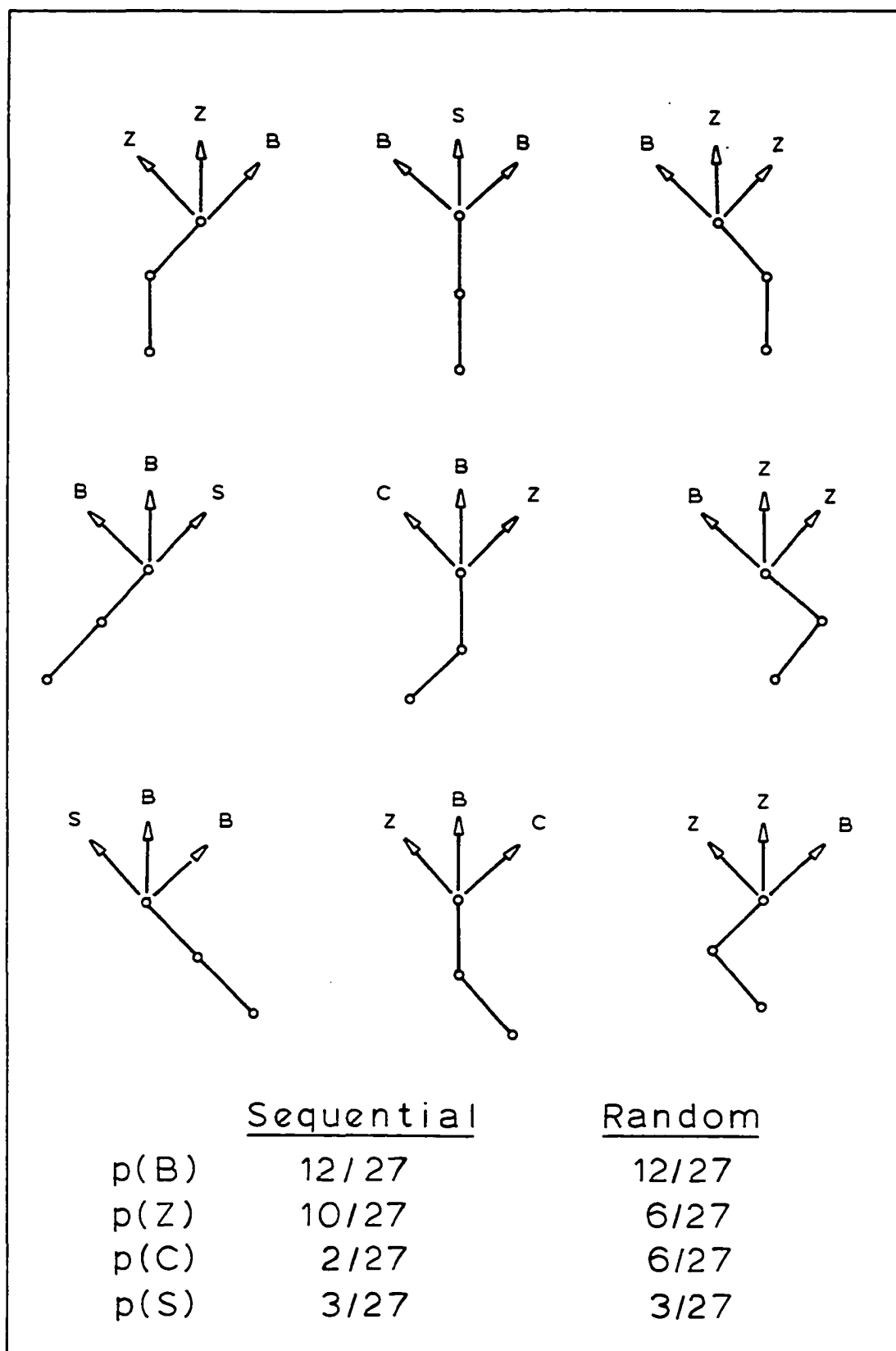
turn-angle relationships, I must first discuss these sampling problems.

In most studies involving turn angles, all turns in a sequence are pooled to form a single sample. This procedure is perfectly permissible so long as the process corresponds to a correlated walk (as is usually assumed, at least implicitly); the turns are then equivalent to the deflection angles, which are independent of one another by definition. If, on the other hand, the walk obeys any other process, this assumption must fail; there will inevitably be some sort of sequential dependency among the turns.

In menotaxis, for instance, the turns are equivalent to differences between deflections. Turns that are adjacent to one another in the sequence will hence share a deflection (Figure 5.5). Thus the first turn of a pair tends to be followed by a counter turn, since any deviation away from the mean deflection can be expected to be followed by a return to the mean value (there is, however, no active counterturning, as in various atactic processes). Only non-consecutive turns will therefore be independent of one another. Random sampling must be accomplished by selecting at least every other turn in a sequence, as shown.

These same arguments also apply to higher-order turns. Again for menotaxis, only turns that do not share steps in common will be independent of one another. Here, however, adjacent turns will be independent (Figure 5.6). The general rule now, for any series of  $k$ -th order turns, is that every other set of  $k$  steps must be skipped in order to form an independent random sample.

**FIGURE 5.5** Demonstration of the bias introduced into a sample of turns drawn sequentially from a menotactic series of steps. All 27 possible three-step sequences are illustrated for the case where  $p(\delta = -45^\circ) = p(\delta = 0^\circ) = p(\delta = 45^\circ) = 1/3$ , and Z = zig-zagged; C = curved; B = bent; S = straight. As compared to random sampling of turns (where successive turns do not share any steps), the probability of zig-zagged sequences is increased, while the probability of curved sequences is correspondingly decreased.



**FIGURE 5.6** Sampling rules for selecting independent turn angles from sequences produced by menotactic and correlated walks. The turns for each sequence occur in order across the page from left to right; alternative samples of independent turns occur on different lines.

A.

Since in menotaxis

$$\theta_{ij} = \delta_j - \delta_i$$

for all  $i < j$ , then the following alternative sets will represent independent samples of turns taken from a given series of steps:

1st order turns

$$(\delta_2 - \delta_1) (\delta_3 - \delta_2) (\delta_4 - \delta_3) (\delta_5 - \delta_4) (\delta_6 - \delta_5) \dots$$

2nd order turns

$$(\delta_3 - \delta_1) (\delta_4 - \delta_2) (\delta_5 - \delta_3) (\delta_6 - \delta_4) (\delta_7 - \delta_5) (\delta_8 - \delta_6) \dots$$

3rd order turns

$$(\delta_4 - \delta_1) (\delta_5 - \delta_2) (\delta_6 - \delta_3) (\delta_7 - \delta_4) (\delta_8 - \delta_5) (\delta_9 - \delta_6) \dots$$

B.

For correlated walks

$$\theta_{ij} = \sum_i^{j-1} \delta_{ij}$$

Consequently, the following sets represent independent samples of turns:

1st order turns

$$\delta_1 \delta_2 \delta_3 \delta_4 \delta_5 \delta_6 \delta_7 \dots$$

2nd order turns

$$(\delta_1 + \delta_2) (\delta_2 + \delta_3) (\delta_3 + \delta_4) (\delta_4 + \delta_5) (\delta_5 + \delta_6) \dots$$

3rd order turns

$$(\delta_1 + \delta_2 + \delta_3) (\delta_2 + \delta_3 + \delta_4) (\delta_3 + \delta_4 + \delta_5) (\delta_4 + \delta_5 + \delta_6) \dots$$



For the correlated walk similar considerations must be made. Higher-order turns no longer correspond to simple deflections. On the contrary, they are equivalent to sums of deflections. Just as for the differences between deflections in the menotactic walk, sums that share deflections in common will not be independent of one another. For example, only every other second-order turn in a series can be used to form an independent random sample. As a consequence, the sampling rule is very different from the one that applied to the menotactic walk: for higher orders of turns within a correlated walk, only every  $k$ -th turn in the series will make up an independent sample (this rule is another consequence of the cumulative effects of deflections in this type of walk).

Complicating matters still further, tests that examine the predictions for higher-order turns based on information obtained from lower-order ones should be based on samples for the two orders that are also independent of one another. That way any biases present in the lower-order samples will not automatically bias the findings in the higher-order. As a consequence, further selectivity must be exercised in forming the samples. Again, the rule governing the choice will depend on the type of walk, as is shown in Figure 5.7.

Figure 5.7 also illustrates the possibility of choosing samples that meet the requirements for independence for both correlated and menotactic walks, depending on the orders of turns. This selection will involve a decrease in sampling efficiency for one or both of the walks, relative to what could be achieved by treating them separately. This method allows, though, the same samples to be used to test the competing hypotheses that the process is either the one kind of walk

**FIGURE 5.7** Independent samples of first- and second-order turns under the hypothesis of a correlated walk or a menotactic walk, or either one. Note that alternative schemes are possible. I chose to start with the initial second-order turn of the sequence and to then alternate between selecting the next available first- and second-order turns.

### First-order Turns

$\theta_{12}$	$\theta_{23}$	$\theta'_{34}$	$\theta'''_{45}$	$\theta_{56}$	$\theta'_{67}$	$\theta_{78}$	$\theta_{89}$	$\theta'''_{910}$	$\theta_{1011}$	$\theta_{1112}$
$\delta_2 - \delta_1$	$\delta_3 - \delta_2$	$\delta_4 - \delta_3$	$\delta_5 - \delta_4$	$\delta_6 - \delta_5$	$\delta_7 - \delta_6$	$\delta_8 - \delta_7$	$\delta_9 - \delta_8$	$\delta_{10} - \delta_9$	$\delta_{11} - \delta_{10}$	$\delta_{12} - \delta_{11}$
$\delta_1$	$\delta_2$	$\delta_3$	$\delta_4$	$\delta_5$	$\delta_6$	$\delta_7$	$\delta_8$	$\delta_9$	$\delta_{10}$	$\delta_{11}$

### Second-order Turns

$\theta'''_{13}$	$\theta_{24}$	$\theta_{35}$	$\theta'_{46}$	$\theta_{57}$	$\theta'''_{68}$	$\theta'_{79}$	$\theta_{810}$	$\theta_{911}$	$\theta'_{1012}$	$\theta'''_{1113}$
$\delta_3 - \delta_1$	$\delta_4 - \delta_2$	$\delta_5 - \delta_3$	$\delta_6 - \delta_4$	$\delta_7 - \delta_5$	$\delta_8 - \delta_6$	$\delta_9 - \delta_7$	$\delta_{10} - \delta_8$	$\delta_{11} - \delta_9$	$\delta_{12} - \delta_{10}$	$\delta_{13} - \delta_{11}$
$\delta_1 + \delta_2$	$\delta_2 + \delta_3$	$\delta_3 + \delta_4$	$\delta_4 + \delta_5$	$\delta_5 + \delta_6$	$\delta_6 + \delta_7$	$\delta_7 + \delta_8$	$\delta_8 + \delta_9$	$\delta_9 + \delta_{10}$	$\delta_{10} + \delta_{11}$	$\delta_{11} + \delta_{12}$

' Turns independent under the hypothesis of a correlated walk

" Turns independent under the hypothesis of a menotactic walk

''' Turns independent under both the above hypotheses

or the other.

Some constraints of rigorous independent sampling of turns should be evident by now: a sequence needs to contain a great many actual deflections (or steps) in order to provide minimum sample sizes for the tests, particularly those that involve higher-order turns. In a menotactic walk, for example, a series of 13 steps produces a sample of just 6 independent first-order turns and a sample of only 5 second-order ones. Similarly, a correlated walk 11 steps long produces only 5 independent second-order turns, even though all 10 of its first-order turns are independent by definition. When the samples of the two orders of turns are further required to be independent of one another, and when it is also desired to look for evidence of either a correlated or menotactic walk, then 25 steps will be required to produce just 5 first- and 5 second-order turns that are independent.

Such rigorous conditions for independence raise practical problems for sampling; even 25 steps in a homogeneous series can be hard to come by. Furthermore, since not all the turns in a series will be included in a given sample (except for first-order turns in a correlated walk), the particular turn representing the change in target will sometimes be skipped; the results then might wrongly indicate homogeneity where it in fact does not occur!

More than one independent sample of turns can, of course, be obtained from a given series of steps, and if one does not include the discontinuity, another one will. In menotaxis, for example, there are always two alternative, independent samples for turns of any order (Figure 5.6). The turns skipped to form one independent sample themselves compose a second one, possessing presumably the same sorts

of features. For the correlated walk there will be  $k$  alternative samples for any sequence of  $k$ -th order turns. By testing all such possibilities, the presence of a discontinuity cannot go unnoticed.

That procedure, however, seems cumbersome and does not reduce the number of steps in the sequence required for testing. The fact that the alternate samples of turns should represent the same sort of behavior (within homogeneous sequences, at least) suggests another approach: why not pool all turns after all? The lack of independence between turns may not be as significant as the similarities they possess overall.

The results of simulating both menotactic and correlated walks tend to support this hypothesis (Table 5.1). These findings indicate that even a sequence as short as seven steps can produce pooled samples of first- or second-order turns whose statistics do not differ markedly from those expected under the parameters of the models. At least with regard to  $c$ , the unbiased estimator of the concentration parameter,  $\rho$  (see Table 4.1), the relationships between the samples of azimuths and the samples of both the first- and second-order turns show no significant departure from the simple exponential function described in Chapter IV.

At the same time it should be noticed that the predictions do not hold when the sample statistic  $r_a$  is used instead of  $c_a$ . Unfortunately this is the statistic that must be employed in most cases since the actual target heading is usually unknown. Whereas the average value of  $c$  over all sequences will approach the population value  $\rho$  as the number of sequences grows large, the values of  $r$  for a sample will always be larger on the average than the corresponding

**TABLE 5.1 EFFECTS OF SEQUENTIAL SAMPLING ON TURN STATISTICS IN A  
HEMOTACTIC WALK**

Fifty sequences of seven steps each were formed by random sampling from a semi-circular uniform distribution of deflections:

$$\delta = 270, 290, 310, 33, 350, 10, 30, 50, 70, 90$$

$$p(\delta = x) = 0.1$$

$$\rho_{\delta} = 0.567 \quad \mu_{\delta} = 0^{\circ}$$

$$\rho_{\theta} = 0.322 \quad \mu_{\theta} = 0^{\circ}$$

run	azimuths			turns	
	$c_{\alpha}$	$c_{\alpha}^2$	$r_{\alpha}$	$c_{\theta 1}$	$c_{\theta 2}$
1	0.472	0.223	0.256	-0.124	0.400
2	0.670	0.449	0.476	0.196	0.629
3	0.742	0.551	0.659	0.642	0.353
4	0.546	0.298	0.304	0.250	-0.188
5	0.405	0.164	0.181	0.388	-0.053
6	0.481	0.231	0.282	-0.026	0.606
7	0.455	0.207	0.248	0.044	0.023
8	0.701	0.491	0.557	0.579	0.494
9	0.421	0.177	0.216	-0.063	0.053
10	0.435	0.189	0.282	0.112	0.106
11	0.594	0.353	0.386	0.412	0.441
12	0.687	0.472	0.481	0.451	0.257
13	0.744	0.554	0.565	0.706	0.370
14	0.606	0.367	0.372	-0.068	0.565
15	0.568	0.323	0.506	0.352	0.335
16	0.579	0.335	0.554	0.573	0.564
17	0.472	0.223	0.285	-0.005	0.445
18	0.469	0.220	0.253	0.254	0.047
19	0.456	0.208	0.401	0.099	0.253
20	0.287	0.082	0.084	-0.550	0.257
21	0.702	0.493	0.496	0.511	0.200
22	0.635	0.403	0.432	0.073	0.441
23	0.484	0.234	0.295	0.313	0.000
24	0.437	0.191	0.194	-0.313	0.776
25	0.652	0.425	0.591	0.730	0.611
26	0.531	0.282	0.361	0.381	0.218
27	0.643	0.413	0.484	0.599	0.653
28	0.445	0.198	0.427	0.255	0.518
29	0.606	0.367	0.381	0.112	0.418
30	0.428	0.183	0.224	0.292	-0.237
31	0.546	0.298	0.298	0.437	0.165
32	0.572	0.327	0.328	0.524	0.135
33	0.477	0.228	0.227	0.122	-0.237
34	0.778	0.605	0.606	0.524	0.606
35	0.627	0.393	0.401	0.167	0.406
36	0.546	0.298	0.300	0.339	0.023

TABLE 5.1 CONTINUED

run	azimuths			turns	
	$c_a$	$c_a^2$	$r_a$	$c_{\theta 1}$	$c_{\theta 2}$
37	0.597	0.356	0.559	0.304	0.572
38	0.660	0.436	0.487	0.226	0.300
39	0.622	0.387	0.410	0.157	0.241
40	0.770	0.593	0.681	0.594	0.488
41	0.621	0.386	0.386	0.131	-0.135
42	0.680	0.462	0.474	0.422	0.200
43	0.735	0.540	0.541	0.608	0.276
44	0.405	0.164	0.210	0.485	0.082
45	0.635	0.403	0.587	0.514	0.257
46	0.762	0.581	0.587	0.631	0.476
47	0.603	0.364	0.407	0.480	0.035
48	0.405	0.164	0.169	0.300	-0.196
49	0.382	0.146	0.313	-0.099	0.311
50	0.645	0.416	0.471	0.378	0.035

Friedman Two-way ANOVA:

$$r_a^2 \text{ vs } c_{\theta 1} \text{ vs } c_{\theta 2} \quad \chi_r^2 = 6.76, p < 0.05$$

$$c_a^2 \text{ vs } c_{\theta 1} \text{ vs } c_{\theta 2} \quad \chi_r^2 = 2.44, \text{ n.s.}$$

Wilcoxon Matched Pairs Test:

$$r_a^2 - c_{\theta 1} \quad T = -320.5, z = 3.06, p < 0.01$$

$$r_a^2 - c_{\theta 2} \quad T = -260.5, z = 3.64, p < 0.001$$

$$c_{\theta 1} - c_{\theta 2} \quad T = -548.0, z = 0.864, \text{ n.s.}$$

values of  $c$ , since  $r \geq r (\cos \mu - m) = c$ . Thus the square of  $r$  will also be larger on the average than the values of  $c_\theta$ . Single sequence tests of the menotactic hypothesis based on this relationship should therefore be restricted to situations where the sample is very large, that is, where  $m_\alpha$  is close to  $\mu_\alpha$  and hence both  $r_\alpha$  and  $c_\alpha$  are close to  $\mu_\alpha$ .

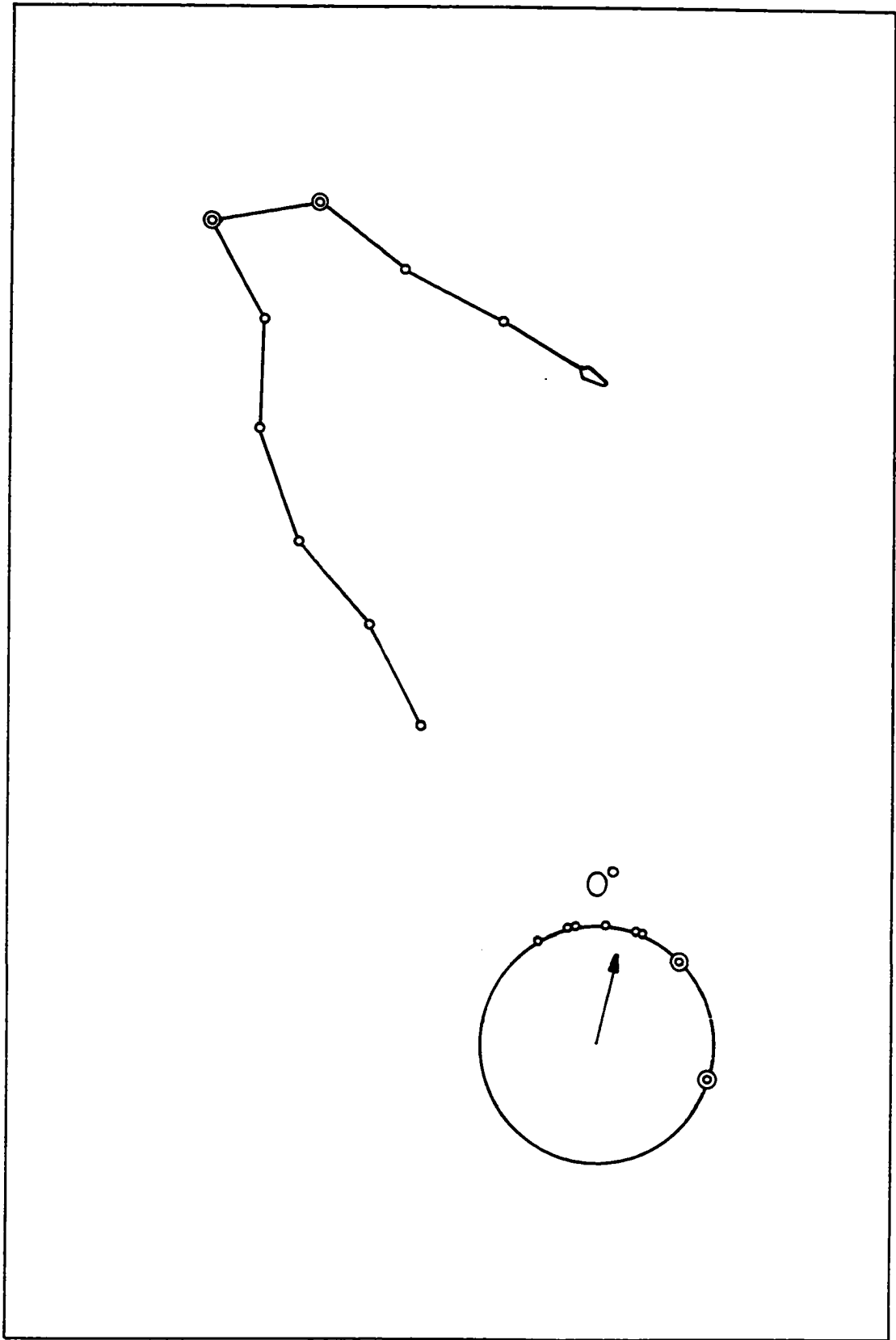
Small samples, however, still suffice in screening for discontinuities if only the turns are considered. As indicated in the table, the equality of  $c$  between the two orders of turns does not appear to be affected by their lack of independence. Also unaffected would be the more basic prediction that turns of a menotactic series should always be symmetrically distributed about  $0^\circ$ . If anything the zig-zagging introduced by sequential sampling should contribute to this feature, making tests for unbiasedness very conservative. Even the large change in target heading illustrated in Figure 5.8 results in only a small shift in  $m_\theta$  away from  $0^\circ$ . Since such conservatism seems wise in screening samples for the likely presence of discontinuities, tests for unbiased turning, both in the first- and second-order samples of turns, were what I used in this study.

Suitable tests abound in the literature on orientational analysis (see Batschelet, 1965, 1972, 1981; and Mardia, 1972, for a general discussion). The specific ones I employed were the following.

- (1) The V-test. This simple non-parametric test is used to check the null hypothesis that there is no concentration of values (turns in this case) towards a particular heading (here equal to  $0^\circ$ ). Significant results indicate a general concentration within the semi-circle centered on the chosen heading. It



**FIGURE 5.8** The effects of unbalanced changes in target heading on the distribution of turns in a menotactic sequence. Even two fairly large turns affect the mean heading only slightly.



is thus not a direct test of the hypothesis that  $0^\circ$  is the actual mean heading, but serves as a useful precursor; it requires only a minimum of five sample values. Insignificance is usually attributed to the sample's being random, but alternatively there could be some modal value other than the predicted mean heading, or the sample could have its actual mean where expected but with the value of  $c_\theta$  too low to differ noticeably from zero. Useful back-up procedures in these situations employ the less specific Rayleigh Test to examine both the sample of step azimuths (if the process is menotactic then  $r_\alpha$  might differ significantly from zero whereas  $c_\theta$  - or,  $r_\alpha^2$  - may not) and the sample of turns (in case the concentration of values is not where expected).

(2) Stephens' Test of the Mean Direction. When a sample has been found to show a concentration of values towards the predicted heading, the next step, logically, would be to see whether that direction is indeed the mean. Stephens' is one of many parametric tests designed for this purpose; they are particularly appropriate for menotactic samples, where a wrapped bell-shaped distribution of turns is usually expected. The main attraction of this particular test is the existence of nomographs (in Batschelet, 1965) that allow rapid evaluation of the significance of the findings. Again, only a small sample size is needed (the exact number varies).

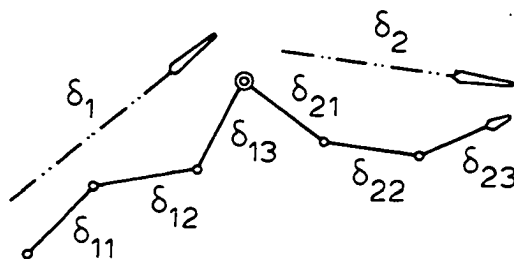
(3) Watson's Goodness of Fit Test. When the samples of turns are fairly large, then a test of how well they fit a Von Mises Distribution, with mean direction equal to  $0^\circ$  is an especially sensitive one for the hypothesis of menotaxis; the

samples of turns can here be evaluated not only for their mean direction, but also for their symmetry and general bell-shaped conformation. Watson's Test is a Smirnov-type test for circular data and thus detects any sort of departures from the predicted features. While only samples of six values are required for this test, I only employed it for much larger samples.

In theory, these tests can be applied to samples of turns of any order. As long as the first order turns are unbiased, then so will all higher orders. When discontinuities are present, on the other hand, the higher-order turns will be more sensitive to their biasing effects. As shown in Figure 5.9, a single change in target will effect only a single first-order turn, but two second-order, three third-order, and so on. Thus, any independently selected sample of higher-order turns will be more likely to capture the effects of the discontinuity than a comparable sample of lower-order turns. Furthermore, if all turns of a particular order are pooled over the sequence, then the effects of a given discontinuity within a sample will be magnified with each increase in the order of the turns.

In practice, I used samples of both the pooled first- and second-order turns from a given sequence to look for signs of discontinuities. Sequences that showed signs of biased turning in the first-order samples I set aside for later comparison to either the random or biased-correlated walks. Those that passed the first screening were then examined with respect to their second-order turns. Any samples passing this step I considered homogeneous as could be determined. Any that failed I treated as possessing discontinuities of some sort, although not necessarily the same as those that failed

**FIGURE 5.9** Effects of a discontinuity on samples of turns in a menotactic sequence. The higher-order arrows indicate top level headings which in this case are unknown to the observer; their influences, thus, get added to those of the deflections at the level lower down (the change in targets goes undetected). Among the first-order turns, only one turn is affected (underlined); in the other first-order turns the higher-level effect cancels out. Likewise, among the second- and third-order turns, two and three turns are affected respectively.



### Azimuths

$$\alpha_{11} = \delta_1 + \delta_{11}$$

$$\alpha_{12} = \delta_1 + \delta_{12}$$

$$\alpha_{13} = \delta_1 + \delta_{13}$$

$$\alpha_{21} = \delta_2 + \delta_{21}$$

$$\alpha_{22} = \delta_2 + \delta_{22}$$

$$\alpha_{23} = \delta_2 + \delta_{23}$$

### 1st-order Turns

$$\begin{array}{l} \delta_1 + \delta_{12} - \delta_1 - \delta_{11}^* \\ \delta_1 + \delta_{13} - \delta_1 - \delta_{12}^{**} \\ \delta_2 + \delta_{21} - \delta_1 - \delta_{13}^* \\ \delta_2 + \delta_{22} - \delta_2 - \delta_{21}^{**} \\ \delta_2 + \delta_{23} - \delta_2 - \delta_{22}^* \end{array}$$

### 2nd-order Turns

$$\begin{array}{l} \delta_1 + \delta_{13} - \delta_1 - \delta_{11}^* \\ \delta_2 + \delta_{21} - \delta_1 - \delta_{12}^* \\ \delta_2 + \delta_{22} - \delta_1 - \delta_{13}^{**} \\ \delta_2 + \delta_{23} - \delta_2 - \delta_{21}^{**} \end{array}$$

### 3d-order Turns

$$\begin{array}{l} \delta_2 + \delta_{21} - \delta_1 - \delta_{11}^* \\ \delta_2 + \delta_{22} - \delta_1 - \delta_{12}^* \\ \delta_2 + \delta_{23} - \delta_1 - \delta_{13}^* \end{array}$$

\* } alternate independent samples  
\*\* }

the first screening; they were not pooled with the earlier failures. These procedures appeared to be the best possible that would still keep the sequences as short as possible. Only seven-step sequences were required (and even these proved to be not short enough).

Wherever I could obtain large samples of first- and second-order turns, I felt justified in taking their analysis yet one step further, to test more specifically the hypotheses of correlated or menotactic walks. This analysis requires fairly good estimates of the value of  $\rho_{\theta k}$  for the two orders of turns, something not obtainable in just seven-step sequences. Although ideally the samples used in these tests should be acquired through use of independent, random sampling, as described previously, in practice I simply pooled all first- and second-order turns available. Any lack of independence within any one of the smaller samples or between those of the first- and second-order turns for a given sequence, I hoped would be lost in the very large numbers of turns making up the combined samples.

The basis for these tests lies in the relationships between  $\rho_{\theta k}$  and  $\rho_{\theta 1}$  described in Section IV. C. For menotaxis this relationship is simply,

$$\rho_{\theta k} = \rho_{\theta 1}$$

and for an unbiased correlated walk,

$$\rho_{\theta k} = \rho_{\theta 1}^k$$

Given estimates of  $\rho_{\theta 1}$  and  $\rho_{\theta k}$ , it should then be fairly easy to distinguish between these two possibilities, especially when high values of  $k$  are used (but even second-order turns provide a sufficient

basis for the test when the sample sizes are large).

For unbiased walks, the distribution of second-order turns (and higher) can be well fit by the Von Mises Distribution, even when the distribution of the deflections themselves has a markedly different form; hence parametric tests may be employed in their analysis. Since, furthermore, their mean directions will always be equal to zero (by definition), the single most appropriate test to use for the above relationships is Stephens' Test of the Concentration Parameter when the Mean Direction is Known (Stephens, 1969; Mardia, 1972). This test looks simply at the observed value of  $c_0$  for a sample of turns, comparing it directly to an expected value; no extra uncertainties are added by having to estimate other parameters of the distribution.

This is the same test I mentioned above as being suitable for examining the relationship between  $\rho_\delta$  and  $\rho_0$  for menotactic series. However, since applying the same sort of test to the samples of turns produces equivalent results and can be used in more situations, this approach is the one I adopt here. It can be used not only for unbiased correlated walks, but also for menotactic samples from series not all possessing the same (or even known) target headings

It should be noted, however, that it is limited only to unbiased walks; biased correlated walks produce samples of turns (of any order) that depart too far from symmetry about the mean, the least requirement for a parametric approach. There is, on the other hand, a non-parametric method for both biased and unbiased walks. First, for menotactic series, it should be recalled that all orders of turns have the same expected distribution. A test that compares the frequencies across any two such samples therefore provides an appropriate test of



the hypothesis of menotaxis. It examines not only the relationship between the values of  $c$ , but all other parameters besides. Watson's Two Sample Test (Watson, 1962; Batschelet, 1965) takes just this sort of omnibus approach, although of course it sacrifices the ability to pin down exactly what the nature of any departures might be.

A similar comparison can be used to test the hypothesis of a correlated walk, whether biased or unbiased, but by way of a more round-about approach: first the sample of first-order turns must be used to generate an expected distribution for the second- (or higher-) order turns. This can be done simply by modifying the algorithm described in Section IV. E, substituting sums for the differences determined in step 2; in a correlated walk, second-order turns are expected to have the same probabilities as the sums of first-order turns. Once the expected distribution is obtained, then the comparison using Watson's Two Sample Test can be carried out as above.

#### **V.D. Mean Squared Distance Analysis of Samples of Artificially Determined Walks**

A single route composed of arbitrarily defined steps might in some cases be both long enough and sufficiently homogeneous for the methods described in the preceding section to decide whether or not the entire string of steps corresponds to either a correlated or menotactic walk. More often than not, however, the route will contain what appear to be discontinuities, i.e., changes in orientational targets (either tactic or atactic). This situation necessitates breaking the sequence down into smaller fragments for analysis, some of which might be sufficiently homogeneous. The homogeneity of each fragment can be checked in a preliminary way as described in the last section.

Once a sample of homogeneous sequences has been obtained, mean squared distance (MSD) analysis is in some ways the best choice for testing hypotheses about the processes that govern the routes. Not only does it consider distance information ignored by the previous, strictly directional tests, but it also looks more closely at the cumulative effects of turning. Whereas the relationship between two different orders of turns captures a part of those effects, MSD analysis examines the effects contained within all orders of turns within the sequences.

Consider for example a spatially constrained "random" walk. Based on the relationships among the turns alone, this process is indistinguishable from a true random walk. All orders of turns are alike in having a nonexistent mean vector, and analysis of the turns alone would not even reveal the existence of the spatial discontinui-

ties (representing the contacts made with the boundaries to movements). With MSD analysis, on the other hand, there is no problem in identifying this type of process; as the number of steps in a series increases, the corresponding mean squared distance of travel will eventually reach a horizontal asymptote, clearly indicating the presence of limits to outward movement.

A key point in the above example is that constraints show up only after a number of steps have been traversed; in other words, the essentially cumulative effects depend on at least a minimum number of steps per walk. Chopping up a series into a large number of small fragments can serve for simple turn analyses but not for MSD analysis. As mentioned, treating a spatially-constrained random walk in that fashion would destroy the evidence for its limits.

As a compromise between maximizing the number of steps per walk or the number of walks per route, at least for arbitrarily partitioned sequences, I chose to carve out of any given route as many samples of at least seven steps as possible. Seven steps produces samples of at least five second-order turns, the minimum needed for some of the tests described in the preceding section. These samples, thus, can be looked at both by methods that examine single sequences or by those that consider several. The two approaches complement one another.

Both approaches may in fact be required even where the sample size is not limiting. MSD analysis, at least in its current state of development, has some weaknesses relative to those of pure turn analysis. Specifically, tests of the goodness of fit of an observed series of MSD's to the expected curves under the hypotheses of correlated or menotactic walks are not as powerful as the corresponding tests for

samples of turns. Although the form of the data suggests that standard methods of regression analysis could be employed — especially for menotaxis, where the expected curves are simple parabolas — there are several problems that stand in the way.

For a correlated walk, there is first of all the difficulty in fitting any data to the complex, asymptotically-linear curve it predicts. And even if that problem could be solved (for instance, by transforming the data into a menotactic series), there are more general problems that have to do with the distribution of the observations about their means: the assumptions that data are normally distributed and homoscedastic are violated in any type of walk, tactic, atactic, or even random. Based on computer simulations, (Table 5.2) the variance increases with step length for all walks examined and in the random and correlated walks the variates do not appear to be normally distributed.

Yet another problem arises if, as is usual (Gail and Boone, 1970; Hall, 1977), the observed sequences are used to provide data points at more than one step number; the data will then be serially-correlated. This sampling problem once again violates the assumption of independent random sampling upon which regression, as well as most other statistical tests, are based.

Of course this problem can be alleviated, at a cost of sample size, by simply measuring only one length per sequence. The other problems of heteroscedasticity and non-normality can possibly also be circumvented through some sort of transformation of the variates. Such solutions, however, complicate the analysis, especially in comparison to the much simpler and direct analyses of turn samples.

**TABLE 5.2 STATISTICS FOR SQUARED DISTANCES OF TRAVEL FROM SIMULATED RANDOM, CORRELATED, AND MENOTACTIC WALKS; TESTS FOR NORMALITY**

**A. Random Walk**

Step <sup>1.</sup> #	m	e <sup>2.</sup>	var	e <sup>3.</sup>	g <sub>1</sub> <sup>4.</sup>	g <sub>2</sub> <sup>5.</sup>
2	1.62	2	1.8	2	0.37	-1.39
4	4.59	4	16.0	12	0.86***	-0.34
6	6.35	6	32.5	30	1.01***	0.22
8	6.90	8	41.2	56	1.71***	2.90***
10	9.38	10	63.2	90	1.10***	1.04***
15	14.64	15	234.5	210	2.28***	7.22***
20	19.43	20	321.3	380	1.79***	4.92***
25	22.53	25	539.9	600	1.75***	3.66***

1. 100 different sequences were averaged at each step; there is no serial correlation to contend with among these data
2. Expected value for the mean equals the number of steps, n
3. Expected value for the variance equals  $n(n - 1)$
4. Skewness statistic as given in Sokal and Rohlf (1981); I used the t-test to see how well the observed value matched its expectation under the hypothesis that the distribution is normal
5. Kurtosis statistic as given in Sokal and Rohlf; the t-test was also used to test the significance of this value

\* Significant at the 0.05 level of significance

\*\* Significant at the 0.01 level

\*\*\* Significant at the 0.001 level

TABLE 5.2 CONTINUED

B. Correlated Walk; the deflections for these walks were drawn from a semi-circular distribution with mean direction equal to  $0^\circ$  (see Table 5.1)

Step #	m	e <sup>1.</sup>	var	g <sub>1</sub>	g <sub>2</sub>
2	3.34	3.27	0.4	-0.81***	-0.75
4	10.04	9.91	9.6	-0.59*	-0.43
6	17.63	17.91	60.0	-0.13	-0.80
8	28.40	26.45	212.2	-0.36	-0.96*
10	34.60	35.20	459.5	0.24	-0.88
15	56.40	57.37	1733.3	0.61*	-0.58
20	74.02	79.62	4358.9	0.89***	-0.37
25	102.17	101.87	8490.7	1.18***	0.72

C. Menotactic Walk; the series of deflections used in this model were the same as for the correlated walk

Step #	m	e <sup>2.</sup>	var	g <sub>1</sub>	g <sub>2</sub>
2	2.80	2.80	1.3	-0.74**	-0.89
4	8.14	8.81	13.6	0.27	-0.71
6	17.58	18.02	42.6	0.17	-0.85
8	28.89	30.45	75.1	0.03	-0.44
10	46.86	47.07	141.3	0.37	-0.16
15	96.08	99.17	599.5	-0.14	-0.58
20	171.68	172.31	1650.6	-0.09	-0.19
25	266.98	265.49	2522.8	0.31	-0.35

1. Expected value as calculated using R. L. Hall's (1977) equation
2. Expected value as calculated using the menotactic equations presented in Chapter IV

There is still one other way around these difficulties. The various problems mentioned have mainly to do with samples of individual data points; their means, in contrast, much more reliably fit the assumptions. According to the Central Limit Theorem, no matter what distribution the variates obey, their sample means are expected to conform to the Normal Distribution, the bigger the samples, the better the fit.

Thus a regression analysis of the means of several different sequences is more appropriate than an analysis of all their separate data points. Neither the problems associated with non-normality or serial-correlation might be important in this case, although heteroscedasticity is still likely to exist. Another reasonable approach would be to examine the mean squared distance at only one step number and compare a sample of means to the expected value using the standard t-test (it should be noted that this suggestion differs from the approach used by Peterson and Noble, 1972, where samples of individual variates were used in a t-test). Alternatively, non-parametric methods could be used to look for biases in the distribution of sample means relative to their expected value. Either of these last two methods should be relatively free of the problems associated with heteroscedasticity as well as serial-correlation and non-normality.

One final problem concerns the power of either MSD or simple turn analysis to detect processes other than menotactic or correlated walks. As shown in Figure 5.10, both telotaxis and anti-telotaxis look remarkably like a menotactic walk, at least based on the information provided by the observed turns and step lengths in a series.

**FIGURE 5.10** Comparison of the mean squared distances of travel for simulated menotactic, telotactic, and anti-telotactic sequences with predictions generated by the menotactic and correlated walk hypotheses. Each observed datum represents the mean of twenty different runs; each type of walk was subjected to the same series of deflections for a given level of deflectivity:

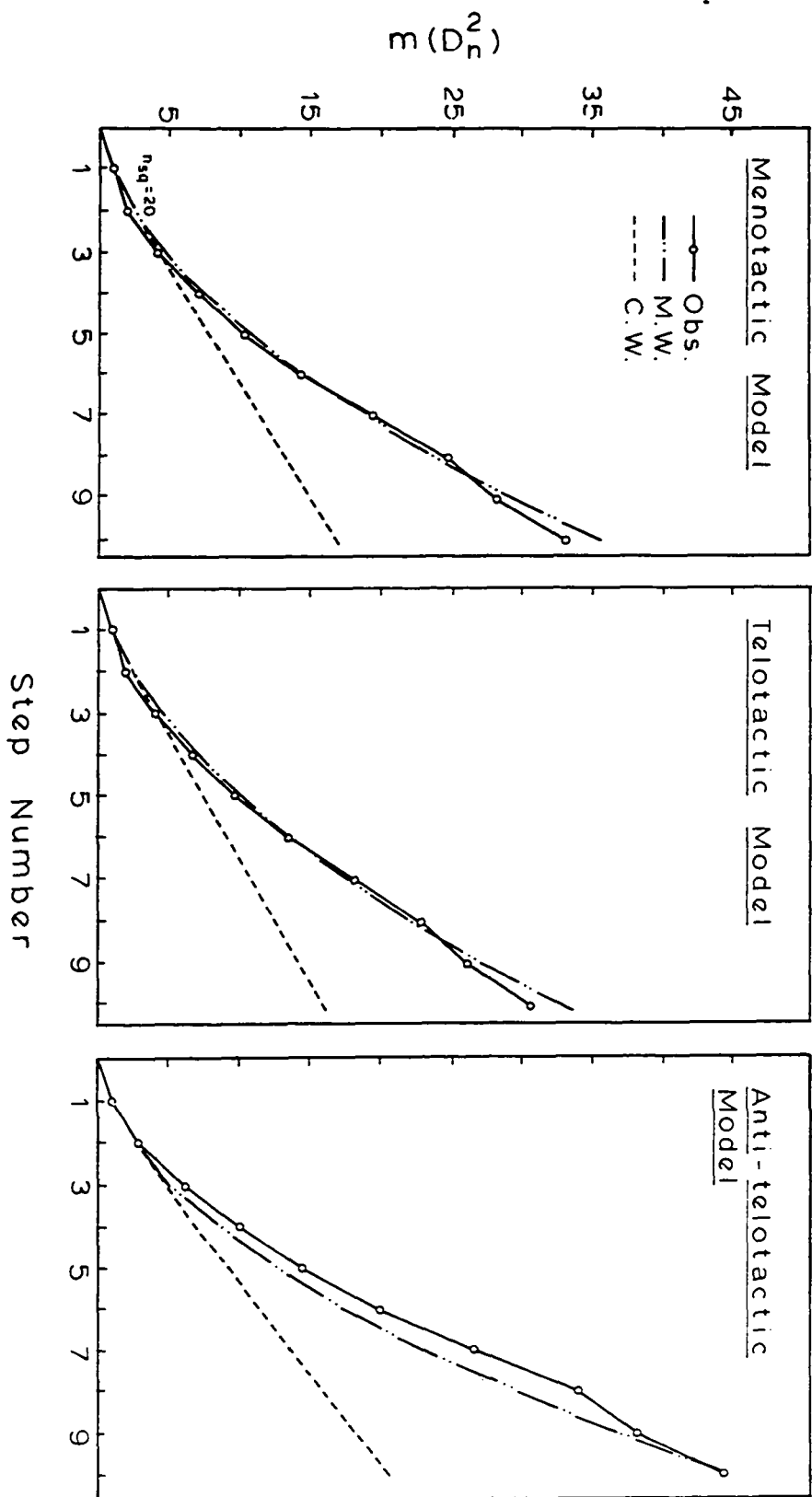
a.  $r_{\delta} = 0.52$

b.  $r_{\delta} = 0.65$

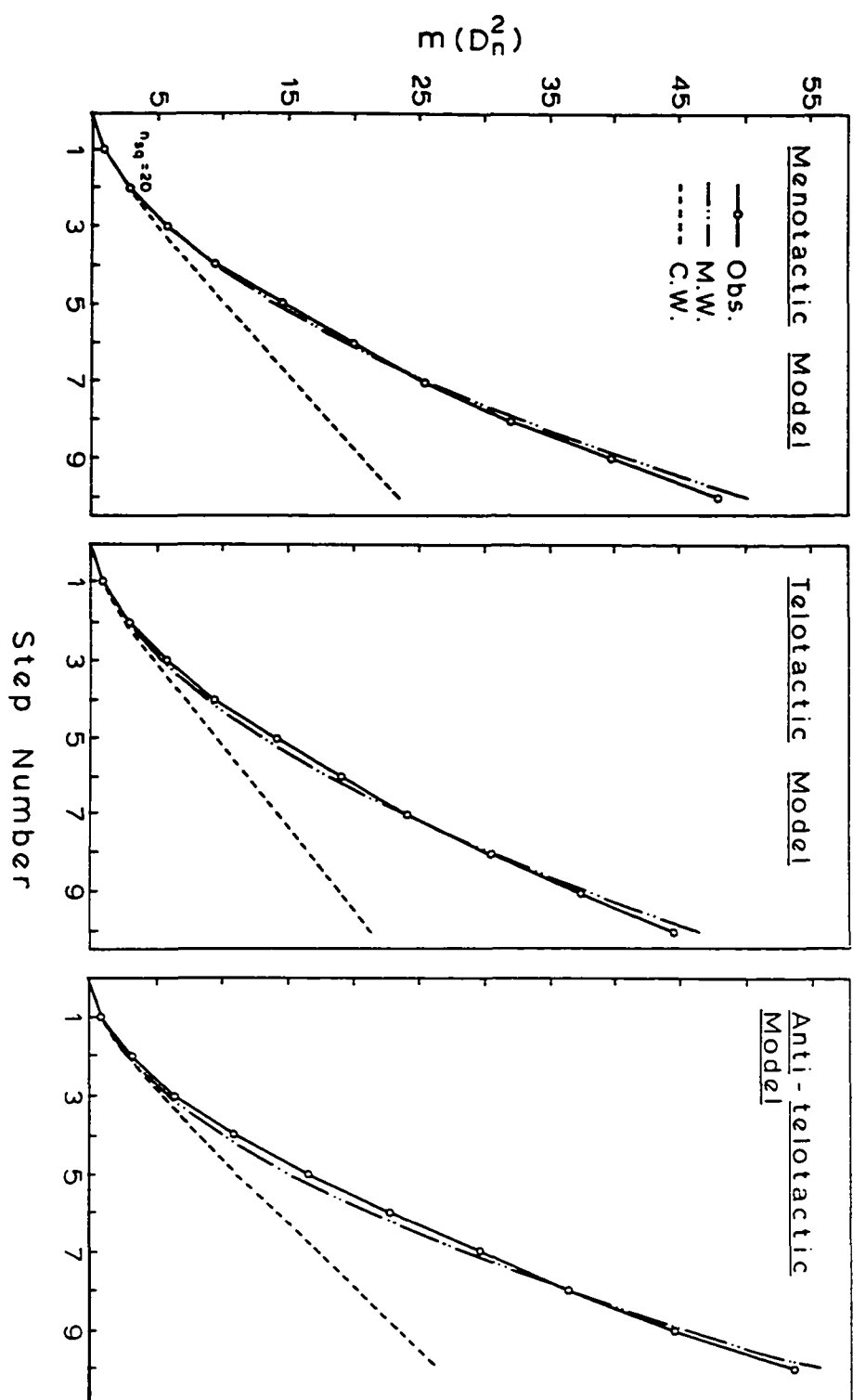
c.  $r_{\delta} = 0.84$



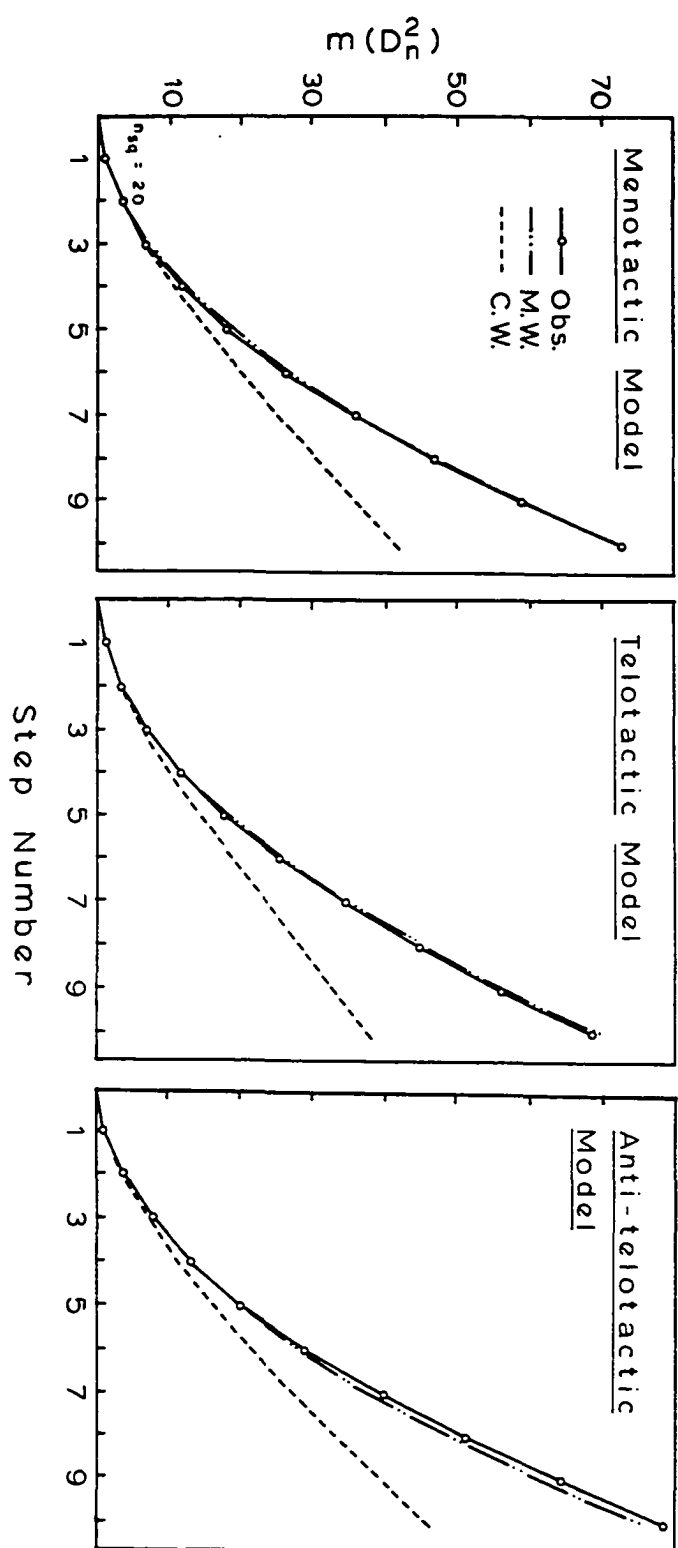
a. Responses of Different Taxes to the Same Series of Deflections;  $r_g = 0.52$



b.  $r_g = 0.65$



c.  $r_g = 0.84$



Of course, if something were known in advance about the actual deflections, then these processes would be easily revealed by their differences in turning behavior from menotaxis: for telotaxis, the turns would be more spread out and the MSD's shorter than expected, whereas for anti-telotaxis the reverse would be true. Without that information, however, there may be no current test available that can distinguish these different models. One possible procedure is to look for trends in the turning magnitudes over a sequence of steps, trends that would not be expected for either a stationary menotactic or correlated walk. In the cases of both telotaxis and anti-telotaxis, the turns should increase in magnitude. In other processes, still other sorts of trends might be expected.

## **CHAPTER VI. RESULTS**

#### VI. A. Analysis of the 25-Foot Partition

As described in Chapter II, constraints on the surveying methods set the basic step length at 25 feet (7.6 m). Although arbitrary, this length seemed nonetheless reasonable for capturing details of the movements at the scale of the residency patterns. As shown in Table 6.1, on the average, seven or more such steps make up a day range. For walks lasting on the order of entire days or longer — the level of events usually associated with residency patterns — the 25-ft partition thus usually supplies the minimum length sequences needed for the sort of statistical analysis described in the last chapter.

Inspection of the thread traces further suggested that a 25-ft step is already long compared to any true deflections it comprises, such as wobbles from micro-detours, adjustments for course errors, or the pursuit of food items. In other words, there did not seem to be any significant sharing of deflectional events between the steps; any discontinuities appearing in these series are thus more likely to indicate changes in target at some level higher than that represented by the basic steps.

Analysis of entire samples. Table 6.2 presents the summary statistics for the overall samples of azimuths and turns collected for each turtle. Examination of the relationship between the values of  $r_a$  and  $r_\theta$  immediately rules out any hope that these routes might correspond to homogeneous menotactic series: the values of  $r_\theta$  are all obviously much higher than predicted by the square of the values of  $r_a$ .

**TABLE 6.1 NUMBER OF 25 FOOT STEPS TRAVELED PER DAY**

Class	No. of Steps Within Days	No. Days*	Steps/Day**
Residents	2245	330	6.80
Transients	698	76	9.18
Experimentals	501	41	12.22
Total	3444	447	7.70

\* Only days with known endpoints are included.

\*\* These averages are underestimates of normally occurring behavior since long day-ranges are more subject to premature ending by the turtles' becoming tethered or breaking free.

**TABLE 6.2 STATISTICS FOR THE OVERALL SAMPLES OF AZIMUTHS AND TURNS**

Turtle	Azimuths			Turns		
	n	m <sub>α</sub>	r <sub>α</sub>	n	m <sub>θ1</sub>	r <sub>θ1</sub>
<b>Residents:</b>						
1	259	246	0.14	254	356	0.68
4	460	340	0.05	451	358	0.64
7	691	355	0.02	687	4	0.58
8r	150	191	0.14	147	3	0.68
9	561	22	0.08	553	1	0.61
10	814	74	0.07	807	358	0.53
16	462	105	0.10	461	3	0.39
26	310	32	0.02	307	358	0.62
<b>Transients:</b>						
2	117	254	0.19	114	0	0.80
8tr	303	87	0.79	296	0	0.84
11	57	211	0.51	56	11	0.72
12	81	253	0.55	79	357	0.84
14	37	137	0.56	35	356	0.78
17	56	353	0.64	55	354	0.89
23	77	0	0.82	76	1	0.84
27	47	331	0.62	46	5	0.75
<b>Experimentals:</b>						
X1	23	291	0.80	22	3	0.78
X2	97	277	0.23	96	2	0.78
X15	141	291	0.62	140	358	0.78
X16	76	8	0.52	75	1	0.58
X17	101	125	0.72	100	357	0.79
X18	31	149	0.81	30	5	0.83
X19	104	107	0.67	103	1	0.79



On the other hand, the series equally fail to match the expectations for simple, unbiased correlated walks (Table 6.3). In all but two cases, the samples of second-order turns have values of  $r_{02}$  greater than  $r_{01}^2$ , contrary to the predictions of this hypothesis. There is, of course, still the possibility that the walks might be correlated but biased, but examination of the mean vectors for the samples of both orders of turns makes this hypothesis also seem unlikely.

There remain two additional possibilities: the routes are governed by some form of tactic or atactic processes other than the ones suggested above, or the routes are punctuated by discontinuities. While there is little hope of making much more progress if the first turns out to be true, the problems posed by the second can be addressed by dividing the routes into smaller series, as was suggested in the preceding chapter.

Analysis of the day-ranges. Even in purely telemetric studies, it is not always necessary to rely solely on arbitrary partitioning schemes. In most tracking studies in which the subjects are monitored continuously, it is usually possible to plot significant halts in movement, especially between daily activity cycles. My study was no exception in this regard; even when I did not actually see a turtle burrowed in for the night, I frequently was able to find traces of their form-sites for several days after they had been vacated.

Before resorting to an arbitrary division of the routes into "walks", I decided to see if these natural punctuations in the temporal patterns of movement corresponded to discontinuities in the spatial patterns as well. The next step would then be to see whether or

**TABLE 6.3 STATISTICS FOR THE OVERALL SAMPLES OF SECOND ORDER TURNS**

Turtle	n	m <sub>02</sub>	r <sub>02</sub>	r <sub>01</sub>	r <sub>01</sub> <sup>2</sup>
<b>Residents:</b>					
1	248	354	0.53	0.68	0.46
4	443	354	0.44	0.64	0.41
7	683	4	0.39	0.58	0.34
8r	144	9	0.53	0.68	0.46
9	532	0	0.43	0.61	0.37
10	793	342	0.43	0.53	0.28
16	460	357	0.15	0.39	0.15
26	257	4	0.47	0.62	0.38
<b>Transients:</b>					
2	110	357	0.66	0.80	0.64
8tr	289	0	0.77	0.84	0.71
11	55	20	0.55	0.72	0.52
12	85	357	0.72	0.84	0.71
14	33	359	0.72	0.78	0.61
17	54	348	0.82	0.89	0.79
23	75	4	0.82	0.84	0.71
27	45	11	0.69	0.75	0.56
<b>Experimentals:</b>					
X1	21	1	0.60	0.78	0.61
X2	95	2	0.61	0.78	0.61
X15	139	0	0.68	0.78	0.61
X16	74	6	0.39	0.58	0.34
X17	99	353	0.67	0.79	0.62
X18	29	5	0.84	0.83	0.69
X19	102	3	0.69	0.79	0.62

not the separate day-ranges now constitute homogenous sequences. The question is whether the discontinuities suspected in the routes only occur at the breaks between days or also occur within the day-ranges.

This analysis produced a lucky break! In Table 6.4, it can be seen that in all but one case (when the sample size was quite small), the turns between the steps leading into and out of the form sites are much more scattered than are the overall samples of turns. The abrupt nature of this change in magnitude of turning was also clearly evident in the thread traces. This sudden alteration in behavior can be demonstrated quantitatively by a comparison (Table 6.5) between the form-site turns and the two turns to either side of them, i.e., the last and first within-day turns. Quite clearly, the form-site turns are the more scattered (their values of  $r_0$  are much smaller).

The comparison between the last within-day turns and the form-site turns is especially interesting. If the turtles were simply being deflected to a greater than normal degree as a part of selecting an appropriate stopping point for the night, this behavior would show up more in the last within-day turns than in the between-day turns. Upon leaving the form the next day, the turtle would then be expected to make, if the route is still homogeneous, a compensatory turn roughly similar in magnitude to the final turn of the preceding day (assuming the process is not a simple correlated walk, as has already been demonstrated). That the form-site turns are typically greater in magnitude is evidence that a actual change in target heading has occurred between days. The form-sites, thus, seem to mark true points of discontinuity within the route processes. They divide the walk(s) of one day range from those of the next.

**TABLE 6.4    TURNS MADE AT THE FORM-SITES COMPARED TO THE REMAINDER OF  
THE OVERALL SAMPLES OF TURNS**

Turtle	Form-sites			Remainder		
	n	m <sub>θ</sub>	r <sub>θ</sub>	n	m <sub>θ</sub>	r <sub>θ</sub>
<b>Residents:</b>						
1	36	0	0.26	218	356	0.75
4	27	19	0.21	424	358	0.67
7	39	84	0.24	648	3	0.61
8r	15	5	0.55	132	3	0.69
9	49	126	0.09	504	355	0.72
10	71	359	0.11	736	0	0.57
16	35	135	0.08	426	2	0.43
26	33	17	0.28	274	357	0.66
total	305	29	0.13	3362	359	0.61
<b>Transients:</b>						
2	10	325	0.54	104	2	0.83
8tr	22	336	0.51	274	1	0.87
11	3	310	0.96	53	15	0.74
12	4	357	0.67	75	357	0.85
14	4	331	0.60	31	358	0.81
17	5	316	0.81	50	357	0.92
23	13	352	0.51	63	2	0.91
27	3	97	0.62	43	2	0.80
total	64	337	0.52	693	1	0.85
<b>Experimentals:</b>						
X1	0	-	-	0	-	-
X2	5	4	0.69	91	2	0.78
X15	5	359	0.66	135	358	0.78
X16	8	18	0.31	67	0	0.61
X17	8	335	0.51	92	358	0.82
X18	1	354	1.00	91	358	0.82
X19	5	200	0.30	98	1	0.84
total	32	354	0.39	534	0	0.78

**TABLE 6.5 COMPARISON OF THE FORM-SITE TURNS TO THE FIRST AND LAST WITHIN-DAY TURNS**

Turtle	Within-days						Form-sites		
	n	First		n	Last		n	m <sub>0</sub>	r <sub>0</sub>
		m <sub>0</sub>	r <sub>0</sub>		m <sub>0</sub>	r <sub>0</sub>			
<b>Residents:</b>									
1	33	346	0.73	33	355	0.76	36	0	0.26
4	22	8	0.75	23	25	0.58	27	19	0.21
7	37	345	0.49	33	345	0.56	39	84	0.24
8r	12	343	0.71	11	23	0.66	15	5	0.55
9	14	46	0.59	44	2	0.58	49	126	0.09
10	59	0	0.58	59	350	0.69	71	359	0.11
16	52	6	0.37	34	19	0.68	35	135	0.08
26	24	335	0.62	29	354	0.47	33	17	0.28
total	258	356	0.54	266	1	0.61	305	29	0.13
<b>Transients:</b>									
2	10	16	0.93	12	353	0.90	10	325	0.54
8tr	18	10	0.76	21	23	0.74	22	336	0.51
11	3	42	0.83	3	25	0.77	3	310	0.96
12	5	2	0.85	5	4	0.88	4	357	0.67
14	4	338	0.88	4	359	0.87	4	331	0.60
17	4	354	0.97	5	5	0.91	5	316	0.81
23	8	350	0.92	8	14	0.92	13	352	0.51
27	2	225	0.11	3	345	0.94	3	97	0.62
total	54	5	0.80	61	9	0.82	64	337	0.52
<b>Experimentals:</b>									
X1	0	-	-	0	-	-	0	-	-
X2	4	18	0.95	4	344	0.54	5	4	0.69
X15	5	357	0.93	5	19	0.81	5	359	0.66
X16	9	341	0.50	8	356	0.82	8	18	0.31
X17	8	329	0.81	7	29	0.79	8	335	0.51
X18	2	7	0.96	1	332	1.00	1	354	1.00
X19	6	355	0.63	5	356	0.58	5	200	0.30
total	34	350	0.71	30	6	0.71	32	354	0.39

While the exact nature of these changes that occur between days can only be assessed at a higher level in the analysis, it is worthwhile at this point to note the differences that separate the three classes of turtles with regard to their behavior at the form-sites. The Residents appear to be much more radical in their between-day turning tendencies than the other two classes. In fact, their samples do not differ greatly from random. Table 6.6 presents the results of applying the Rayleigh and V-Tests to these data. Only two Residents showed any significant concentration of values towards  $0^{\circ}$  (as indicated by the results of the V-Test) and none showed a concentration towards some other point around the circle (indicated by the results of the Rayleigh Tests).

The Transients, in contrast, all appear to have decidedly non-uniform samples; all samples large enough to be tested showed significant concentrations of values, and even the smaller samples clearly have large values for  $r_0$ . While the results for the Experimentals are more equivocal, they are all based on small samples. When the three classes were compared using the Mann-Whitney U Test, no significant difference was found between the Transients and Experimentals, while both were different from the Residents (Table 6.7).

This picture is somewhat muddled when only the initial series of steps taken by the Residents is used in the comparison. In trying to see whether Residents were different from the very first observations, I examined their initial 85 steps separately from the rest of their samples. This number was chosen because of its close match to the average number available for the other two groups, 88 steps. As can be seen in Table 6.8., these samples do not differ as significantly

**TABLE 6.6 TESTS FOR THE CONCENTRATION PARAMETERS OF THE FORM-SITE TURNS**

Turtle	n	$r_{\theta}$	$c_{\theta}$	V Test <sup>1.</sup>	Rayleigh Test <sup>2.</sup>
<b>Residents:</b>					
1	36	0.26	0.26	$p < 0.05$	n.s.
4	27	0.27	0.20	n.s.	n.s.
7	39	0.24	0.03	n.s.	n.s.
8r	15	0.55	0.55	$p < 0.01$	$p < 0.01$
9	49	0.09	-0.05	n.s.	n.s.
10	71	0.11	0.11	n.s.	n.s.
16	35	0.08	-0.06	n.s.	n.s.
26	33	0.28	0.27	$p < 0.05$	n.s.
total	305	0.13	0.11	$p < 0.01$	$p < 0.01$
<b>Transients:</b>					
2	10	0.54	0.44	$p < 0.05$	$p < 0.05$
8tr	22	0.51	0.47	$p < 0.01$	$p < 0.01$
11	3	0.96	0.62	-	-
12	4	0.67	0.67	-	-
14	4	0.60	0.52	-	-
17	5	0.81	0.58	$p < 0.05$	$p < 0.05$
23	13	0.51	0.51	$p < 0.01$	$p < 0.01$
27	3	0.62	-0.08	-	-
total	64	0.52	0.48	$p < 0.01$	$p < 0.01$
<b>Experimentals:</b>					
X1	0	-	-	-	-
X2	5	0.69	0.69	$p < 0.05$	$p < 0.05$
X15	5	0.66	0.66	$p < 0.05$	$p < 0.05$
X16	8	0.31	0.29	n.s.	n.s.
X17	8	0.51	0.46	$p < 0.05$	$p < 0.05$
X18	1	1.00	0.99	-	-
X19	5	0.30	-0.28	n.s.	n.s.
total	32	0.39	0.39	$p < 0.01$	$p < 0.01$

<sup>1</sup>  $H_0: c_{\theta} = 0$  ;  $H_a: c_{\theta} > 0$ , where  $\mu_{\theta} = 0$ .

<sup>2</sup>  $H_0: r_{\theta} = 0$

**TABLE 6.7 INTERCLASS COMPARISONS OF THE CONCENTRATION PARAMETER FOR  
THE FORM-SITE TURNS**

Kruskall-Wallis One-way Analysis of Variance:  $H = 11.9$ ,  $p < 0.01$

Mann-Whitney U Test:

Residents vs. Transients:  $U = 3$ ,  $p = 0.001$

Residents vs. Experimentals:  $U = 3$ ,  $p = 0.005$

Transients vs. Experimentals:  $U = 11$ ,  $p = 0.111$



**TABLE 6.8 COMPARISONS OF FORM-SITE TURNS BETWEEN CLASSES WHEN ONLY THE FIRST 85 STEPS OF THE RESIDENTS ARE USED**

Residents	1st 85 Steps			Remainder		
	n	m <sub>θ</sub>	r <sub>θ</sub>	n	m <sub>θ</sub>	r <sub>θ</sub>
1	12	359	0.30	24	0	0.24
4	6	69	0.13	21	12	0.24
7	3	64	0.28	36	86	0.23
9	8	172	0.57	41	56	0.08
10	14	7	0.42	57	346	0.04
16	6	321	0.58	29	138	0.22
26	11	0	0.67	22	61	0.14
total	60	2	0.26	230	57	0.10

Kruskall-Wallis One-Way Analysis of Variance (over all three classes):

$H = 4.06$ , n.s.

Mann-Whitney U Test:

Residents vs Transients:  $U = 12$ ,  $p = 0.036$

Residents vs Experimentals:  $U = 13$ , n.s.

from those of the Transients and Experimentals. A possible explanation for this is that handling a subject for the first time creates a greater than normal tendency to keep traveling the same direction between days; this only "relaxes" to a normal pattern after a period of habituation. Nonetheless, it should also be noted that the average turning tendencies for the Residents are still greater than those of the other two groups, which suggests some other difference does in fact distinguish the Residents right from the start.

An immediate difference is clearer in the within-day samples of turns. The same sort of inter-class differences, already noticeable in the overall samples presented in Table 6.2 and in the samples of the first and last within-day turns presented in Table 6.5, are just as characteristic of the complete samples of within-day turns shown in Table 6.9. Moreover, Table 6.10 demonstrates that for the majority of the Residents, their initial series of within-day turns do not differ significantly from the rest of their samples. The two exceptions, Turtles 1 and 10, that showed more concentration in their initial samples were perhaps actually transients during these sample periods. Turtle 1 was on an egg-laying trip for much of this interval, and Turtle 10's movements during the first two years I followed him were also wide-ranging and transient-like. On the other hand, Turtle 16 also appeared to be a transient when I first found her (see Figure 2.5h), but showed no appreciable difference between her initial and later samples.

The nature of these differences between classes is hard to assess. Table 6.11 indicates that the day-ranges, like the overall routes, might contain points of discontinuity: the concentration

TABLE 6.9 STATISTICS FOR THE SAMPLES OF WITHIN-DAY TURNS

					Goodness of Fit* To Circular Normal,
	No. Days	n	$m_{\theta}$	$r_{\theta}$	$\mu_{\theta} = 0^{\circ}$
Residents:					
1	36	179	358	0.769	n.s.
4	34	256	359	0.709	n.s.
7	37	245	3	0.696	n.s.
8r	11	93	5	0.727	n.s.
9	51	315	0	0.669	n.s.
10	41	325	2	0.620	n.s.
16	38	208	9	0.521	n.s.
26	24	186	358	0.720	n.s.
total	272	1807	1	0.670	n.s.
Transients:					
2	12	103	2	0.835	n.s.
8tr	20	180	3	0.868	n.s.
11	3	29	21	0.752	n.s.
12	5	74	358	0.854	n.s.
14	5	32	358	0.818	n.s.
17	5	50	355	0.937	n.s.
23	8	63	2	0.912	n.s.
27	4	42	2	0.804	n.s.
total	62	573	2	0.855	n.s.
Experimentals:					
X1	1	22	3	0.781	n.s.
X2	6	67	355	0.784	n.s.
X15	8	134	359	0.791	n.s.
X16	11	65	358	0.658	n.s.
X17	9	92	358	0.814	p < 0.05
X18	2	29	5	0.825	n.s.
X19	6	98	1	0.844	n.s.
total	43	507	359	0.788	n.s.

\* .Watson's Goodness of Fit Test.  $H_0$ : Sample does not differ significantly from the theoretical Circular Normal (von Mises) Distribution

**TABLE 6.10 COMPARISON OF RESIDENTS' WITHIN-DAY TURNS FOR DAYS OCCUR-  
RING IN THE FIRST 85 STEPS AND THOSE IN THE REMAINDER  
OF THE SAMPLE**

Turtle:	1st 85 Days			Remainder		
	n	$m_{\theta}$	$r_{\theta}$	n	$m_{\theta}$	$r_{\theta}$
1	66	2	0.870	113	355	0.712
4	54	349	0.701	202	2	0.714
7	51	4	0.659	194	3	0.706
9	42	8	0.634	273	359	0.676
10	62	358	0.750	263	3	0.590
16	63	8	0.520	145	9	0.522
26	66	354	0.735	120	0	0.713
total	404	0	0.697	1310	1	0.657

Wilcoxon Signed Rank Test (two-tailed) comparing values of  $r_{\theta}$ :  
T = -13, n.s.

**TABLE 6.11 WITHIN-DAY SAMPLES OF SECOND ORDER TURNS COMPARED TO PREDICTIONS UNDER MENOTACTIC AND CORRELATED WALK HYPOTHESES**

Turtle	n	$m_{\theta 2}$	$r_{\theta 2}$	$r_{\theta 1}^*$	$r_{\theta 1}^{2**}$
<b>Residents:</b>					
1	139	357	0.671	0.769	0.591
4	243	352	0.506	0.709	0.503
7	299	0	0.466	0.696	0.484
8r	82	10	0.612	0.727	0.528
9	276	0	0.513	0.669	0.448
10	283	4	0.381	0.620	0.384
16	176	4	0.265	0.521	0.271
26	172	0	0.555	0.720	0.518
total	1670	0	0.476	0.670	0.449
<b>Transients:</b>					
2	91	2	0.688	0.835	0.697
8tr	194	1	0.842	0.868	0.753
11	26	31	0.564	0.752	0.566
12	169	353	0.766	0.854	0.729
14	25	3	0.810	0.818	0.669
17	44	350	0.890	0.937	0.878
23	55	4	0.887	0.912	0.832
27	38	7	0.715	0.804	0.646
total	542	1	0.785	0.855	0.731
<b>Experimentals:</b>					
X1	21	1	0.603	0.781	0.610
X2	84	0	0.629	0.784	0.615
X15	101	357	0.694	0.791	0.626
X16	54	358	0.506	0.658	0.433
X17	82	355	0.732	0.814	0.663
X18	2	42	0.946	0.825	0.681
X19	92	1	0.750	0.844	0.712
total	436	359	0.672	0.788	0.621

\* The value expected for  $r_{\theta 2}$  under the menotactic hypothesis.

\*\* The value expected under the hypothesis of a correlated walk.

values for the second-order turns are again intermediate between those expected for menotactic and correlated walks.

Furthermore, there is some hint of non-stationarity in the turning behavior at both the beginnings and the ends of the day-ranges, at least among the Residents. In a comparison of Tables 6.9 and 6.5, the samples of both their first and last within-day turns seem to be more scattered than their within-day samples overall. Table 6.12 compares specifically the initial and terminal within-day turns to the remainder. Although the Wilcoxon Test indicates that only the first within-day turns of the Residents are significantly more scattered than the non-terminal samples, the same trend is reasonably evident in their final turns as well. In contrast, the samples for the Transients and Experimentals show no such findings, which again might be a sign of their overall differences from the Residents.

While the day-range samples do not clearly differentiate the classes with regard to orientational processes, number and level of discontinuities, or even deflectivity at one or more levels, they are still the only behaviorally defined samples I was able to obtain. They were also the only samples that I could attempt to correlate with aspects of the routes' context, such as weather conditions, and with behavioral indicators, such as the path lengths of the day-ranges. It seems worthwhile then to examine the day-range samples further. For simple comparative purposes, the fact that they perhaps represent mixtures of different distributions or contain minor amounts of non-stationarity does not cause any serious problems, as will be confirmed by later analyses.

**TABLE 6.12 COMPARISON OF FIRST AND LAST WITHIN-DAY TURNS TO REMAINDER OF THE SAMPLE**

Turtle	First			Last			Remainder		
	n	m <sub>θ</sub>	r <sub>θ</sub>	n	m <sub>θ</sub>	r <sub>θ</sub>	n	m <sub>θ</sub>	r <sub>θ</sub>
<b>Residents:</b>									
1	33	346	0.728	33	355	0.758	113	2	0.790
4	22	8	0.746	23	25	0.578	211	356	0.728
7	37	345	0.486	33	345	0.556	175	8	0.780
8r	12	343	0.708	11	23	0.658	257	358	0.755
9	14	46	0.594	44	2	0.581	257	358	0.698
10	59	0	0.580	59	350	0.689	207	6	0.617
16	52	6	0.369	34	19	0.683	122	6	0.544
26	24	335	0.616	29	354	0.472	133	2	0.804
total	258	356	0.545	266	1	0.611	1283	2	0.708

Wilcoxon Test comparing values of  $c_{\theta} = r_{\theta} (\cos m_{\theta})$ :

first vs remainder,  $T = -1$ ,  $p < 0.05$

last vs remainder,  $T = -5$ , n.s.

**Transients:**

2	10	16	0.931	12	353	0.900	81	1	0.819
8tr	18	10	0.765	21	23	0.737	141	0	0.910
11	3	42	0.832	3	25	0.772	23	17	0.748
12	5	2	0.846	5	4	0.877	64	357	0.853
14	4	338	0.880	4	359	0.866	24	2	0.811
17	4	354	0.972	5	5	0.911	41	354	0.939
23	8	350	0.924	8	14	0.915	55	4	0.914
27	2	225	0.113	3	345	0.942	37	4	0.844
total	54	5	0.796	61	9	0.817	458	1	0.868

Wilcoxon Test:

first vs remainder,  $T = -11$ , n.s.

last vs remainder,  $T = +16$ , n.s.

**Experimentals:**

X1	0	-	-	0	-	-	22	3	0.781
X2	4	18	0.946	4	344	0.535	59	354	0.796
X15	5	357	0.927	5	19	0.812	124	358	0.787
X16	9	341	0.503	8	356	0.825	48	1	0.664
X17	8	329	0.810	7	29	0.789	77	358	0.837
X18	2	7	0.964	1	332	1.00	26	6	0.814
X19	6	355	0.626	5	356	0.585	87	2	0.874
total	34	350	0.707	30	6	0.708	443	359	0.801

Wilcoxon Test:

first vs remainder,  $T = -3$ , n.s.

last vs remainder,  $T = -6$ , n.s.

The pooled frequency distributions for each of the three classes (Figure 6.1) are plainly symmetric, unimodal about  $0^{\circ}$ , and bell-shaped — all features expected in turning distributions if the walks are menotactic (the inclusion of discontinuities should not disrupt these features too much). Table 6.9 further confirms these findings; all but one turtle's samples do not differ significantly from the Von Mises Distribution with mean direction equal to  $0^{\circ}$ . The distribution of Turtle X17 (Figure 6.2) appears to differ only slightly from the rest, probably due to a greater asymmetry and more values near  $180^{\circ}$ .

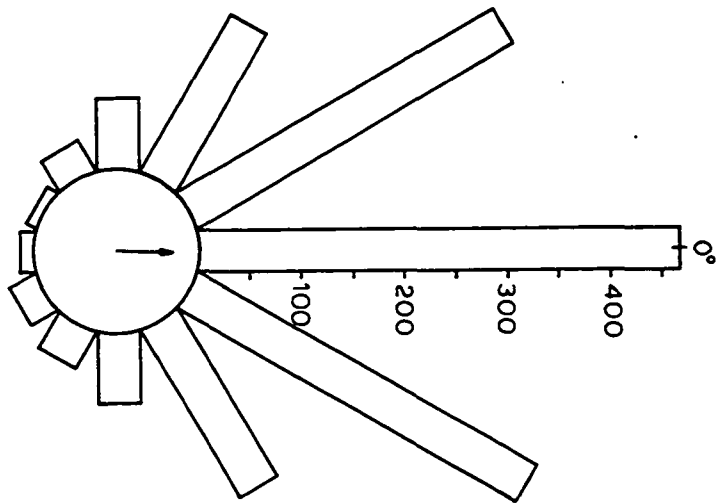
This approximation to the Von Mises Distribution is particularly useful in that it allows of parametric methods of comparison. Since the mean directions all appear to be equal to zero, by the results of Watson's Goodness of Fit Test just presented, the important differences between the samples lie solely in the concentration parameters,  $r_{\theta}$ . Appropriate tests for making comparisons between the samples are thus Mardia's Multi-sample Test of the Concentration Parameter, for examining intra-class homogeneity, and Mardia's Two Sample Test, for making pair-wise comparisons between the pooled samples for each class (Mardia, 1972). Additionally, I made use of the Kruskal-Wallis Test and the Mann-Whitney U Test (Siegel, 1956) to supplement the inter-class comparisons without resorting to the use of the pooled data.

The results of the intra-class comparisons (Table 6.13a) indicate that the Residents, but not the other two classes, are a heterogeneous assemblage. But although the Residents vary widely in the spread of their distributions, they nonetheless appear to be a natural group when compared to the other two classes, as shown in Table 6.13b.

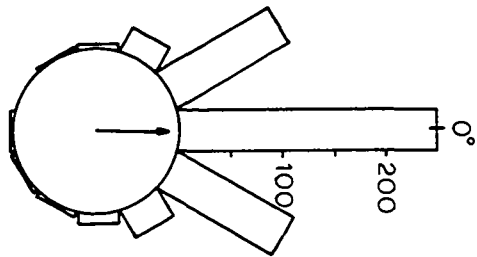


**FIGURE 6.1** Frequency distributions for the pooled samples of within-day turns. Observed values falling on the boundaries between adjacent intervals were assigned by coin toss, following Batschelet, 1965.

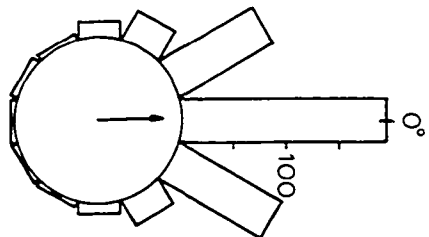
Residents



Transients



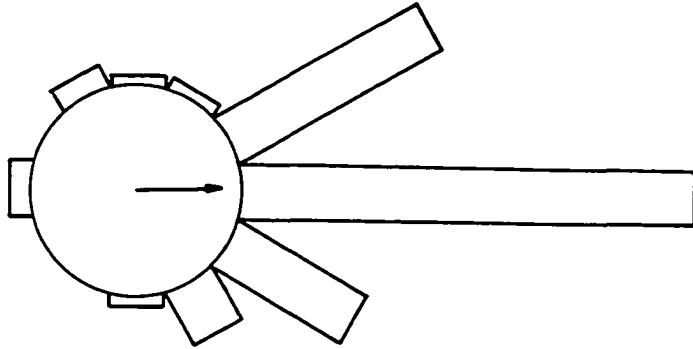
Experimentals



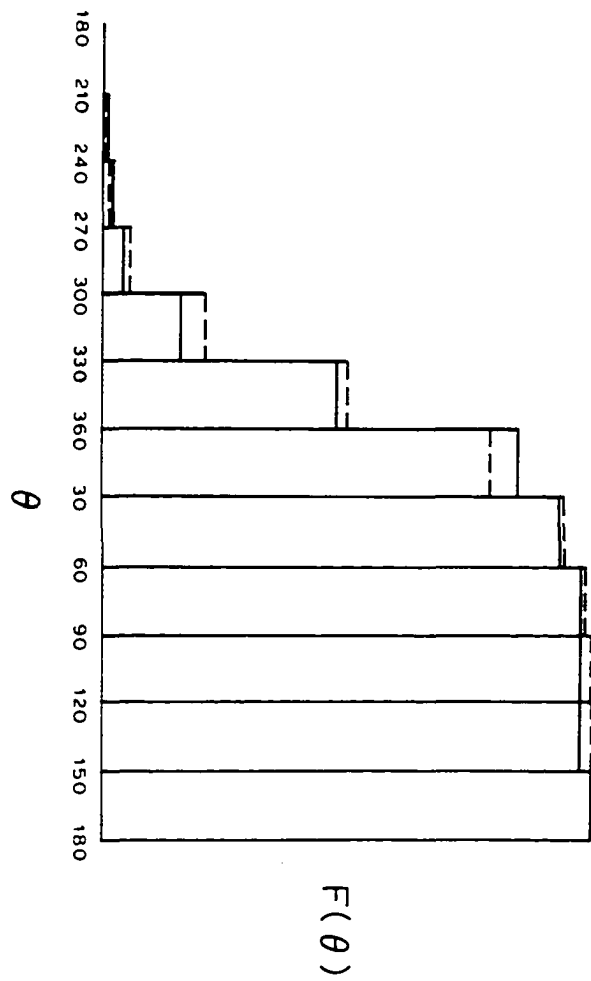
**FIGURE 6.2** Departure of Turtle X17's sample of within-day turns from the von Mises Distribution.

- a. Frequency distribution showing some amount of asymmetry and perhaps more turns near  $180^\circ$  than expected.
- b. Comparison of the observed cumulative frequencies (solid lines) to the cumulative probabilities for the von Mises Distribution,  $k = 3.0$  (dashed lines).

a.



b.



**TABLE 6.13a. INTRA-CLASS COMPARISONS OF THE CONCENTRATION PARAMETER  
FOR WITHIN-DAY SAMPLES OF TURNS**

Mardia's Multi-sample Test for the Equality of  $r_{\theta}$ :

Residents:  $U_2 = 34.9$ ,  $p < 0.001$

Males:  $U_2 = 6.39$ ,  $p < 0.05$

Females:  $U_2 = 26.7$ ,  $p < 0.001$

Transients:  $U_2 = 12.79$ , n.s.

Experimentals:  $U_2 = 6.2$ , n.s.

**TABLE 6.13b INTER-CLASS COMPARISONS**

Kruskall-Wallis One-way Analysis of Variance:  $H = 13.75$ ,  $p < 0.01$

Two-Sample Tests:

Comparison	Mardia's Two-sample Test	Mann-Whitney U Test
Res vs Tran	$p < 0.001$	$U = 1$ , $p < 0.001$
Res vs Exp	$p < 0.001$	$U = 6$ , $p < 0.01$
Tran vs Exp	$p < 0.01$	$U = 12$ , $p < 0.05$
Males vs. Females*	n.s.	$U = 29$ , n.s.
Residents	n.s.	$U = 5$ , n.s.
Transients	n.s.	$U = 4$ , n.s.

\* Experimentals (all females) were not considered in this comparison

(given the within-class heterogeneity of the Residents, the non-parametric tests provide the most appropriate comparisons). In fact, all three classes appear to differ significantly from one another, whereas sex, another grouping that is usually important, provides no comparable discrimination.

Another factor that has no apparent effect on the concentration of turns, although it does have a dramatic effect on activity, is rainfall (Table 6.14). My weather records were not sufficiently exact to rule out all possible effects on orientation, but at least these findings indicate that the differences observed between the classes cannot be explained simply on the basis of different amounts of rainfall occurring within their sampling periods.

Table 6.15 discounts the possibility that the length of the day-range can account in a simple way for the differences observed between the classes. If it were just the number of discontinuities in a sample that create these differences, then there might be some inverse correlation between day-range length and magnitude of  $r_0$ . However, exactly the opposite appears to be the case. Although the Kruskal-Wallis and Mann-Whitney U Tests do not indicate any significant differences among the classes with respect to day-range length, the Residents do generally travel shorter distances per day than the others, definitely not longer ones as would be expected under the above hypothesis. Moreover, path length appears to vary independently of the concentration of turns. Rainfall has a marked effect on path length, at least among the Residents and Transients (Table 6.16), but as mentioned above has no noticeable effect on the turning behavior.

**TABLE 6.14 COMPARISON OF WET DAY AND DRY DAY SAMPLES OF WITHIN-DAY TURNS**

Turtle	Wet Days			Dry Days		
	n	m <sub>0</sub>	r <sub>0</sub>	n	m <sub>0</sub>	r <sub>0</sub>
<b>Residents:</b>						
1	59	358	0.786	120	358	0.761
4	91	358	0.715	165	359	0.706
7	120	4	0.699	125	2	0.694
8r	45	2	0.703	48	7	0.751
9	121	4	0.613	194	348	0.705
10	179	5	0.654	146	348	0.580
16	74	7	0.410	134	10	0.583
26	109	1	0.704	77	344	0.745
total	802	2	0.658	1005	0	0.680

Wilcoxon Test comparing values of r<sub>0</sub>: n.s.

<b>Transients:</b>						
8tr	121	2	0.907	59	5	0.789
11	0	-	-	29	21	0.752
12	22	349	0.709	52	1	0.920
14	8	0	0.930	24	357	0.781
17	47	354	0.935	3	6	0.980
23	22	0	0.936	41	3	0.900
27	26	359	0.779	16	7	0.850
total	246	359	0.882	327	4	0.836

Wilcoxon Test: n.s.

<b>Experimentals:</b>						
X1	22	7	0.745	0	-	-
X2	38	354	0.844	29	358	0.707
X15	37	358	0.702	97	359	0.825
X16	37	350	0.668	28	8	0.662
X17	19	11	0.664	73	355	0.858
X18	0	-	-	29	5	0.825
X19	5	357	0.859	93	1	0.843
total	158	358	0.729	349	0	0.815

Wilcoxon Test: too few samples

**TABLE 6.15 DAY-RANGE PATH LENGTHS**

Turtle	n	$\bar{x}$	s
<b>Residents:</b>			
1	33	136	101
4	32	196	182
7	33	194	160
8r	15	182	168
9	48	164	124
10	46	174	170
16	36	147	108
26	24	165	137
total	267	169	144
<b>Transients:</b>			
2	12	240	150
8tr	19	173	191
11	3	260	191
12	4	377	223
14	5	174	86
17	5	264	312
23	13	137	130
27	4	279	82
total	65	208	175
<b>Experimentals:</b>			
X2	6	280	136
X15	6	344	246
X16	11	157	127
X17	6	140	122
X19	5	351	226
total	34	237	183

Kruskall-Wallis One-way Analysis of Variance:  $H = 3.15$ ; n.s.



**TABLE 6.16 COMPARISON OF PATH-LENGTHS FOR WET AND DRY DAYS**

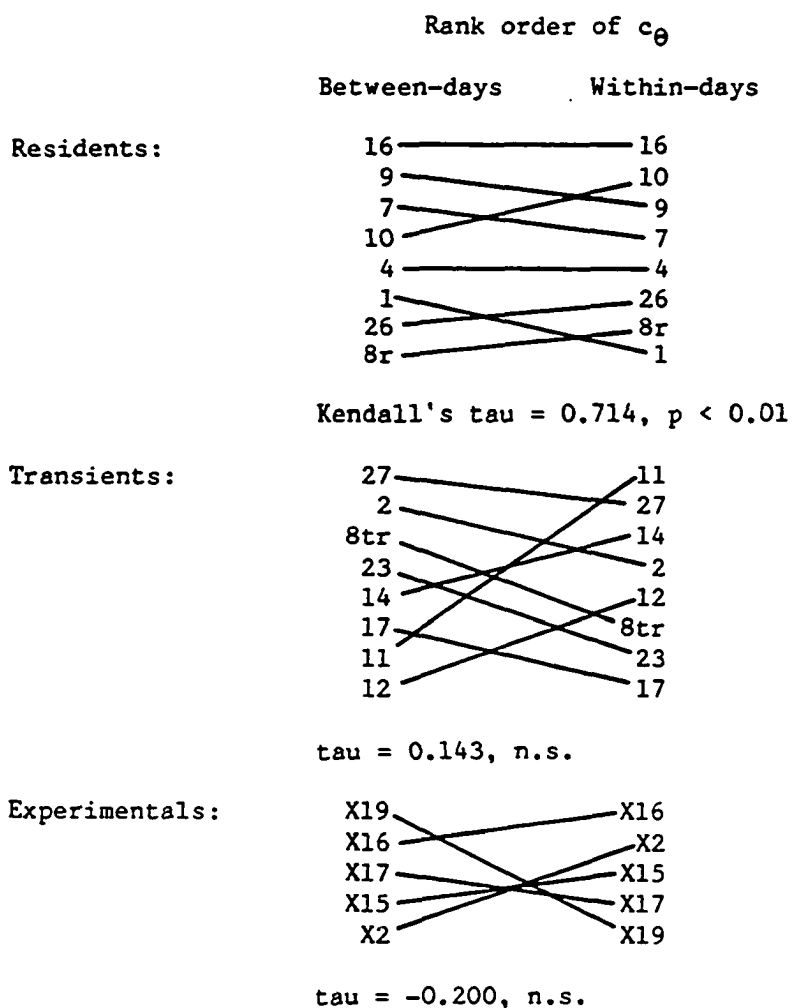
Turtle	Wet Days			Dry Days		
	n	$\bar{x}$	s	n	$\bar{x}$	s
<b>Residents:</b>						
1	9	169	101	24	124	100
4	8	307	251	24	158	140
7	12	275	178	21	147	131
8r	5	237	172	10	155	168
9	19	167	108	29	161	136
10	21	220	195	25	136	138
16	10	203	143	26	125	85
26	13	193	132	11	132	141
total	97	214	162	170	142	126
<b>Transients:</b>						
8tr	7	206	215	12	153	182
11	-	-	-	3	260	53
12	2	450	283	2	304	218
14	1	229	-	4	160	93
17	3	406	344	2	50	13
23	4	240	148	9	91	97
27	2	344	32	2	215	54
total	19	286	214	34	153	142
<b>Experimentals:</b>						
X2	4	244	155	2	354	64
X15	3	289	289	3	398	64
X16	5	190	168	6	130	88
X17	2	133	54	4	143	154
X19	1	135	-	4	406	221
total	15	213	168	19	257	197
<b>Kruskall-Wallis</b>						
	H = 4.66, n.s.			H = 2.9, n.s.		

While these findings do not exclude the possibility that the number of discontinuities still plays some role in differentiating the three classes, it at least does not appear to be the only such factor. Indeed, the differences already noticed in the form-site turns suggests that the magnitude of the turns at the discontinuities might also play an important role. On the other hand, with the exception of the Residents, there is no clear correlation between the values of  $c_0$  for the form-site turns and those for the within-day turns (Table 6.17). The fact that there does appear to be some correlation for the Residents when treated separately further suggests that the differences separating them from the other two classes are quite complex.

Analysis of seven step sequences. Continuing under the working hypothesis that the presence of discontinuities causes the samples to depart from the expectations of the menotactic walk, the next step is to divide the day-ranges into still shorter units. As discussed in Chapter V, the intention is to isolate the discontinuities within sections of the path that are as small as possible but still large enough to apply the screening tests for sequential homogeneity. As was suggested in that chapter, seven step sequences provide the bare minimum samples for this purpose.

A problem now arises as to how best to divide the day-ranges into such samples. Only rarely will they be evenly divisible by seven, so what do you do with the remainder? I chose first to determine how many seven step-samples could be created from a given day-range and then to distribute the remainder as evenly as possible over the samples, beginning with the first. For example, a 15-step day-range would be divided into samples of eight and seven steps, and a 26-step

**TABLE 6.17 CORRELATION OF THE MAGNITUDE OF TURNING BETWEEN AND WITHIN DAYS**



day-range into samples of nine, nine, and eight steps. This scheme thus ensures the maximum number of samples of the minimum length, while not including the known points of discontinuity at the form-sites. It also utilizes all the information available for estimating the parameters of the circular distributions, which is of particular importance in the statistical tests used to screen the samples for discontinuities.

In order to maximize the number of samples still further, I applied this same procedure to path sections that had been excluded from the day-range analysis, those series for which the form-sites could not be ascertained. The samples created from these portions of the routes differ from the others only in that some of the heterogeneity that they contain will be due to unknown form-sites, not just the within-day changes in target.

The only sequences left out of this analysis now are thus any that are less than seven steps between either known form-sites or route termini. This procedure yielded the following total numbers of samples for each class: Residents, 359; Transients, 76; and Experimentals, 62.

The results of the first screening are summarized in Table 6.18. As described in Chapter V, the V-Test determines the significance of concentration of angular values towards one direction, here set at  $0^{\circ}$ . The samples identified in this table are therefore those that fail to meet the simplest expectation for any unbiased oriented walk, including menotaxis. To the contrary, the presumption is that they do not differ significantly from those produced by a purely random process.

**TABLE 6.18 RELATIVE NUMBERS OF RANDOM-APPEARING, SEVEN-STEP-MINIMUM SEQUENCES**

Turtle	No. of Sequences Failing V-Test*	% of Total No. of Sequences
Residents:		
1	0	0
4	5	11
7	12	17
8r	1	8
9	4	8
10	27	33
16	24	53
26	4	13
total	77	22

Correlation between within-day  $c_0$  (Table 6.9) and percentage of sequences failing the V-Test:

Kendall's tau = -0.714,  $p < 0.01$

Transients:		
2	0	0
8tr	0	0
11	1	17
12	0	0
14	0	0
17	0	0
23	0	0
27	0	0
total	1	1
Experimentals:		
X1	0	0
X2	1	9
X15	2	12
X16	0	0
X17	1	9
X18	0	0
X19	0	0
total	4	6

As is quite clear, these findings are consistent with the differences between the classes that were discussed in the last section: the Residents show the greatest number of these apparently random sequences, the Transients the least, with the Experimentals intermediate but closer to the Transients. Additionally, there is a strong inverse correlation between the percentage of a Resident's sample that show no clustering of values towards zero degrees and the within-day values of  $c_0$  (Table 6.18).

But are these samples truly random? The majority of these sequences also appear to be so when either their azimuths or turns are further subjected to the standard Rayleigh Test; only 12 out of the 77 have significantly concentrated azimuths and only three others show some degree of clustering of turns when no mean direction is specified.

However, when the sequences appearing most random — those showing no clustering of values under any of these tests — are subjected to MSD analysis, then another answer seems probable. Although the results (Table 6.19 and Figure 6.3) indicate that the differences from the random predictions are indeed only slight (the results of a test applied to the pooled sample of Residents' means at step seven show no significant difference from the expectations for the random walk:  $z = 0.3217$ ), it can also be seen that virtually all the observed MSD values lie above the predicted line for the random walk. This result is actually contrary to the direction expected for samples under the hypothesis of randomness: as a result of skewness of the distributions of the individual variates, mentioned in the last chapter, more of the means should lie towards the bottom of the graph. The Sign Test (Sie-

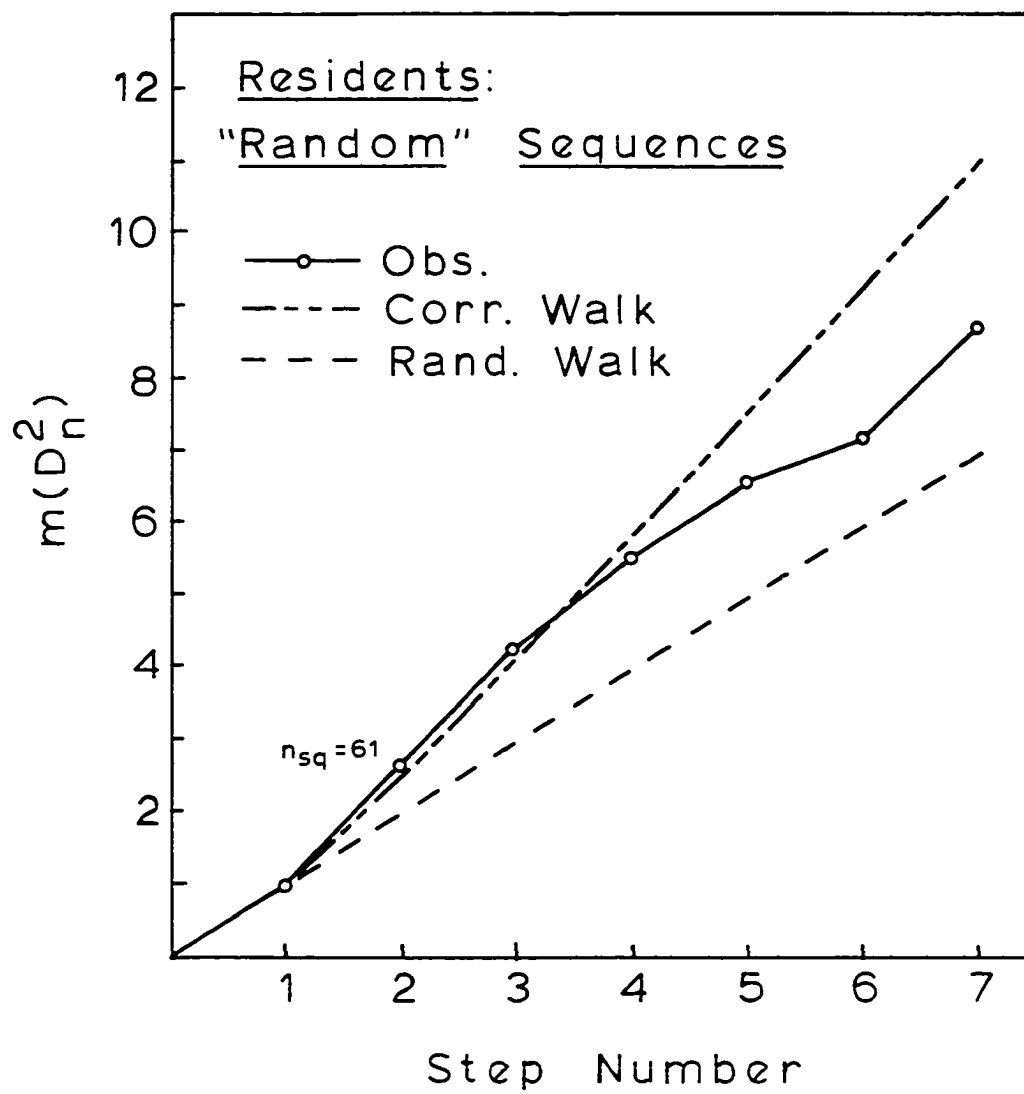
**TABLE 6.19 MEAN SQUARED DISTANCES OF TRAVEL FOR "RANDOM" SEQUENCES  
COMPARED TO EXPECTATIONS UNDER THE CORRELATED WALK HYPOTHESIS**

		Mean Squared Distance of Travel						
Turtle	$n_{sq}^*$	$n_{st}^{**} =$	2	3	4	5	6	7
Residents:								
4	5	o	3.37	4.26	4.04	4.30	6.46	7.96
		$e_{cw}$	2.77	4.83	7.00	9.21	11.44	13.67
7	8	o	3.36	4.93	7.40	8.13	9.60	11.23
		$e_{cw}$	2.45	4.00	5.58	7.16	8.74	10.32
8r	1	o	1.28	3.53	5.99	5.72	6.45	7.97
		$e_{cw}$	2.83	4.82	6.70	8.45	10.12	11.75
9	3	o	2.28	4.41	6.91	8.54	11.39	13.35
		$e_{cw}$	2.58	4.29	6.02	7.73	9.44	11.14
10	22	o	2.34	4.08	5.25	5.83	6.03	7.10
		$e_{cw}$	2.51	4.15	5.82	7.49	9.17	10.85
16	18	o	2.81	4.38	4.85	6.16	6.20	7.95
		$e_{cw}$	2.46	4.02	5.60	7.18	8.77	10.35
26	4	o	1.45	3.66	6.90	10.58	11.20	13.90
		$e_{cw}$	2.63	4.42	6.24	8.06	9.87	11.68
total	61	o	2.62	4.27	5.52	6.55	7.19	8.73
		$e_{cw}$	2.52	4.19	5.88	7.59	9.30	11.01
Experimentals:								
X2	1	o	1.72	5.14	7.23	9.17	4.60	2.33
		$e_{cw}$	2.88	4.34	4.92	4.95	5.06	5.52
X17	1	o	2.78	6.53	11.70	6.53	6.70	12.73
		$e_{cw}$	2.76	4.65	6.47	8.21	9.91	11.58
total	2	o	2.25	5.84	9.46	7.85	5.65	7.53
		$e_{cw}$	2.82	4.56	5.92	7.00	8.01	9.04

\*  $n_{sq}$  = number of sequences contributing to the observed averages  
 \*\*  $n_{st}$  = number of steps; the first step is not indicated since for uniform steps it will always be equal to one

**FIGURE 6.3** Pooled samples of the Residents' series partitioned under the seven-step-minimum rule that were not significantly different from random under the V- or Rayleigh Test.





gel, 1956) indicates that these departures from the random walk are quite significant:  $p = 0.04$  overall, and for the Residents alone,  $p = 0.016$ . It is this consistency of the departures, over all the step numbers, rather than their magnitudes, that rules out the purely random walk as the governing process; there is a tendency even in these samples for the animal to show some maintenance of heading from one step to the next.

These data further suggest that this tendency is not explained by predictions from simple correlated walks. Even though it does not require much of an ongoing tendency for a correlated walk to make significant progress compared to a purely random walk (something that would be missed if only simple orientational analyses were used), the observed curves still do not appear to fit the expectations. Although they now appear to lie above and below the predicted curves in about equal numbers, the curves that fall below seem to be more sharply bent or curved than would be expected of truly homogeneous sequences, whereas the smoother curves (as indicated in Table 6.19, those of Turtles 7, 9, and 26) all lie above the expected lines.

The jagged appearance of the lower curves is most clearly shown in those that represent single sequences (the ones having the least meaning statistically, although also the ones in which the effects of discontinuities would be most likely to show up); the observed MSD's for Turtles 8, X2, and X17 show what strongly appear to be one or two sharp changes in behavior within the sequence. Even in the samples composed of the greatest number of separate sequences, those of Turtles 10 and 16, the observed curves show an initial rise followed by a decline towards the predictions of the random walk. This pattern

could reflect the accumulated effects of discontinuities during the course of the sequences, although in these cases the effect of any one discontinuity occurring at a given step within one sequence is balanced to some degree by the within-sequence behavior occurring at corresponding points in the other sequences.

While I cannot present strong statistical proof that these sequences fail to fit the correlated walk model, given the evidence presented earlier that the routes or day-ranges overall also fail to show any such fit, it seems parsimonious at least to rule out this model here as well. There is simply too little evidence to suggest that these sequences represent qualitative shifts in behavior from that in other parts of the routes. As I have suggested above, the presence of discontinuities within otherwise homogeneous sequences can account equally well, if not better, for the behavior seen in these most "convoluted" sequences.

Excluding now the above sequences, the surviving series do not show many further departures from the directional predictions for unbiased oriented walks. There are very few additional sequences that show evidence of having a mean direction significantly different from  $0^\circ$ : 2% (4/359) of the Residents' total samples; 1% (1/62) of the Experimentals'; and none of the Transients' (Table 6.20).

Although these samples are "bent" in some fashion, the results of the simple Binomial Test show no significant imbalances in turns either to the right or the left. Again it is perhaps the presence of discontinuities that biases these samples, not any fundamental difference in their behavioral processes from those of the unbiased samples. At any rate, the evidence suggests that if path curvature exists at

**TABLE 6.20 OVERALL RESULTS OF SCREENING SEVEN-STEP-MINIMUM SEQUENCES FOR BIAS AMONG FIRST-ORDER TURNS**

Turtle	No. of "Random" <sup>1</sup> . Sequences	No. of "Curved" <sup>2</sup> . Sequences	No. of "Unbiased" <sup>3</sup> . Sequences
<b>Residents:</b>			
1	0	0	20
4	5	1	40
7	12	1	59
8r	1	0	12
9	4	2	44
10	27	0	55
16	24	0	21
26	4	0	26
total	77 ( = 22%)	4 ( = 1%)	277 ( = 77%)
<b>Transients:</b>			
2	0	0	11
8tr	0	0	27
11	1	0	5
12	0	0	9
14	0	0	3
17	0	0	6
23	0	0	7
27	0	0	5
total	1 ( = 1%)	0	73 ( = 99%)
<b>Experimentals:</b>			
X1	0	0	3
X2	1	0	10
X15	2	0	15
X16	0	0	5
X17	1	0	10
X18	0	0	3
X19	0	1	12
total	4 ( = 4%)	1 ( = 2%)	58 ( = 92%)

1. Sequences whose turns show no significant concentration of values around  $0^\circ$  under the V-Test.
2. Sequences passing the V-Test but whose mean turn angle is significantly different from  $0^\circ$  under Stephens' Test for the Mean Direction.
3. Sequences passing the first two tests.

all, it plays only a very minor role in box turtles' routes of travel.

The remaining sequences, those that appear to have distributions of first-order turns unimodally symmetric about  $0^{\circ}$ , constitute the majority of samples for each class, which is not surprising given the features of the entire day-ranges. Among the Residents, these samples compose 77% of the total, among the Experimentals 92%, and among the Transients 99%.

Even in these samples, differences in turning magnitude follow the same pattern as before (Table 6.21). Does this mean that there are still hidden points of discontinuity within these series that account for the differences between the classes? Or do these differences now indicate real distinctions in either deflectivity or the control processes in truly homogeneous sequences?

When the MSD's of these sequences are examined, all three classes now show strong evidence for active orientation (Table 6.22 and Figure 6.4). At step seven, the curves for all but two Residents and one Transient lie above the predicted line for the correlated walk. Given the arguments in Chapter V for the expected symmetrical distribution of the means about the predicted values, these results indicate that all classes of turtles make significantly more forward progress than would be expected for a correlated walker.

However, it is equally apparent that these sequences also fall short of values expected for menotaxis. Furthermore, there appear to be differences between the classes as to where their observed values fall between the correlated or menotactic predictions (it should be noted that the absolute distances from one or the other of the two models will vary with deflectivity, and hence will not necessarily

**TABLE 6.21 STATISTICS FOR THE TURN ANGLES IN FIRST-ORDER "UNBIASED" SEVEN-STEP-MINIMUM SEQUENCES**

Turtle	Unbiased Sequences			Within-days
	n	m <sub>θ</sub>	r <sub>θ</sub>	r <sub>θ</sub>
<b>Residents:</b>				
1	155	356	0.789	0.769
4	295	0	0.738	0.709
7	451	2	0.684	0.696
8r	110	3	0.742	0.727
9	352	2	0.724	0.669
10	423	358	0.691	0.620
16	174	359	0.615	0.521
26	189	1	0.712	0.720
total	2149	0	0.706	0.670
<b>Transients:</b>				
2	80	1	0.866	0.835
8tr	195	1	0.904	0.868
11	42	8	0.826	0.752
12	64	358	0.863	0.854
14	23	359	0.897	0.818
17	44	355	0.931	0.937
23	50	2	0.900	0.912
27	41	1	0.800	0.804
total	539	1	0.880	0.855
<b>Experimentals:</b>				
X1	20	6	0.766	0.781
X2	78	0	0.805	0.784
X15	108	1	0.833	0.791
X16	38	4	0.722	0.658
X17	71	355	0.865	0.814
X18	24	3	0.798	0.825
X19	75	0	0.868	0.844
total	414	0	0.823	0.788

**TABLE 6.22 MEAN SQUARED DISTANCES OF TRAVEL FOR FIRST-ORDER UNBIASED SEQUENCES COMPARED TO EXPECTATIONS UNDER MENOTACTIC AND CORRELATED WALK HYPOTHESES**

		Mean Squared Distance of Travel						
Turtle	$n_{sq}$	$n_{st} =$	2	3	4	5	6	7
Residents:								
1	20	$e_{mw}$	3.57	7.22	13.44	20.73	29.59	40.03
		$o$	<b>3.54</b>	<b>7.19</b>	<b>11.67</b>	<b>17.47</b>	<b>24.90</b>	<b>33.50</b>
		$e_{cw}$	3.57	7.38	12.13	17.63	23.69	30.19
4	40	$e_{mw}$	3.48	7.43	12.86	19.76	28.14	37.99
		$o$	<b>3.53</b>	<b>7.12</b>	<b>11.14</b>	<b>15.99</b>	<b>21.59</b>	<b>28.78</b>
		$e_{cw}$	3.48	7.03	11.38	16.30	21.62	27.24
7	59	$e_{mw}$	3.37	7.10	12.20	18.67	26.50	35.71
		$o$	<b>3.47</b>	<b>6.96</b>	<b>11.16</b>	<b>15.54</b>	<b>20.56</b>	<b>26.23</b>
		$e_{cw}$	3.37	6.67	10.60	14.97	19.63	24.49
8r	12	$e_{mw}$	3.48	7.45	12.89	19.82	28.23	38.12
		$o$	<b>3.32</b>	<b>6.89</b>	<b>12.31</b>	<b>18.92</b>	<b>26.23</b>	<b>34.49</b>
		$e_{cw}$	3.48	7.06	11.44	16.42	21.83	27.56
9	44	$e_{mw}$	3.45	7.34	12.68	19.47	27.71	37.39
		$o$	<b>3.37</b>	<b>6.70</b>	<b>10.84</b>	<b>15.62</b>	<b>20.32</b>	<b>26.25</b>
		$e_{cw}$	3.45	6.94	11.19	15.98	21.17	26.64
10	55	$e_{mw}$	3.38	7.14	12.30	18.82	26.72	36.01
		$o$	<b>3.41</b>	<b>6.82</b>	<b>11.22</b>	<b>15.81</b>	<b>20.93</b>	<b>24.46</b>
		$e_{cw}$	3.38	6.72	10.71	15.16	19.92	24.89
16	21	$e_{mw}$	3.23	6.69	11.38	17.30	24.45	32.83
		$o$	<b>3.41</b>	<b>6.55</b>	<b>10.08</b>	<b>14.66</b>	<b>19.38</b>	<b>23.89</b>
		$e_{cw}$	3.23	6.22	9.67	13.40	17.32	21.34
26	26	$e_{mw}$	3.42	7.27	12.54	19.23	27.35	36.89
		$o$	<b>3.30</b>	<b>6.83</b>	<b>11.82</b>	<b>17.65</b>	<b>23.62</b>	<b>28.57</b>
		$e_{cw}$	3.42	6.86	11.01	15.68	20.72	26.01
total	277	$e_{mw}$	3.41	7.24	12.54	19.13	27.19	36.66
		$o$	<b>3.43</b>	<b>6.88</b>	<b>11.18</b>	<b>16.09</b>	<b>21.50</b>	<b>27.17</b>
		$e_{cw}$	3.41	6.82	10.94	15.55	20.51	25.72

**TABLE 6.22 CONTINUED**

			Mean Squared Distance of Travel					
Turtle	n <sub>sq</sub>	n <sub>st</sub> =	2	3	4	5	6	7
Transients:								
2	11	e <sub>mw</sub>	3.73	8.20	14.39	22.32	31.98	42.37
		o	<b>3.78</b>	<b>7.91</b>	<b>13.76</b>	<b>20.23</b>	<b>28.17</b>	<b>37.21</b>
		e <sub>cw</sub>	3.73	7.96	13.49	20.14	27.76	36.21
8tr	27	e <sub>mw</sub>	3.81	8.43	14.85	23.09	33.13	44.98
		o	<b>3.75</b>	<b>8.36</b>	<b>14.80</b>	<b>22.97</b>	<b>32.83</b>	<b>44.30</b>
		e <sub>cw</sub>	3.81	8.25	14.18	21.44	29.90	39.47
11	5	e <sub>mw</sub>	3.63	7.90	13.81	21.35	30.52	41.33
		o	<b>3.24</b>	<b>7.44</b>	<b>13.33</b>	<b>20.44</b>	<b>28.17</b>	<b>31.28</b>
		e <sub>cw</sub>	3.63	7.58	12.54	18.27	24.57	31.28
12	9	e <sub>mw</sub>	3.73	8.18	14.35	22.26	31.88	43.24
		o	<b>3.86</b>	<b>8.32</b>	<b>14.20</b>	<b>22.01</b>	<b>36.05</b>	<b>38.05</b>
		e <sub>cw</sub>	3.73	7.94	13.43	20.03	27.58	35.94
14	3	e <sub>mw</sub>	3.79	8.38	14.76	22.94	32.91	44.67
		o	<b>3.97</b>	<b>8.48</b>	<b>15.05</b>	<b>23.27</b>	<b>31.47</b>	<b>43.16</b>
		e <sub>cw</sub>	3.79	8.20	14.04	21.17	29.46	38.78
17	6	e <sub>mw</sub>	3.86	8.57	15.13	23.56	33.84	45.97
		o	<b>3.80</b>	<b>8.50</b>	<b>15.02</b>	<b>23.13</b>	<b>33.20</b>	<b>43.74</b>
		e <sub>cw</sub>	3.86	8.42	14.55	22.09	30.90	40.84
23	7	e <sub>mw</sub>	3.80	8.40	14.80	22.99	32.99	44.79
		o	<b>3.76</b>	<b>7.98</b>	<b>13.91</b>	<b>21.85</b>	<b>31.17</b>	<b>41.92</b>
		e <sub>cw</sub>	3.80	8.22	14.08	21.25	29.58	38.95
27	5	e <sub>mw</sub>	3.60	7.80	13.60	21.00	30.01	40.61
		o	<b>3.85</b>	<b>8.40</b>	<b>14.87</b>	<b>22.62</b>	<b>32.01</b>	<b>39.75</b>
		e <sub>cw</sub>	3.60	7.48	12.38	18.11	24.48	31.38
total	73	e <sub>mw</sub>	3.76	8.20	14.56	22.60	32.41	43.97
		o	<b>3.75</b>	<b>8.20</b>	<b>14.42</b>	<b>22.22</b>	<b>31.26</b>	<b>40.94</b>
		e <sub>cw</sub>	3.76	8.07	13.74	20.62	28.54	37.40

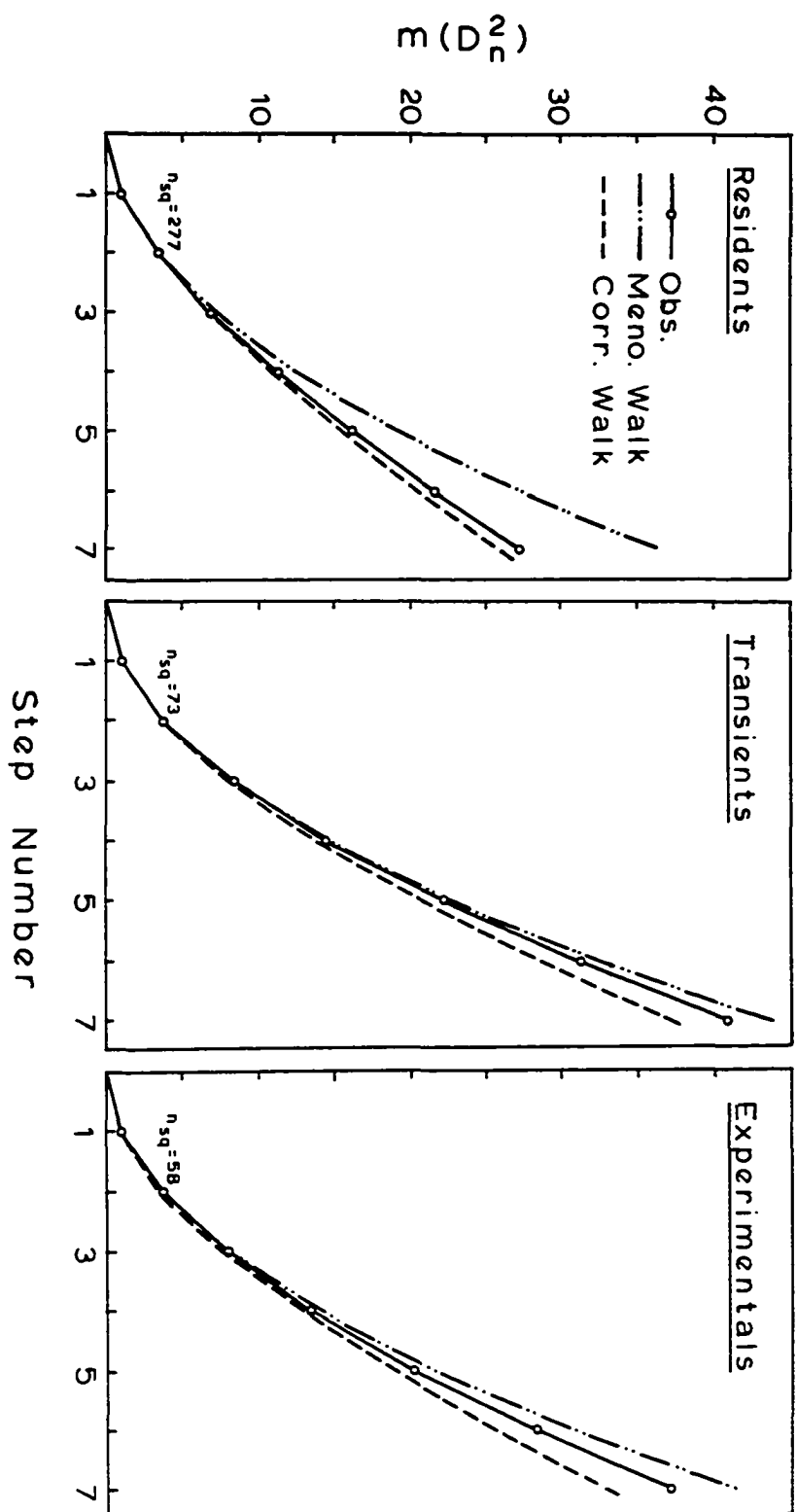


TABLE 6.22 CONTINUED

			Mean Squared Distance of Travel					
Turtle	n <sub>sq</sub>	n <sub>st</sub> =	2	3	4	5	6	7
Experimentals:								
X1	3	e <sub>mw</sub>	3.52	7.57	13.14	20.24	28.86	39.00
		o	3.01	6.73	12.78	20.60	30.35	34.78
		e <sub>cw</sub>	3.52	7.20	11.73	16.90	22.53	28.50
X2	10	e <sub>mw</sub>	3.61	7.83	13.66	21.11	30.16	40.83
		o	3.02	6.47	11.71	18.12	26.30	35.19
		e <sub>cw</sub>	3.61	7.52	12.47	18.27	24.74	31.76
X15	15	e <sub>mw</sub>	3.66	7.99	13.99	21.65	30.97	41.96
		o	3.57	7.80	13.42	19.88	21.22	37.83
		e <sub>cw</sub>	3.66	7.72	12.92	19.08	26.04	33.67
X16	5	e <sub>mw</sub>	3.44	7.32	12.65	19.41	27.62	37.26
		o	3.82	8.64	12.97	19.33	25.61	33.79
		e <sub>cw</sub>	3.44	6.91	11.12	15.86	20.96	26.32
X17	10	e <sub>mw</sub>	3.72	8.17	14.35	22.25	31.87	43.22
		o	3.75	8.38	14.73	22.34	31.70	40.35
		e <sub>cw</sub>	3.72	2.93	13.38	19.90	27.30	35.44
X18	3	e <sub>mw</sub>	3.59	7.78	13.57	20.94	29.92	40.48
		o	3.41	8.00	13.52	21.12	28.42	34.98
		e <sub>cw</sub>	3.59	7.46	12.32	17.98	24.26	31.04
X19	12	e <sub>mw</sub>	3.74	8.21	14.42	22.36	32.04	43.46
		o	3.85	8.28	13.77	20.02	27.61	37.37
		e <sub>cw</sub>	3.74	7.98	13.53	20.22	27.89	36.42
total	58	e <sub>mw</sub>	3.65	7.94	13.88	21.46	30.70	41.58
		o	3.55	7.80	13.36	20.08	28.26	37.06
		e <sub>cw</sub>	3.65	7.65	12.77	18.80	25.59	33.01

**FIGURE 6.4** Pooled samples of seven-step-minimum sequences whose first-order turns ( $\theta_1$ ) show significant concentration of values towards  $0^\circ$ .

# Sequences of at Least Seven Steps Unbiased in $\theta_1$



indicate much about the degree of departure from the expectations). The Residents seem to show the greatest relative discrepancy from menotaxis, the Transients the least, with the Experimentals once more in between. Again, the simplest answer for these inter-class differences, as well as for the lack of fit to the menotactic walk, could lie in the action of yet undetected discontinuities within these series.

To look for evidence of "subtle" discontinuities (changes in target close to  $0^\circ$ ), I subjected this set of sequences to the same sort of screening procedures as before, but now using their samples of second-order turns. The results, however, are similar to those obtained for the first-order turns: the Residents again show the highest proportion of sequences that fail to show a significant clustering of values about  $0^\circ$ , the Transients again show the smallest proportion, and the Experimentals, as usual, occupy an intermediate position (Table 6.23).

The removal of the samples showing second-order departures from an unbiased oriented walk also fails to bring the observed MSD curves for the remainder up to the expectations for menotaxis (Figure 6.5). In addition, the classes still seem to have the same order of relative decrement from menotaxis as found for the corresponding first-order samples. This difference is dramatically shown just within Turtle 8's data (Figure 6.6). Compare her "transient" sequences with her "resident" ones.

Given the resemblance of these findings to previous ones, the screening procedures do not seem to have resolved anything; there still may be undetected discontinuities within these samples, just as

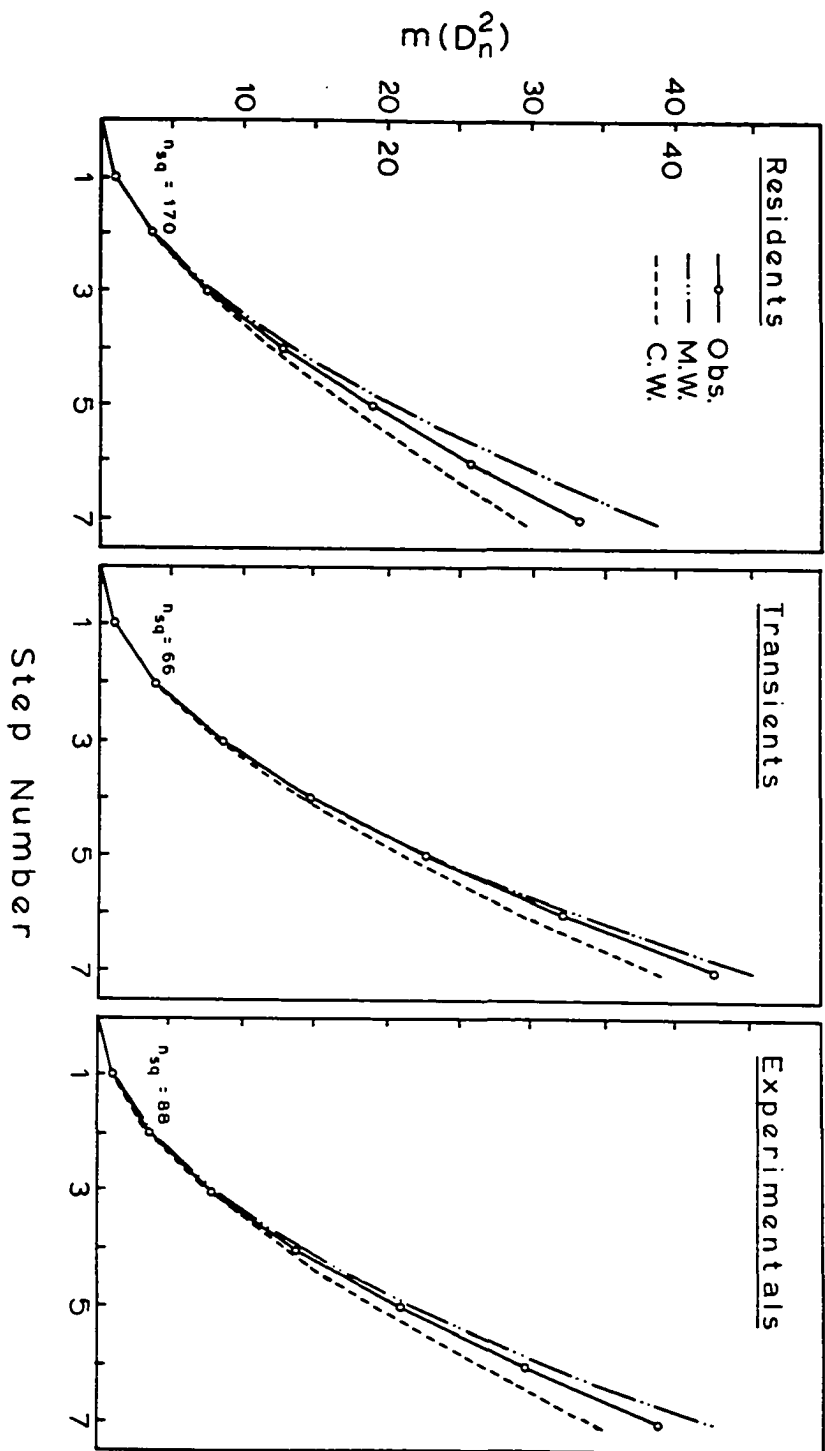
**TABLE 6.23 RESULTS OF SCREENING THE SEVEN-STEP-MINIMUM SEQUENCES FOR BIAS IN THE SECOND-ORDER TURNS**

Turtle	No. of "Bent" <sup>1</sup> Sequences	No. of "Straight" <sup>2</sup> Sequences	Turn Statistics for "Straight" Sequences		
			n	m <sub>0</sub>	r <sub>0</sub>
Residents:					
1	5	15	112	359	0.857
4	11	29	218	357	0.775
7	30	29	231	3	0.765
8r	1	11	102	3	0.753
9	13	31	252	2	0.746
10	24	31	241	359	0.767
16	12	9	74	354	0.675
26	11	15	107	359	0.785
total	107 ( = 30%)	170 ( = 47%)	1337	0	0.766
Transients:					
2	2	9	68	1	0.902
8tr	1	26	186	0	0.919
11	4	1	8	347	0.887
12	0	9	64	358	0.863
14	0	3	23	359	0.897
17	0	6	44	355	0.931
23	0	7	50	2	0.900
27	0	5	41	1	0.800
total	7 ( = 9%)	66 ( = 89%)	484	0	0.896
Experimentals:					
X1	1	2	13	1	0.845
X2	2	8	64	1	0.820
X15	2	13	93	2	0.855
X16	1	4	32	11	0.794
X17	1	9	65	356	0.854
X18	0	3	24	3	0.798
X19	3	9	57	359	0.911
total	10 ( = 16%)	48 ( = 76%)	348	1	0.846

1. Sequences whose second-order turns either showed no concentration of values towards 0° under the V-Test or had a mean significantly different from 0° under Stephens' Test for the Mean Direction.
2. Sequences that passed the above-mentioned tests.

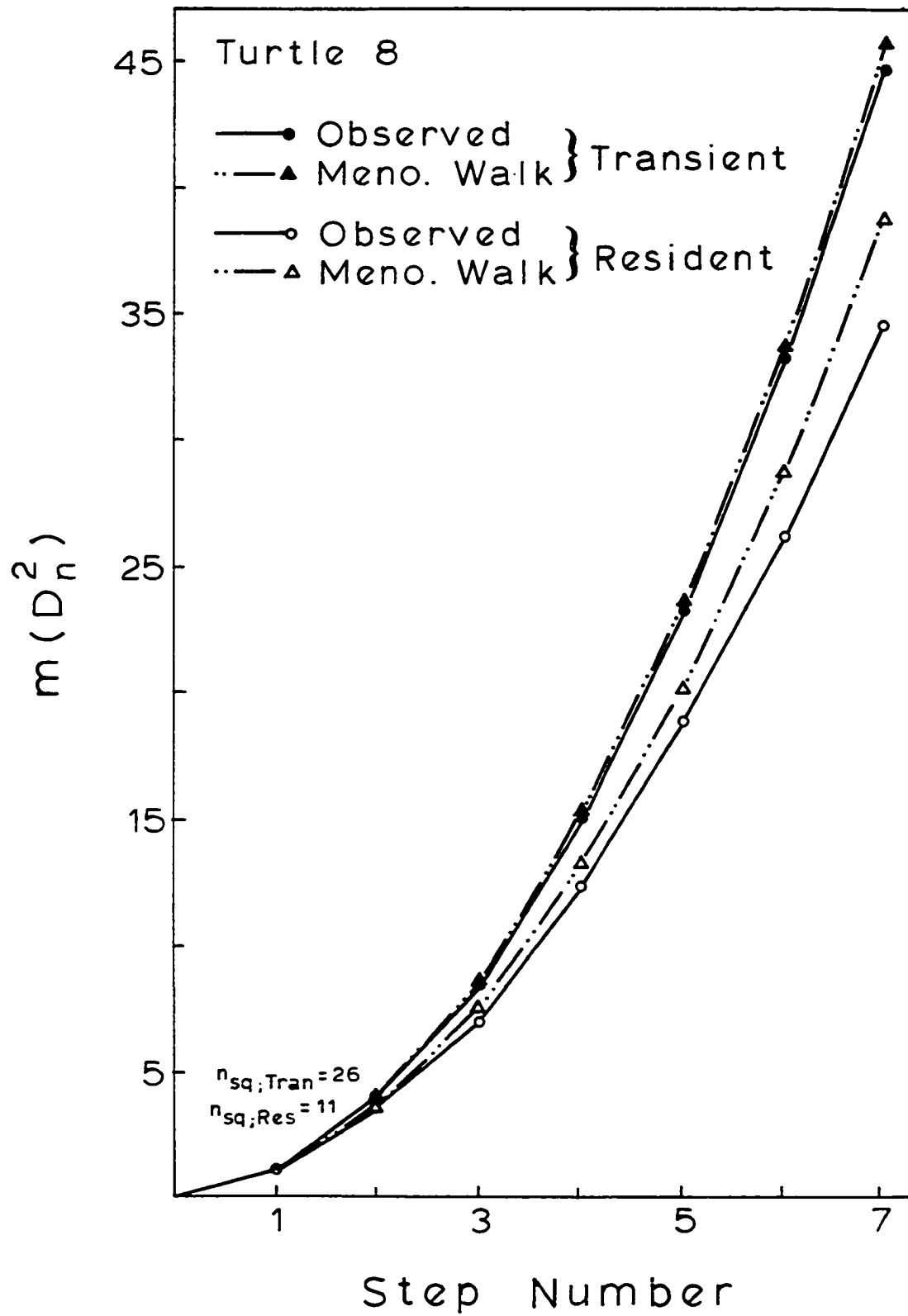
**FIGURE 6.5** Pooled samples of seven-step-minimum sequences whose first- and second-order turns both show significant concentration of values towards  $0^\circ$ .

# Sequences of at Least Seven Steps Unbiased in $\theta_1$ and $\theta_2$



**FIGURE 6.6** A comparison of the goodness-of-fit to a menotactic walk of Turtle 8's resident and transient samples of seven-step-minimum sequences that were unbiased in both first- and second-order turns.





possibly for all previous samples. Although justifiable in theory, an examination of third- or even higher-order turns would appear to be a waste of effort. Not only are there few samples left with a sufficient number of steps to provide a minimum sample size for such analysis, but any results obtained would probably be too rarified to be viewed without skepticism. The limits to a rigorously objective approach have been reached at this point.

Given the continued likelihood of discontinuities within even my most "homogeneous" sequences, the basic questions about the nature of the differences between the classes remain:

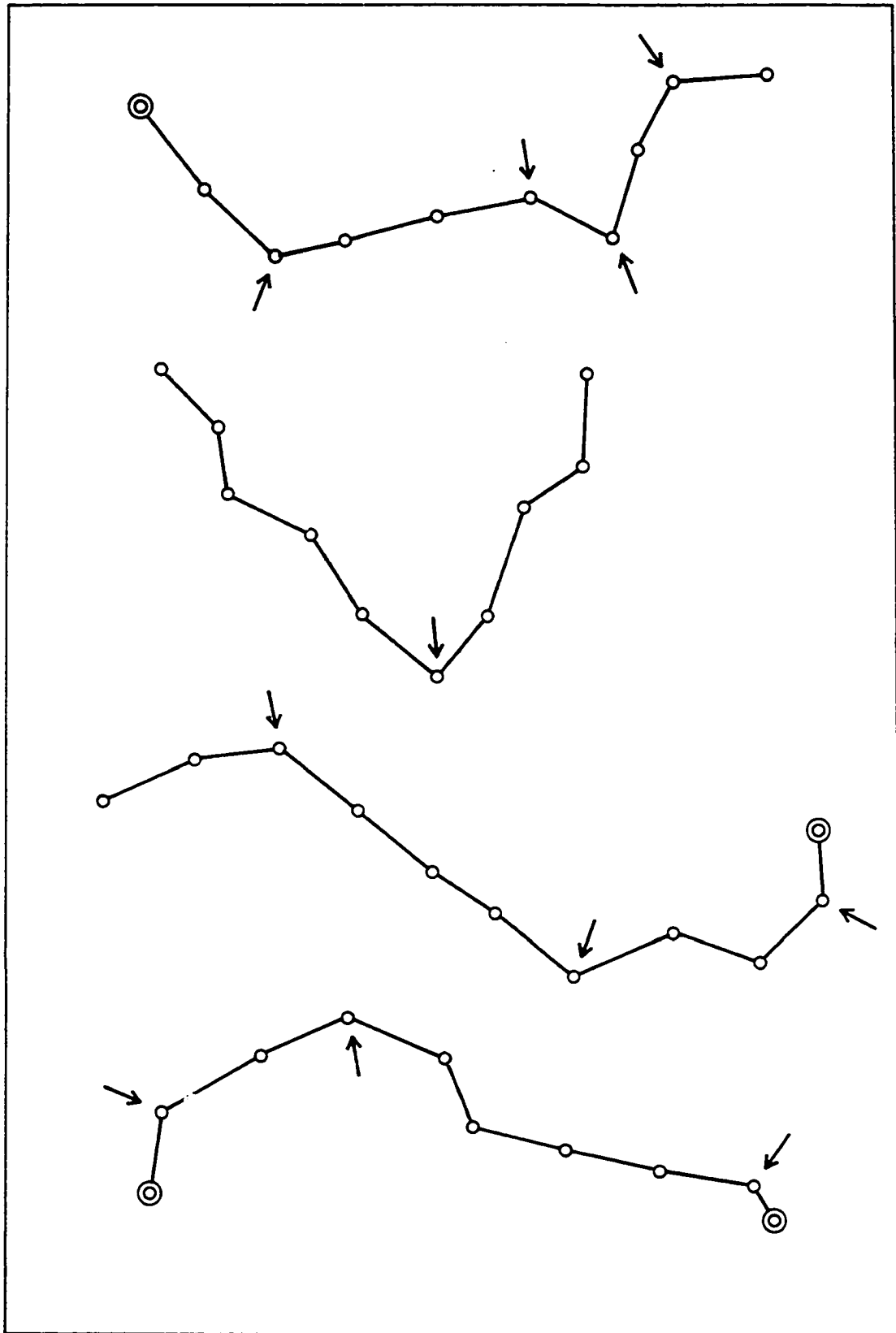
- (1) Do the Residents show a higher frequency of discontinuities than the other classes, i.e., do they travel shorter distances before changing target headings?
- (2) Do they make more radical changes in direction at the points of discontinuity?
- (3) Do they have a higher true deflectivity (i.e., a lower value of  $\rho_\delta$ ) between the points of discontinuity?
- (4) Do they still show a greater apparent discrepancy from the menotactic model for sequences occurring between the points of discontinuity?
- (5) Does the intermediate position of the Experimentals for most measures indicate that they are intermediate with respect to all or only part of the factors that distinguish the Residents from the Transients?

A subjective sampling scheme. With regard to the occurrence of discontinuities, simple visual inspection of the maps is revealing. As suspected, the examples illustrated in Figure 6.7 appear to show definite points of discontinuity even though they represent samples that passed the final screening for homogeneity. While these sequences are generally "straight" in the sense that their turns, both first- and second-order, show a relatively balanced concentration about  $0^\circ$ , they nonetheless appear to contain more than one significant change in orientation. Such "discontinuities" could easily account for the lower MSD's than those expected under the hypothesis of monotaxis; even a single change in heading will result in a shorter overall path length while changing the estimate of the mean vector for turns only slightly.

Consequent to these findings, I proceeded to treat these visually apparent discontinuities as though they were real. The results of this subjective method turned out to be quite informative.

In defining the points of apparent discontinuity, rather than rely on a fixed, arbitrarily chosen measure for departure from a straight course (as did Gail and Boone, 1970; Hall, 1977; Lemkau, 1970; Michener and Walcott, 1967), I used a relative method, making use of the sequences of both first and second-order turns (Figure 6.8). This approach is less likely to confuse a large detour with a true change in target and also allows for the existence of differences in deflectivity. The absolute methods, in contrast, would automatically "discover" more changes of target in sequences possessing large magnitude deflectivities than in those with smaller values, even when all sequences are actually homogeneous.

**FIGURE 6.7** Examples of visually-apparent discontinuities, indicated by arrows, in Turtle 7's sequences that showed no biases among either the first- or second-order turns. Note that discontinuities can occur adjacent to one another, either where they occur next to form-sites (as in the last two examples) or in the middle of the sequences (as in the first example).



I took as my basic model for a discontinuity the known, context-dependent changes in target that occur at the form-sites (Figure 6.8a). At these points, the change in heading is larger, on the average, than those both immediately preceding and following it in the series. Moreover, the second-order turns that straddle a single discontinuity of this kind will be similar in magnitude and direction, both to one another and to the first-order turn marking the spot. In addition, if the sequences are long enough, these second-order turns will also be bracketed by smaller turns of the same order. In contrast to all these features of true discontinuities, those associated with simple deflections are quite different in pattern with respect to both orders of turns, as is illustrated.

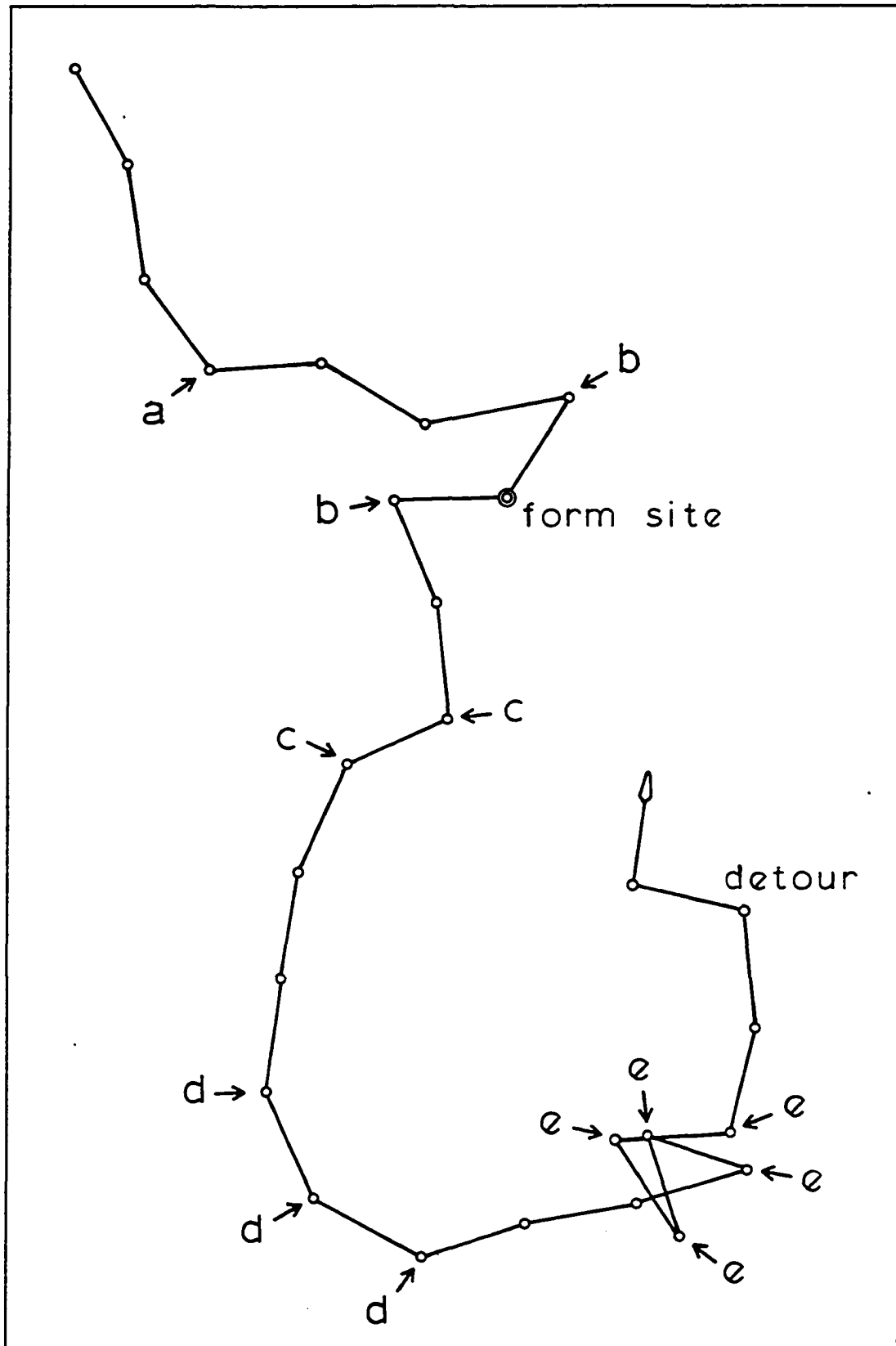
Wherever the single-target sequences are two or more steps in length, the above features should identify even slight changes in targets, discriminating them from large deflections. Where the sequences are extremely long, even higher order turns can be employed to confirm the identifications.

On the other hand, when the "sequences" are shorter than two steps, as where discontinuities occur adjacent to one another in sequence, the above method will not work. Such discontinuities, however, also have a context-defined model: at the points marking the last and first within-day turns of the Residents. Correspondingly, I discarded any of the final or initial points of a day-range that were marked by first- and second-order turns that were noticeably larger than the ones preceding or following them, respectively (Figure 6.8b). In similar fashion, I looked for this sort of behavior in the vicinity of the primary "discontinuities" determined on the basis of the form-

**FIGURE 6.8** Types of visually-apparent discontinuities.

- a. "Form-like" discontinuities.
- b. Final and intial turns within a day-range if markedly larger from those adjacent to them.
- c. Adjacent sharp changes in direction bounded by straighter sections.
- d. Curves.
- e. Tangles

Also note the large turn marked "detour"; unlike the case for the discontinuities, the higher-order turns here indicate a return to the previous heading.





site model, although with more caution than for the primary "discontinuities" themselves.

The two models just described are defined primarily with respect to relative changes in magnitude within a series of turns. Another important type of visually apparent discontinuity are curves, distinguished more by the direction of turning within a series (Figure 6.8d). For example a series of turns could all have the same magnitude, which would disqualify them for detection by the above methods, but if they all had the same signs would also represent a departure from the expectations of independence.

Rather than use the first or second-order turns to define this type of "discontinuity", I was more conservative, resorting to the sequence of third-order turns: for a curve to be defined as representing a "discontinuity", the difference between the directions of the first step going into the curve and the fourth step following it would have to be larger than either the first, second, or third-order turns preceding and succeeding it in sequence.

One final type of discontinuity that is far easier to pick out visually than to describe in terms of a pattern of turns can be termed a "tangle" (Figure 6.8e). Here a tight clustering of turns occurs which possesses no particular arrangement of magnitudes or signs, but which is bounded by much "straighter" sections of path.

Although a computer algorithm could be devised to make the procedures outlined more completely replicable, the results I obtained from even simple visual inspection are in accord with my previous findings. The following results should spur on the search for more objective methods capable of detecting discontinuities in the routes.

Table 6.24 and Figure 6.9 present the MSD analysis of just those sequences that passed the final statistical screening but which are now further broken up after having taken the visually identified "discontinuities" into account. The fit to the menotactic model is now obviously improved in all cases. No longer is there any systematic downward departure from the predictions of the model; on the contrary, there are now curves that lie completely above the predicted lines or that fluctuate about it. In addition, there no longer seem to be any differences between the three classes as to how well they fit the model.

There are, however, still important differences between the classes with respect to deflectivity. Although removal of the the turns associated with the "discontinuities" has raised the value of  $r_0$  for all three classes, the same inter-class rank order persists: Transients have the highest value; Residents the lowest; and Experimentals intermediate. These differences are reflected in the distances expected and actually reached for each class, particularly at the higher step numbers.

Encouraged by these results, I went on to remove "discontinuities" from the entire data set in order to increase the sample sizes for comparative purposes. Rather than use the MSD analysis for these data, however, I chose to test the menotactic hypothesis by examining the values of  $r_0$  for the first- and second-order turns, as described in Chapter V. As can be seen in Figure 6.9 from the number of sequences averaged at each step, most of the apparently homogeneous sequences are quite short, two or three steps being predominant. Turn analysis thus looks specifically at lengths of sequence where most of

**TABLE 6.24 MEAN SQUARED DISTANCES OF TRAVEL FOR SECOND-ORDER UNBIASED SEQUENCES FURTHER DIVIDED AT POINTS OF VISUALLY APPARENT "DISCONTINUITIES"**

		Mean Squared Distance of Travel							
Turtle	$n_{st} =$	2	3	4	5	6	7	8	9
Residents:									
1	$n_{sq}^*$	29	14	8	3	2	2		
	$e_{mw}$	3.85	8.55	15.10	23.50	33.76	45.86		
	$o$	<b>3.90</b>	<b>8.41</b>	<b>14.50</b>	<b>23.42</b>	<b>33.83</b>	<b>45.28</b>		
	$e_{cw}$	3.85	8.40	14.52	22.06	30.90	40.90		
4	$n_{sq}$	69	29	14	4	2	1	1	
	$e_{mw}$	3.68	8.05	14.09	21.82	31.23	42.32	55.10	
	$o$	<b>3.78</b>	<b>8.08</b>	<b>13.70</b>	<b>20.34</b>	<b>24.33</b>	<b>27.21</b>	<b>37.85</b>	
	$e_{cw}$	3.68	7.78	13.06	19.35	26.48	34.31	42.74	
7	$n_{sq}$	71	47	22	12	5	4	3	1
	$e_{mw}$	3.76	8.27	14.54	22.56	32.34	43.88	57.17	72.22
	$o$	<b>3.80</b>	<b>8.23</b>	<b>14.19</b>	<b>21.86</b>	<b>31.40</b>	<b>43.35</b>	<b>55.27</b>	<b>71.93</b>
	$e_{cw}$	3.76	8.05	13.70	20.54	28.42	37.21	46.79	52.08
8r	$n_{sq}$	30	17	11	6	4	3	1	
	$e_{mw}$	3.80	8.40	14.81	23.01	33.02	44.83	58.44	
	$o$	<b>3.84</b>	<b>8.38</b>	<b>14.41</b>	<b>22.31</b>	<b>32.40</b>	<b>44.30</b>	<b>57.88</b>	
	$e_{cw}$	3.80	8.23	14.11	21.31	29.70	39.15	49.56	
9	$n_{sq}$	78	43	13	6	4	2		
	$e_{mw}$	3.80	8.41	14.83	23.84	33.06	44.89		
	$o$	<b>3.88</b>	<b>8.51</b>	<b>15.09</b>	<b>22.67</b>	<b>31.85</b>	<b>47.08</b>		
	$e_{cw}$	3.80	8.24	14.13	21.36	29.77	39.26		
10	$n_{sq}$	69	35	15	9	4	2	2	
	$e_{mw}$	3.80	8.39	14.79	22.98	32.96	44.75	58.33	
	$o$	<b>3.85</b>	<b>8.40</b>	<b>14.52</b>	<b>23.44</b>	<b>35.00</b>	<b>48.17</b>	<b>60.09</b>	
	$e_{cw}$	3.80	8.21	14.07	21.24	29.58	38.96	49.29	
16	$n_{sq}$	19	13	7	3	2	2		
	$e_{mw}$	3.83	8.48	14.96	23.27	33.41	45.37		
	$o$	<b>3.82</b>	<b>8.65</b>	<b>15.04</b>	<b>23.85</b>	<b>33.78</b>	<b>45.00</b>		
	$e_{cw}$	3.83	8.32	14.33	21.72	30.37	40.15		

\* As a result of the divisions, the number of sequences now available for averaging will vary from step to step. It should be noted that there may be a few sequences longer than seven steps even though only the first seven steps of these sequences had been considered in the tables and figures previously.

TABLE 6.24 CONTINUED

Turtle	$n_{st}$	Mean Squared Distance of Travel							
		2	3	4	5	6	7	8	9
26	$n_{sq}$	33	18	9	3	2	1		
	$e_{mw}$	3.68	8.05	14.09	21.82	31.23	42.52		
	$o_{mw}$	<b>3.73</b>	<b>7.87</b>	<b>13.56</b>	<b>21.94</b>	<b>31.89</b>	<b>39.22</b>		
	$e_{cw}$	3.68	7.77	13.03	19.26	26.30	33.95		
total	$n_{sq}$	398	216	99	46	25	17	7	1
	$e_{mw}$	3.77	8.31	14.61	22.69	32.53	44.14	57.53	72.68
	$o_{mw}$	<b>3.83</b>	<b>8.31</b>	<b>14.34</b>	<b>22.44</b>	<b>32.07</b>	<b>43.75</b>	<b>54.53</b>	<b>71.98</b>
	$e_{cw}$	3.77	8.10	13.82	20.76	28.78	37.76	47.58	58.15

## Transients\*:

8tr	$n_{sq}$	57	30	19	7	6	5	3	
	$e_{mw}$	3.92	8.77	15.54	24.24	34.86	47.40	61.87	
	$o_{mw}$	<b>3.94</b>	<b>8.74</b>	<b>15.58</b>	<b>24.20</b>	<b>34.79</b>	<b>46.96</b>	<b>61.21</b>	
	$e_{cw}$	3.92	8.70	15.25	23.51	33.41	44.81	57.86	
11	$n_{sq}$	2	2	1	1				
	$e_{mw}$	3.72	8.17	14.35	22.24				
	$o_{mw}$	<b>3.98</b>	<b>8.80</b>	<b>14.39</b>	<b>22.92</b>				
	$e_{cw}$	3.72	7.92	13.38	19.89				
12	$n_{sq}$	20	10	3	2	2	1	1	1
	$e_{mw}$	3.89	8.68	15.36	23.94	34.40	46.76	61.02	77.17
	$o_{mw}$	<b>3.91</b>	<b>8.72</b>	<b>15.65</b>	<b>24.38</b>	<b>34.61</b>	<b>46.64</b>	<b>61.20</b>	<b>77.76</b>
	$e_{cw}$	3.89	8.58	14.96	22.95	32.46	43.41	55.73	69.33
14	$n_{sq}$	8	3	2	1				
	$e_{mw}$	3.97	8.90	15.79	24.65				
	$o_{mw}$	<b>3.96</b>	<b>8.91</b>	<b>15.77</b>	<b>24.68</b>				
	$e_{cw}$	3.97	8.86	15.65	24.31				
17	$n_{sq}$	12	6	3	2	1	1	1	
	$e_{mw}$	3.92	8.77	15.53	24.22	34.83	47.36	61.81	
	$o_{mw}$	<b>3.94</b>	<b>8.74</b>	<b>15.10</b>	<b>23.99</b>	<b>35.35</b>	<b>48.12</b>	<b>62.97</b>	
	$e_{cw}$	3.92	8.69	15.23	23.48	33.36	44.81	57.77	

\* Turtle 2 drops out of the analysis at this point since his routes were surveyed before the control lines were in place and before I decided to record elevational changes; all further analysis requires mapped data or at least accurate projections onto the x-y plane.

TABLE 6.24 CONTINUED

Turtle		Mean Squared Distance of Travel							
		$n_{st} = 2$	3	4	5	6	7	8	9
23	$n_{sq}$	16	8	3	1				
	$e_{mw}$	3.90	8.71	15.43	24.05				
	$o$	3.98	8.71	14.90	24.81				
	$e_{cw}$	3.90	8.62	15.06	23.13				
27	$n_{sq}$	13	7	4	1	1			
	$e_{mw}$	3.94	8.81	15.62	24.37	35.06			
	$o$	3.94	8.77	15.65	24.28	34.65			
	$e_{cw}$	3.94	8.75	15.38	23.77	33.87			
total	$n_{sq}$	128	66	35	15	10	7	5	1
	$e_{mw}$	3.92	8.75	15.49	24.16	34.74	47.23	61.64	77.97
	$o$	3.94	8.75	15.47	24.19	34.80	47.08	61.56	77.76
	$e_{cw}$	3.92	8.67	15.18	23.37	33.17	44.52	57.34	71.58

## Experimentals:

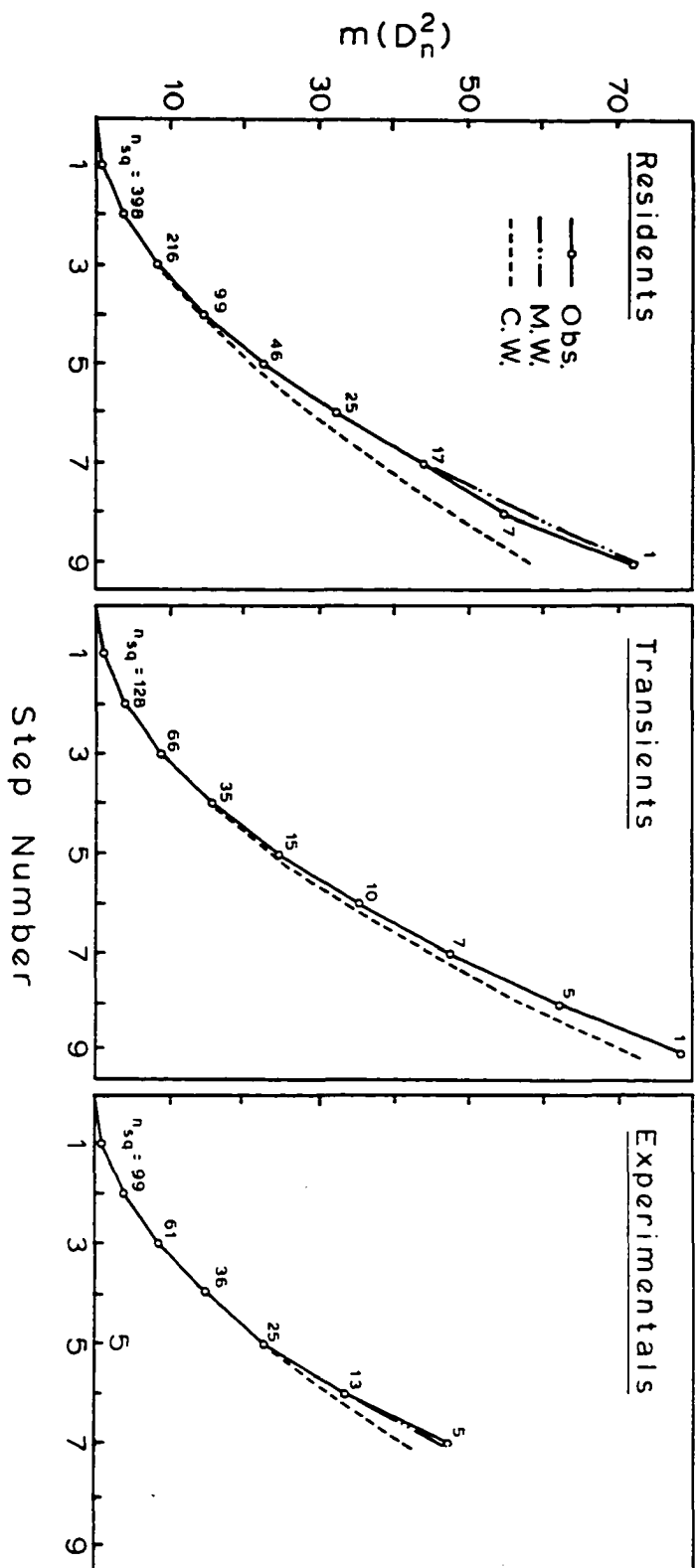
X1	$n_{sq}$	4	1						
	$e_{mw}$	3.98	8.93						
	$o$	3.97	8.96						
	$e_{cw}$	3.98	8.89						
X2	$n_{sq}$	16	9	6	5	3	2		
	$e_{mw}$	3.91	8.72	15.45	24.08	34.62	47.06		
	$o$	3.93	8.78	15.56	24.16	34.27	47.67		
	$e_{cw}$	3.91	8.63	15.10	23.21	32.90	44.08		
X15	$n_{sq}$	24	18	12	8	6	2		
	$e_{mw}$	3.82	8.46	14.92	23.20	33.30	45.22		
	$o$	3.84	8.54	14.81	22.86	32.66	46.91		
	$e_{cw}$	3.82	3.30	14.28	21.63	30.23	39.96		
X16	$n_{sq}$	9	7	3	2	1			
	$e_{mw}$	3.73	8.20	14.39	22.32	31.98			
	$o$	3.95	8.82	13.52	20.07	28.78			
	$e_{cw}$	3.73	7.96	13.47	20.08	27.62			
X17	$n_{sq}$	19	10	7	5	2			
	$e_{mw}$	3.90	8.71	15.42	24.03	34.54			
	$o$	3.87	8.68	15.27	24.02	35.61			
	$e_{cw}$	3.90	8.61	15.04	23.08	32.66			
X18	$n_{sq}$	8	3	2	1				
	$e_{mw}$	3.79	8.38	14.75	22.92				
	$o$	3.84	8.31	14.29	23.02				
	$e_{cw}$	3.79	8.19	14.02	21.14				

**TABLE 6.24 CONTINUED**

Turtle	$n_{st}$	Mean Squared Distance of Travel						
		2	3	4	5	6	7	8
X19								
	nsq	19	13	6	4	1	1	
	$e_{mw}$	3.85	8.56	15.11	23.52	33.78	45.90	
	$\sigma$	<b>3.87</b>	<b>8.69</b>	<b>15.50</b>	<b>24.06</b>	<b>34.21</b>	<b>46.17</b>	
	$e_{cw}$	3.85	8.42	14.56	22.17	31.12	41.31	
total								
	nsq	99	61	36	25	13	5	
	$e_{mw}$	3.85	8.55	15.10	23.49	33.74	45.84	
	$\sigma$	<b>3.88</b>	<b>8.66</b>	<b>15.00</b>	<b>23.33</b>	<b>33.31</b>	<b>47.07</b>	
	$e_{cw}$	3.85	8.41	14.55	22.15	31.11	41.31	

**FIGURE 6.9** Pooled sequences that showed no biases among their first- and second-order turns, here further divided at points of visually-apparent discontinuities.

# Unbiased Sequences Divided at Visually Determined Discontinuities





the information is concentrated. Unlike the MSD analysis, moreover, there are appropriate statistical approaches for evaluating these findings.

The results of eliminating all known and suspected discontinuities from the routes are given in Table 6.25. Again, the fit to the menotactic model is very close, which is here supported by Wilcoxon's Tests, comparing the concentration parameters for the first- and second-order turns. In fact, rather than showing any residual effect of yet undetected discontinuities (which would tend to produce relatively lower values of  $r_{02}$  ) there are more values of  $r_{02}$  that exceed  $r_{01}$  than vice versa!

This goodness-of-fit to menotaxis suggests that comparisons made between the three classes at this point will be more meaningful than any made previously (with the exception of the samples of turns determined by the context of the form-sites). The same pattern of inter-class differences remains, however, even though the within-sequence  $r_0$  have all been raised compared to those of previous samples in which the discontinuities had not been removed. As shown in Table 6.25, the Residents as a group still show significantly greater within-sequence turning than do the other two classes, while the Transients and Experimentals are still quite close together and not significantly different from one another.

Not only are these findings similar to earlier results obtained through more strictly objective methods, but they are also difficult to explain in terms of any bias I might have had in selecting the "discontinuities".

**TABLE 6.25 STATISTICS FOR TURN ANGLES WITHIN "HOMOGENEOUS" SEQUENCES**

Turtle	n	m <sub>01</sub>	r <sub>01</sub>	n	m <sub>02</sub>	r <sub>02</sub>
<b>Residents:</b>						
1	140	1	0.862	64	4	0.853
4	224	6	0.837	82	0	0.803
7	402	1	0.821	223	359	0.842
8r	89	0	0.887	48	4	0.891
9	253	0	0.904	96	2	0.932
10	333	359	0.857	138	357	0.886
16	174	1	0.890	64	359	0.939
26	149	0	0.847	72	358	0.839
total	1764	1	0.857	787	0	0.867

Wilcoxon Test comparing r<sub>01</sub> to r<sub>02</sub>:  
T = +10, n.s.

<b>Transient:</b>						
8tr	168	0	0.960	89	1	0.962
11	30	1	0.935	15	3	0.925
12	44	358	0.946	24	2	0.968
14	20	359	0.838	9	359	0.776
17	33	359	0.964	20	4	0.971
23	35	358	0.955	13	5	0.956
27	27	1	0.967	15	1	0.957
total	357	359	0.967	185	2	0.951

Wilcoxon Test: T = -24, n.s.

<b>Experimentals:</b>						
X1	9	4	0.962	2	5	0.999
X2	53	359	0.950	27	355	0.964
X15	91	358	0.840	61	1	0.823
X16	57	359	0.871	19	1	0.792
X17	56	0	0.941	33	0	0.930
X18	18	1	0.911	9	358	0.986
X19	64	0	0.956	37	0	0.986
total	328	359	0.908	188	359	0.896

Wilcoxon Test: T = +12.5, n.s.

Between-class comparisons of r<sub>01</sub>:

Kruskall-Wallis: H = 7.90, p < 0.05

Mann-Whitney:

Residents vs Transients: U = 6, p < 0.01  
Residents vs Experimentals: U = 9, p < 0.05  
Transients vs Experimentals: U = 16, n.s.

One such bias would have been to produce the straighter segments for the Transients and Experimentals by "discovering" a greater number of discrepant turns among their routes. Just the opposite is the case: I weeded the Residents' samples much more extensively: 42% of their turns were considered to represent discontinuities, as opposed to only 36% for the Experimentals and 35% for the Transients.

Nor does it appear that I biased the results by pulling out larger turns from the samples of the Transients and Experimentals. As shown in Table 6.26 the reverse again seems to be true: the "discontinuity" (between sequence) turns are largest among the Residents, smallest for the Transients, and intermediate for the Experimentals. These turns, however, are more concentrated than those occurring at the form-sites. This difference could reflect either a true difference between the two types of discontinuities or the inclusion within the visually identified "discontinuities" of straighter turns from within homogeneous sequences. In either case the conclusions about the within-day samples would still hold.

One final difference regarding the "discontinuities" also seems to separate the Residents from the other two classes. As implied by their greater proportion of "discontinuities" per route, they also travel fewer steps and hence shorter distances between points of "discontinuity". This difference is reflected in the class averages shown in Table 6.27. If true, then this is yet another parallel to the results found for entire day-ranges, in which it was also discovered that the Residents traveled generally shorter distances between the known points of discontinuity occurring at the form-sites.

**TABLE 6.26 STATISTICS FOR TURNS OCCURRING AT POINTS OF DISCONTINUITY**

Turtle	"Discontinuities"			Form-sites			Total		
	n	m <sub>θ</sub>	r <sub>θ</sub>	n	m <sub>θ</sub>	r <sub>θ</sub>	n	m <sub>θ</sub>	r <sub>θ</sub>
<b>Residents:</b>									
1	79	341	0.549	35	1	0.302	114	345	0.469
4	196	352	0.521	31	37	0.165	227	344	0.466
7	227	9	0.285	58	73	0.207	285	18	0.248
8r	43	20	0.312	15	5	0.549	58	14	0.370
9	242	2	0.446	54	123	0.084	296	4	0.357
10	371	355	0.338	73	4	0.141	444	356	0.306
16	240	21	0.109	47	275	0.066	287	14	0.089
26	124	351	0.435	34	12	0.319	158	355	0.407
total	1522	358	0.348	347	23	0.141	1869	0	0.307
<b>Transients:</b>									
8tr	103	3	0.758	25	336	0.445	128	359	0.689
11	23	44	0.582	3	310	0.962	26	31	0.519
12	31	355	0.722	4	357	0.671	35	357	0.671
14	11	357	0.760	4	331	0.603	15	351	0.706
17	19	350	0.834	3	302	0.792	22	344	0.796
23	28	8	0.860	13	352	0.509	41	4	0.746
27	15	2	0.505	4	73	0.597	19	17	0.455
total	230	4	0.721	56	341	0.477	286	1	0.667
<b>Experimentals:</b>									
X1	13	2	0.654	0	-	-	13	2	0.654
X2	39	9	0.571	4	3	0.619	43	8	0.575
X15	43	1	0.694	6	339	0.523	49	359	0.668
X16	28	354	0.363	10	62	0.252	38	6	0.298
X17	36	354	0.629	8	335	0.506	44	351	0.602
X18	12	12	0.716	0	-	-	12	12	0.716
X19	34	5	0.638	5	200	0.296	39	4	0.520
total	205	2	0.600	33	354	0.270	238	2	0.554

Between-class comparisons of "discontinuity" r<sub>θ1</sub>

Kruskall-Wallis: H = 11.07, p < 0.01

Mann-Whitney:

Residents vs Transients: U = 2, p < 0.001  
 Residents vs Experimentals: U = 4, p < 0.01  
 Transients vs Experimentals: U = 11, p < 0.05

**TABLE 6.27 AMOUNT OF SEPARATION BETWEEN POINTS OF DISCONTINUITY**

		Net Distance Between Points		No. of Steps Between Points	
Turtle	n	$\bar{x}$	s	$\bar{x}$	s
Residents:					
1	112	51	46.3	2.1	1.2
4	230	43	27.3	2.0	1.2
7	287	54	39.9	2.4	1.6
8r	58	54	36.5	2.4	1.7
9	284	42	33.8	1.8	1.1
10	437	39	29.4	1.8	1.3
16	288	35	25.0	1.6	1.1
26	158	50	34.1	1.9	1.2
total	1854	44	33.5	1.9	1.3
Transients:					
8tr	130	56	45.0	2.3	1.8
11	25	50	35.5	2.1	1.5
12	31	57	53.2	2.4	2.1
14	15	57	34.9	2.4	1.4
17	21	60	55.3	2.5	2.4
23	41	43	25.5	1.8	1.0
27	18	58	40.0	2.4	1.6
total	281	54	42.9	2.3	1.7
Experimentals:					
X1	12	41	20.3	1.8	0.7
X2	42	49	34.1	2.1	1.5
X15	48	62	59.5	2.6	1.8
X16	28	44	34.0	2.0	1.4
X17	43	53	51.2	2.3	2.2
X18	12	50	37.7	2.4	1.5
X19	39	59	45.1	2.6	1.8
total	234	53	45.2	2.3	1.7
Kruskall-Wallis:		H = 1.0013, n.s.		H = 3.67, n.s.	
Mann-Whitney:					
Res vs Tran:		U = 9, p < 0.05		U = 13, p < 0.05	
Res vs Exp:		U = 19, n.s.		U = 15, n.s.	
Tran vs Exp:		U = 18, n.s.		U = 25, n.s.	

The significance of these differences in path lengths is, however, hard to evaluate. On the one hand, the individual mean scores overlap greatly between the classes; only the comparison between the Residents and Transients shows a significant separation of values for both the number of steps per series and net distance of travel. On the other hand, comparison of the pooled frequency distributions for each class does indicate significant differences between all three classes, ( $p < 0.001$  for all three comparisons; Kolmogorov-Smirnov Test; Siegel, 1954).

In summary, these findings appear to indicate that the orientational mechanisms are the same for all three classes (perhaps identical to menotaxis); at any rate, the Residents do not appear to be more "disoriented" than the other two classes, nor do the Experimentals appear to be less oriented than the Transients. On the other hand, the Residents do appear to differ from the others in three distinct ways: they appear to have a greater within-sequence deflectivity; they seem to make more frequent changes in their orientational targets; and they appear to make changes of greater magnitude. The Experimentals appear to differ from the Transients mainly with respect to the magnitude of their changes between target headings; they do not seem to make more changes in target heading. Whether or not they also differ with respect to deflectivity remains open to question.

Strings of "discontinuities". Although the results just presented are quite consistent with an hypothesis of oriented sequences of movements punctuated by changes in target heading, the existence of sequences of adjacent "discontinuities" suggests that more might be going on. Tangles and curves could both be associated with a switch

from extensive to intensive searching. Both could indicate the replacement of a purely sequential pattern with one involving spatial constraints. Particularly disturbing for the theory of discrete walks, they also suggest that some changes in target do not take place at discrete points in space but rather are accomplished only after gradual re-adjustments or a period of trial and error testing of directions.

Table 6.28 indicates that strings of "discontinuities" are at least not very common. Single points of "discontinuity" predominate greatly in all three classes, and only around 10% of the "discontinuities" occur in sequences greater than two. Nonetheless, there are sequences of seven, eight, and nine "discontinuities". There are also curves of up to six turns having the same sign. These appear to be hard to dismiss as simple, accidental clusterings within an otherwise random scattering of points.

Table 6.29 gives the MSD data for within-day sequences of "discontinuities" that are at least three steps in length. Surprisingly, the evidence suggests that some form of orientation is still taking place within even these sequences. The curves definitely lie above the expectations for both the random as well as the simple correlated walk. One possible explanation for this finding is that my visual method of determining points of "discontinuity" has confounded larger detours with real changes in target; I might simply have been missing some compensations for deflections, especially if they took several steps to show up (which would happen if I confounded two different levels in the route hierarchy).

**TABLE 6.28 FREQUENCY OF "DISCONTINUITIES" OCCURRING IN RUNS OF VARIOUS LENGTHS\***

Turtle	Number of Consecutive "Discontinuities"								
	1	2	3	4	5	6	7	8	9
<b>Residents:</b>									
1	50	10	3						
4	94	35	9		1				
7	140	29	7	2					
8r	37	1		1					
9	94	34	17	6	1				
10	111	55	18	10	3	3	2		1
16	57	34	14	3	3	4	2	1	
26	55	21	6	1	1				
total	638	219	74	23	9	7	4	1	1
<b>Transients:</b>									
8tr	59	12	5		1				
11	12	4	1						
12	15	2	4						
14	9	1							
17	7	4		1					
23	12	5	2						
27	8	2	1						
total	122	30	13	1	1				
<b>Experimentals:</b>									
X1	6	1			1				
X2	19	6	1		1				
X15	20	6	2		1				
X16	15	5	1						
X17	18	6	2						
X18	7	1	1						
X19	27	1	1		1				
total	112	26	7	0	4				

\* Form-sites are not included; these are "within-day" runs only



**TABLE 6.29 MEAN SQUARED DISTANCES OF TRAVEL FOR RUNS OF  
"DISCONTINUITIES"**

		Mean Squared Distance of Travel						
Turtle	$n_{st}$	2	3	4	5	6	7	8
Residents	$n_{sq}$	74	74	27	14	9	5	3
	$e_{mw}$	2.26	3.79	5.57	7.62	9.93	12.51	15.34
	$o$	2.23	3.39	4.57	6.93	10.66	12.13	26.07
	$e_{cw}$	2.26	3.56	4.86	6.16	7.46	8.76	10.06
Transients	$n_{sq}$	6	6	2				
	$e_{mw}$	3.45	7.36	12.73				
	$o$	3.54	6.70	13.96				
	$e_{cw}$	3.45	6.92	11.06				
Experimentals	$n_{sq}$	4	4	3	1			
	$e_{mw}$	3.28	6.84	11.69	17.81			
	$o$	3.08	7.07	10.04	17.48			
	$e_{cw}$	3.28	6.35	9.90	13.70			

Another explanation is that the curves actually do represent departures from the normal, linear mode of progression but that in pooling curves of different signs I have underestimated the value of  $r_0$  for any given curved sequence (as mentioned earlier, with regard to the seven-step sequences). For example, pooling a sample of turns having a value of  $\rho_0$  equal to 0.5 and a mean heading of  $45^\circ$  with one having an identical concentration parameter but a mean direction of  $315^\circ$  would produce an overall mean direction of  $0^\circ$  and a concentration parameter of 0.35! If that value for  $r_0$  was used in the computation of the expected squared distances of travel for the two sequences, the observed distances would be much greater (recall that the MSDs are not affected by mean direction of the turns and so will reflect the true value of  $\rho_0$  for each sequence, i.e., 0.5).

Is there some other way, then, for assessing the nature of the curved sequences? In particular, do curves as such (ignoring their signs) appear to be more common than would be expected under an hypothesis of unbiasedness? If they are, then surely some other process is also at work within these sequences than menotaxis or some other form of unbiased orientation. A rather laborious method for dealing with these questions is described below.

If the signs of the curve are ignored, except to distinguish between adjacent runs of turns, then for any particular number  $n$  of turns, the total number of distinguishable sequences is given by the sum of the binomial coefficients for  $n$ . For example, the number of distinguishable sequences of four turns can be calculated as,

$$1 + 3 + 3 + 1 = 8$$

This can be demonstrated by writing out all the possibilities:

RRRR	1 (all one sign)
RRRL	3 (one "odd" sign)
RRLR	
RLRR	
RRLL	3 (two "odd" signs)
RLRL	
RLLR	
RLLL	1 (three "odd" signs)

(remember that it does not matter whether the first turn is to right or left, so long as the signs within the sequence can be distinguished).

The number of possible curves of a particular length,  $q$ , that can occur within a given number of turns also obeys a fairly simple rule.

By induction I found this to be

Number of turns in sequence	Number of curves of $c$ turns	
$n = q + 0$	1	= 1
$q + 1$	2 (1) + 0	= 2
$q + 2$	2 (2) + $2^0$	= 5
$q + 3$	2 (5) + $2^1$	= 12
$q + 4$	2 (12) + $2^2$	= 28
$q + 5$	2 (28) + $2^3$	= 64
$q + 6$	2 (64) + $2^4$	= 144
$q + 7$	2 (144) + $2^5$	= 320

Dividing the number of possible curves by the number of distinguishable sequences gives the expected frequency of curves of length  $q$  per sequence of length  $n$ . Multiplying the observed number of sequences of length  $n$  by the expected frequency thus produces an expected

number of curves of length  $q$ . Summing these expectations over an entire sample of varying length sequences of turns produces an overall expectation for curves of length  $q$ . For example, the expected frequency of three-step curves within sequences of five turns is equal to  $5/12$ ; in sequences of seven turns, it is equal to  $28/64$ . If there is an overall sample of six sequences of five turns each, and three of seven turns each, then the overall expected number of three-turn curves is,

$$5 (5 / 12) + 3 (28 / 64) = 3.4$$

Table 6.30 presents the observed versus the expected number of curves for each possible curve length within the observed samples of "discontinuity" strings. While the results of this test do not indicate that the pattern of curvature is different from random, it is apparent, especially among the Residents, that there are consistently more curves than expected. However, these curves might only represent artifacts of the surveying process, not anything important in terms of the animals' behavior. As illustrated in Figure 6.10, if a true point of discontinuity falls on a section of trail bridged by the arbitrary steps of the survey, then a two-turn curve will result rather than the single turn that really represents the discontinuity. Furthermore, if two-turn curves are more common than expected for this reason, then so will be all curves of greater length.

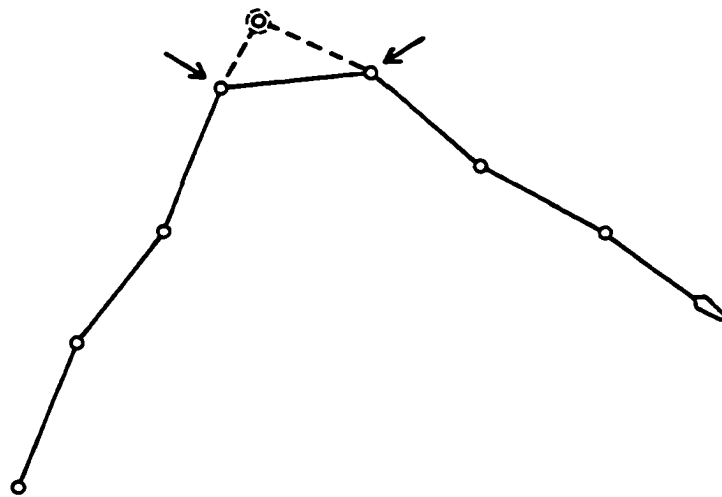
Nonetheless, there are more than twice as many curves of lengths five and six than predicted. These, at least, really do seem to indicate some form of biased turning. But it should also be noted that the evidence for such behavior is miniscule compared to that for

**TABLE 6.30 THE SIGNIFICANCE OF CURVED SEQUENCES WITHIN RUNS OF "DISCONTINUITIES"**

	No. of Steps within "Discontinuity" Run		
	2	3	4 - 9*
Residents			
Observed Number of Curves	184	40	10
Expected Number	180	32	8
	= 2.16, n.s.		
Transients + Experimentals*	2	3 - 5*	
Observed Number	43	10	
Expected Number	42	8	
	= 0.63, n.s.		

\* Pooling was necessary to produce expected frequencies of at least five.

**FIGURE 6.10** An example of a curve artificially introduced into a survey by failure to hit the true point of discontinuity.



⊙ True point of discontinuity

→○ Visually-determined point of discontinuity

unbiased movements. They do not appear to undermine seriously the general picture of animal movements representing discrete, stochastic walks.



## **VI. B. Analysis of Higher Level Partitions**

The presence of discontinuities within the routes implies the sort of hierarchical patterning described in Chapter III. According to the plan of analysis laid out in that chapter, the next step is to treat each walk (a homogeneous sequence) as a single step in a higher-level series. The procedures of walk analysis used at the lower scale of measurement are then repeated on these more inclusive steps.

The most natural points at which to divide the larger steps are at the form-sites. These represent the ideal sort of discontinuity, ones that are behaviorally determined. Moreover, the magnitude of the turns occurring at these points is larger, on the average, than anywhere yet discovered within the day-ranges. That strengthens the idea that entire day-ranges truly represent natural steps within the route hierarchy.

On the other hand, the results of the preceding section indicate the existence of some level intermediate between that of the day-ranges and that of the 25-ft partition. It also seems useful, then, to divide steps at the visually determined "discontinuities" in order to look for evidence of a middle level pattern before examining the entire day-ranges.

Alternatively, it is possible to divide the routes more arbitrarily into larger uniform length steps. This would have the same justifications and limitations as the 25-ft partition. Although not as informative as the cuts made at the form-sites, these arbitrary divisions are more replicable than the visually determined points. Furthermore, they allow 0° in direction to occur between steps, whereas the subjective steps divided at the points of "discontinuity" do not.

They are thus not subject to built-in tendencies to underestimate  $r_0$  or overestimate the lengths of the steps.

In the following sections, I employ each of these three partitioning schemes. In doing so, I was interested not only in what they would tell me about box turtle behavior, but also in how closely they would agree with one another. Any serious disagreements, especially between the arbitrary and natural partitions, would tend to cast doubt on the possibility of applying this entire approach to telemetric data; more information would then have to be acquired on the behavioral events that correspond to the targets and deflections before analysis could proceed. On the positive side, these methods might turn out to be complementary, each supplying slightly different information with which to construct an integrated view of movements.

Analysis of the visually determined "steps". Since the purpose of this particular analysis was to look for intermediate patterns within the day-ranges, I used only those sections of the routes that I was reasonably certain fell within the endpoints of a single day's movements, as in the earlier analysis of the day-range turns. The summary statistics for the turns between the "steps" are given in Table 6.31. As might be expected, given the straightness of the paths between the points of "discontinuity", these results are very similar to those presented in Table 6.25, for samples of turns at the same points but between the steps of the 25-ft partition. All samples show a significant concentration of directions towards  $0^\circ$  and the values of  $r_0$  are highly correlated between the two tables (Kendall's Tau = 0.83,  $p < 0.0001$ ). It is thus not surprising to see once again the now familiar pattern of differences among the three classes.

**TABLE 6.31 STATISTICS FOR THE TURN ANGLES BETWEEN INTER-"DISCONTINUITY" STEPS**

Turtle	n	m <sub>01</sub>	r <sub>01</sub>	n	m <sub>02</sub>	r <sub>02</sub>	r <sub>01</sub> <sup>2</sup>
<b>Residents:</b>							
1	56	339	0.537	35	342	0.808	0.288
4	116	352	0.503	89	328	0.248	0.253
7	116	11	0.259	80	20	0.178	0.067
8r	27	38	0.419	19	46	0.163	0.176
9	160	2	0.438	119	11	0.240	0.192
10	164	359	0.365	129	2	0.127	0.133
16	111	20	0.200	81	109	0.081	0.040
26	82	352	0.535	60	353	0.275	0.286
total	832	0	0.383	612	0	0.179	0.146
<b>Transients:</b>							
8tr	83	5	0.737	59	0	0.749	0.543
11	13	53	0.620	10	25	0.241	0.384
12	29	356	0.692	24	356	0.520	0.479
14	10	343	0.561	5	29	0.921	0.314
17	18	346	0.901	15	332	0.837	0.811
23	28	6	0.859	20	5	0.776	0.738
27	15	9	0.519	11	42	0.268	0.269
total	196	3	0.708	144	0	0.636	0.501
<b>Experimentals:</b>							
X1	11	354	0.638	10	0	0.379	0.407
X2	25	349	0.463	20	322	0.671	0.214
X15	32	3	0.665	26	358	0.457	0.443
X16	27	358	0.342	17	339	0.240	0.117
X17	33	350	0.612	25	338	0.498	0.375
X18	0	-	-	0	-	-	-
X19	33	4	0.616	27	359	0.566	0.380
total	161	1357	0.553	125	345	0.470	0.306

Between-class comparisons of r<sub>01</sub>

Kruskal-Wallis: H = 10.6, p < 0.01

Mann-Whitney:

Res vs Tran: U = 2, p < 0.001

Res vs Exp: U = 9, p < 0.05

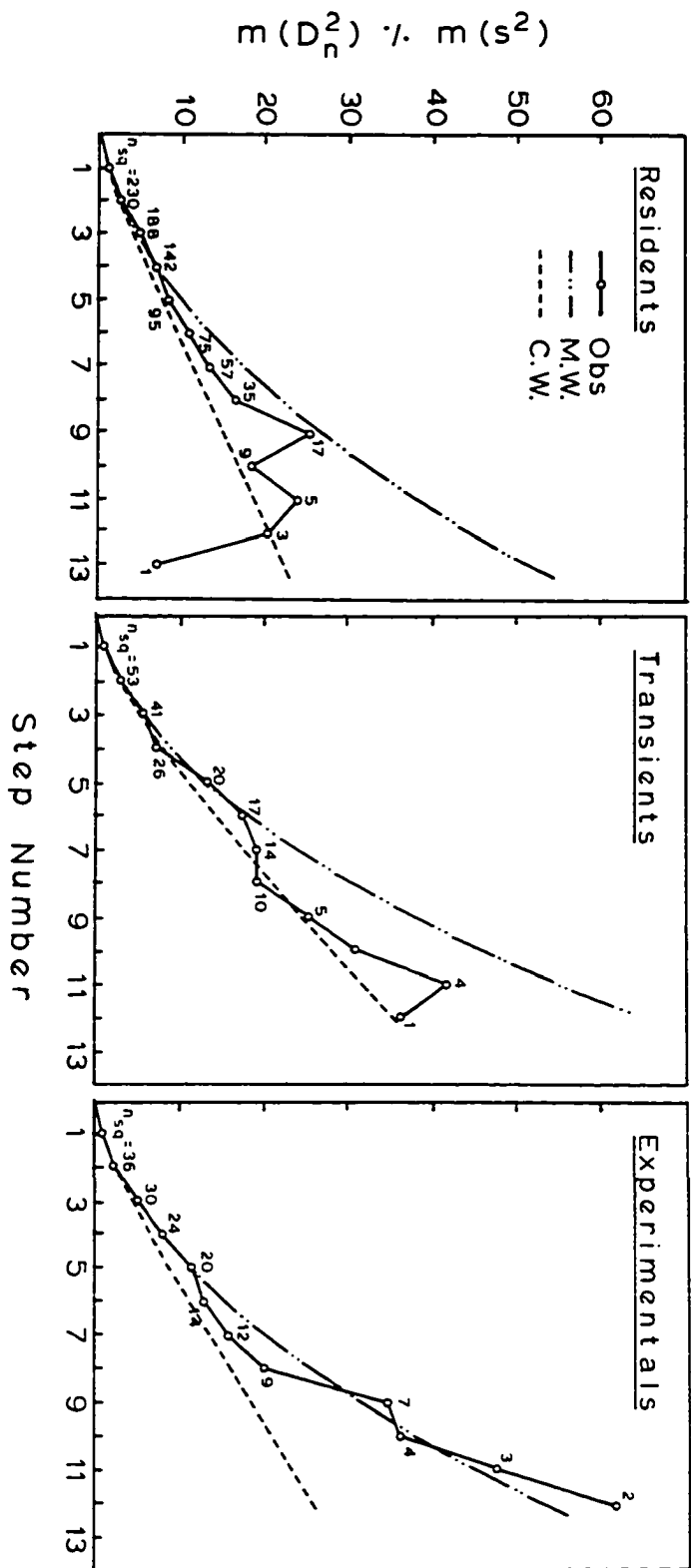
Tran vs Exp: U = 10, n.s.

Also similar to the lower-level pattern, the values of  $r_{\theta 2}$  indicate that orientation is still in operation at this level of measurement, for all classes. In all but five cases, the values of  $r_{\theta 2}$  are higher than the square of  $r_{\theta 1}$ , the expected value under the hypothesis of a simple correlated walk. Although the MSD curves (Figure 6.11) are far more jagged than those of the lower scale — probably as a result of the smaller number of samples available at this level of measurement and the additional variability of the step lengths — they lie mainly above the curve for the correlated walk. That they also fall below the expectations for the menotactic walk perhaps indicates that there are still higher level points of discontinuity within these series.

In order to disentangle some of the sources of variability within these curves, I resorted once again to the statistical screening methods used in the preceding section (although now without the naive hope that truly homogeneous sequences can be isolated through this approach). The outcome is similar once more to the earlier findings, as is shown in Table 6.32. The Residents again have a disproportionately high number of apparently random sequences, while the Transients have the greatest number of apparently unbiased, oriented sequences. The rank order for the values of  $r_{\theta}$  for the 2nd-order unbiased sequences of the three classes is as always, Residents lowest, Experimentals intermediate, Transients highest. These results all suggest that the same sort of factors are operating in these "steps" as at the level of the 25-ft partition.

**FIGURE 6.11** Sequences of steps whose endpoints are visually-  
determined sites of discontinuity.

# Steps Between Visually Determined Discontinuities



**TABLE 6.32. RESULTS OF SCREENING SEQUENCES OF "DISCONTINUITY" STEPS FOR BIASEDNESS AMONG FIRST AND SECOND ORDER TURNS**

Turtle	No. of Random and Curved Seqs. <sup>1</sup>	No. of 1st-Order Unbiased Seqs. <sup>2</sup>	No. of 2nd-Order Unbiased Seqs. <sup>3</sup>
<b>Residents:</b>			
1	0	0	0
4	3	5	2
7	7	1	0
8r	1	0	0
9	4	6	2
10	7	6	0
16	8	0	0
26	3	3	2
total	33 ( = 61%)	21 ( = 39%)	6 ( = 11%)
			$m_{\theta} = 357^{\circ}$
			$r_{\theta} = 0.633$
<b>Transients:</b>			
8tr	0	6	5
11	1	0	0
12	0	2	1
14	0	0	0
17	0	2	2
23	0	2	2
27	1	0	0
total	2 ( = 14%)	12 ( = 86%)	10 ( = 71%)
			$m_{\theta} = 2^{\circ}$
			$r_{\theta} = 0.823$
<b>Experimentals:</b>			
X1	0	1	1
X2	0	2	1
X15	0	3	1
X16	1	0	0
X17	0	2	1
X18	0	0	0
X19	0	3	2
total	1 ( = 8%)	11 ( = 92%)	6 ( = 50%)
			$m_{\theta} = 357^{\circ}$
			$r_{\theta} = 0.666$

1. Sequences whose first order turns did not pass the V-Test, Rayleigh Test, or Stephen's Test for the Mean Direction Equal to  $0^{\circ}$ .
2. Sequences whose first order turns passed the above tests.
3. Sequences whose both first and second order turns passed the above tests.

Figure 6.12 shows, however, additional features of these walks that were not observable at the previous level of analysis, where step lengths were all uniform in length as a result of the surveying methods. There appears to be some positive correlation between a "step's" length and its direction when the actual mean squared distances of travel (scaled by dividing the MSD's by the mean squared step length, MSS) are compared to curves for the mean squared resultants (MSR's), created by holding the step lengths constant and thus allowing only the contribution of the orientational components to be seen.

This result is clearest shown within the "random" sequences of the Residents and to a lesser extent within the second-order unbiased sequences of the Transients. In these two samples (representing the majority of my data at this level of analysis) the azimuthal curves lie below the expectations for a menotactic walk, whereas the actual MSD's (where step length is a variable) run above their predicted curves. Evidently, the lengths of the steps are greater when their directions are closer to the target headings (as explained in Section IV.D). Conversely, the steps that are more divergent in their orientation are likely to be shorter, although often composed of several 25-ft steps themselves (that is what probably induces the discontinuity effects noted in the curves). This interpretation is supported by the examples illustrated in Figure 6.13.

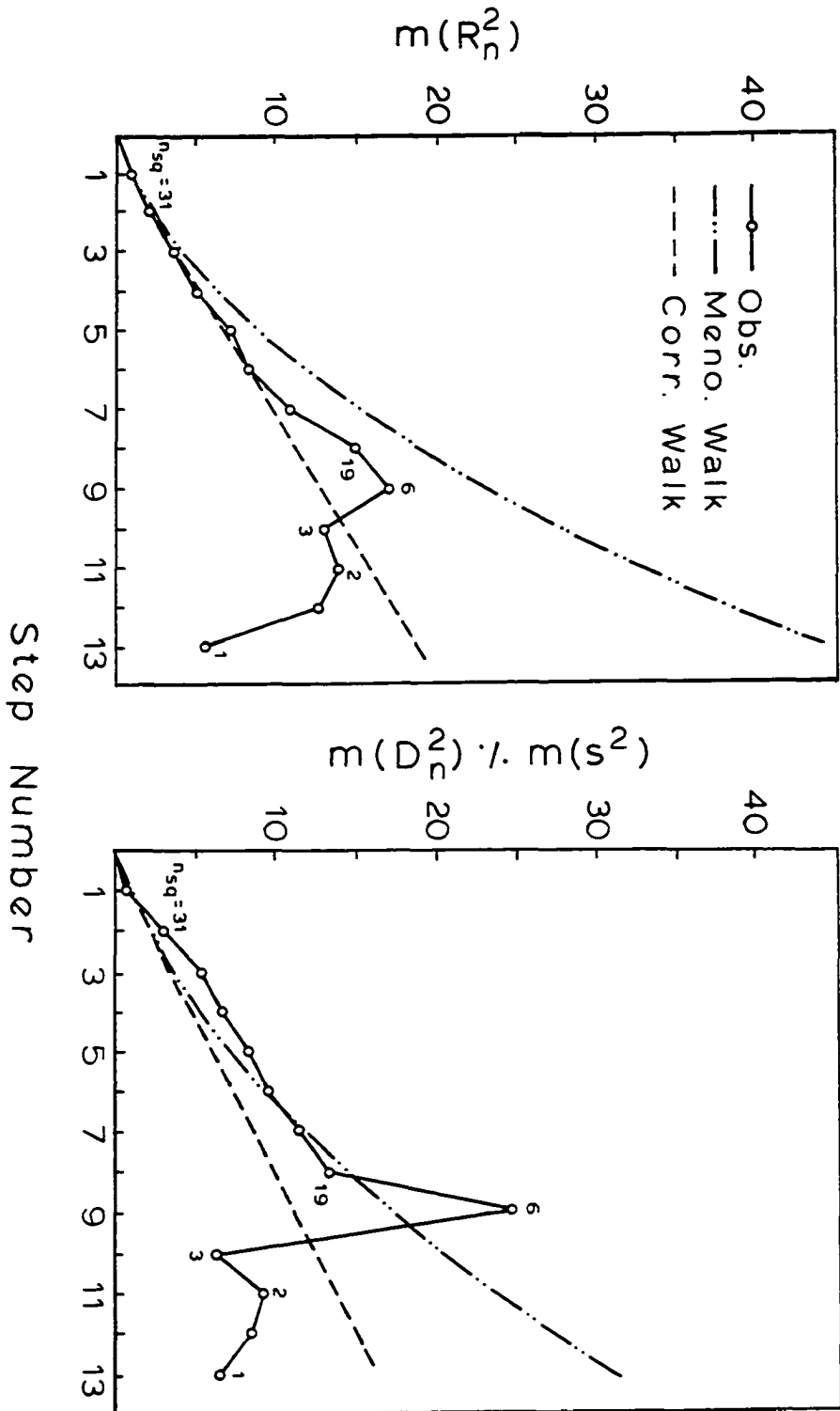
The downward bowing in the MSD / MSS curves compared to the MSR curves for the second-order unbiased sequences of the Residents and Experimentals can be explained in a similar way but with the inclusion of klinokinetic effects: the more disoriented, shorter steps appear



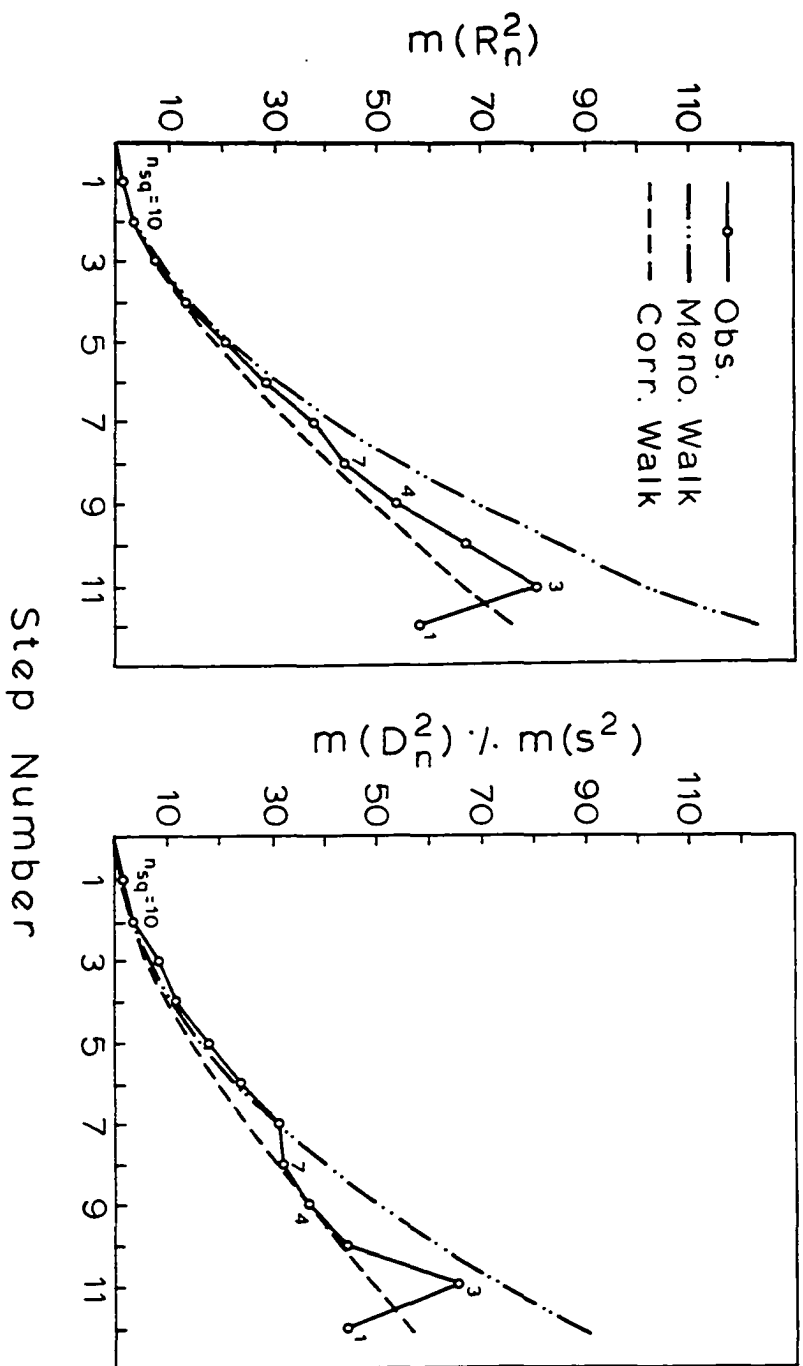
**FIGURE 6.12** MSD analysis of sequences of steps between visually-determined discontinuities. Each sample was examined first by looking only at the directional components of the steps, using the squared resultant,  $R_n$ . Next the combined contribution of step length and direction was considered, using the actual mean squared distance of travel (scaled by dividing by the mean squared step length).

- a. Residents' sequences that showed no significant concentration of turn angles towards  $0^\circ$ .
- b. Transients' sequences that showed significant concentration of values of both first- and second-order turns towards  $0^\circ$ .
- c. Residents' sequences that showed significant concentration of first- and second-order turns towards  $0^\circ$ .
- d. Experimentals' sequences that showed significant concentration of first- and second-order turns towards  $0^\circ$ .

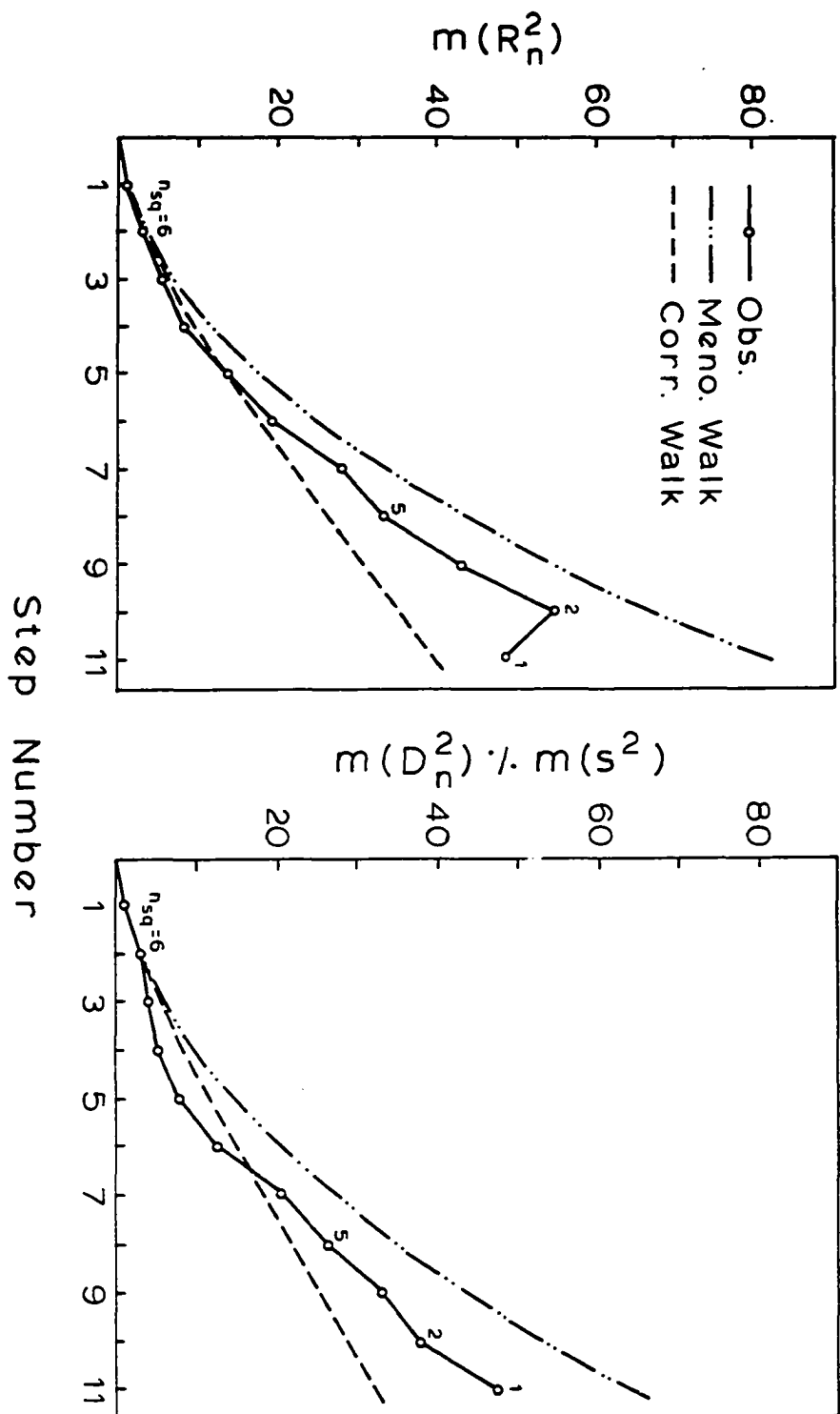
# Residents: "Random" Series of "Discontinuity" Steps



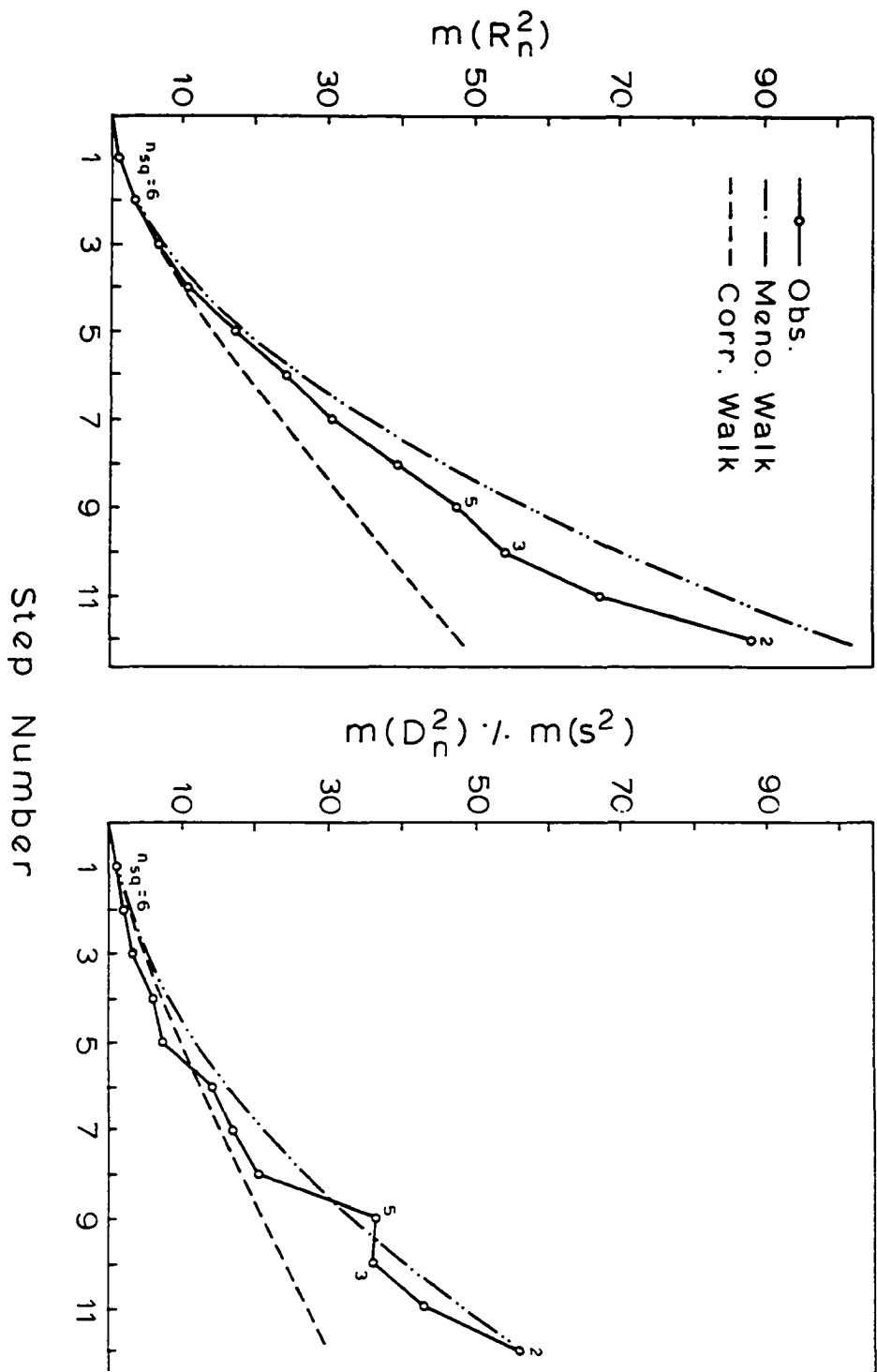
# Transients: Unbiased Series of "Discontinuity" Steps



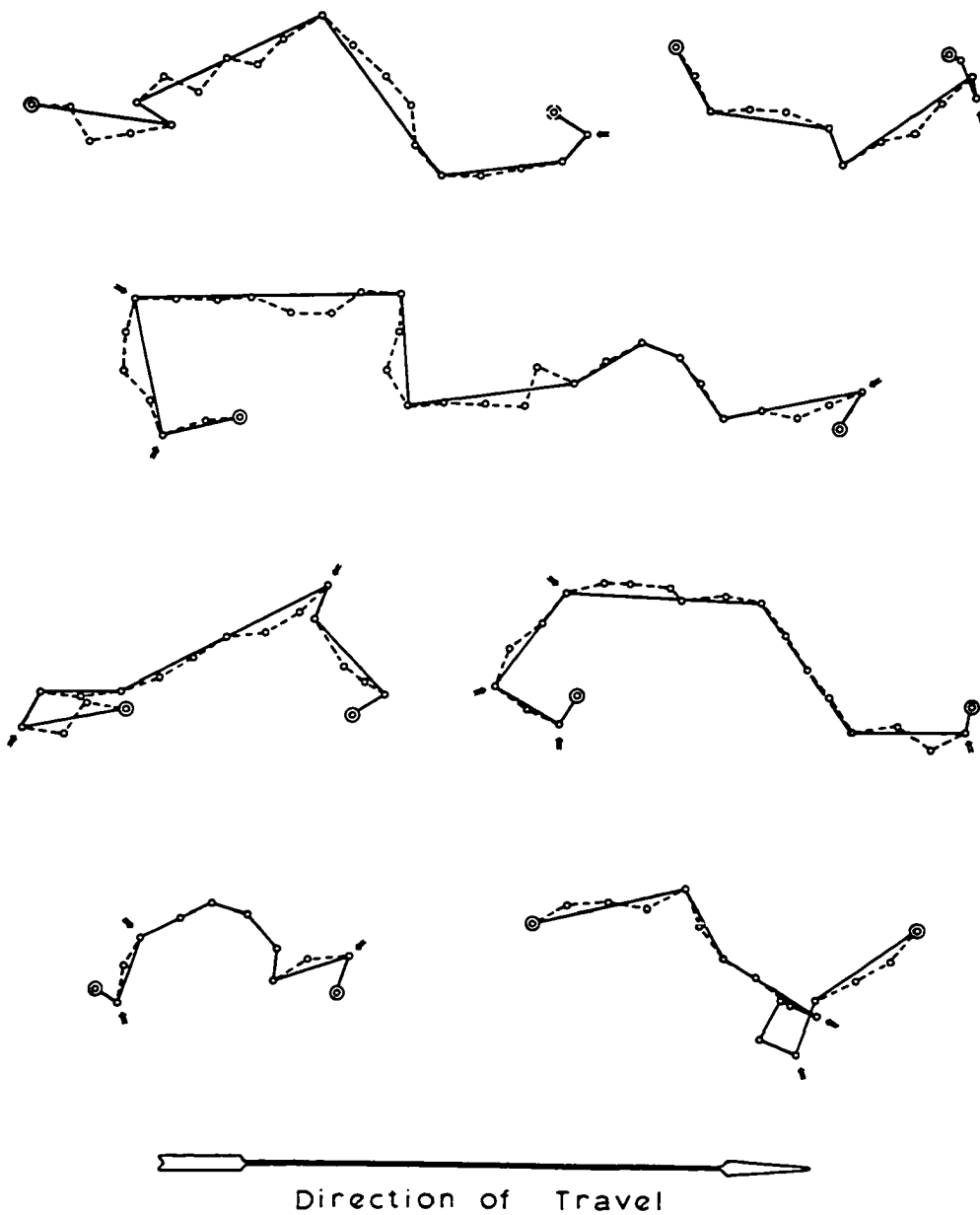
# Residents: Unbiased Series of "Discontinuity" Steps



# Experimentals: Unbiased Series of "Discontinuity" Steps



**FIGURE 6.13** Examples of steps (solid lines) spanning points of visually-determined discontinuity (the paths as originally surveyed are indicated by dashed lines). All series belong to Turtle 7's sample of "random" sequences. Possible points of higher-order discontinuity are indicated by arrows. Note that the steps that depart most radically from the overall heading for the day range (arranged here towards the right) are generally the shortest in the sequence and concentrated near the form-sites (indicated by double circles).



to occur near the beginnings of these sequences and the less deflected, longer steps later on.

Why this trend should show up in these sequences but not the rest of the samples is unclear. Note, however, that all these sequences begin at known form-sites and the first turn at the outset of a day's movements, for the Residents at least, appeared to average larger than those of the rest of the day (with the exception of the final turn). Recall that the initial 25-ft step of a day was for that reason often visually marked off as a single "discontinuity" step in the lower-level subjective analysis.

The choice of a form-site also seemed to result in larger than usual terminal turns, again at least among the Residents. The final 25-ft step (actually usually much shorter) was also frequently treated as a separate "discontinuity". Since this final step would not be synchronized across the series, unlike the first steps, it could contribute to the generally ragged appearance of the curves with increasing step number. Of course, the decrease in number of series to be averaged at high values of  $n$  adds to this picture by increasing the sampling error present at the ends of the curves.



Analysis of the day-range vectors. While the existence of one or possibly two levels of discontinuities can only be tentatively identified within days (due to the subjective nature of the preceding analysis), the presence of discontinuities at the form-sites appears is well established. Not only do these points represent major breaks in activity, but the large magnitude of turns that occur there, especially relative to the within-day turns that bracket them, indicates that important changes in direction also occur at these sites. Moreover, the form-site turns have also been shown to be larger on the average than those taking place at the visually identified "discontinuities" (Table 6.26). Thus entire day-ranges represent steps on at least a third level in the overall route hierarchy, and perhaps even higher, depending on how many distinct levels occur within the day-ranges.

Table 6.33 presents the turn-angle statistics for the vectors spanning entire day-ranges, and Table 6.34 the corresponding information for their lengths. Again, given the relative straightness of the day-ranges, there is a fairly close agreement between these results and those presented in Tables 6.4 and Table 6.15 for the analyses of day-ranges at the 25-ft scale of measurement. The main difference in terms of lengths is that here the Residents are significantly different from the other two classes, resulting from their higher deflectivities over at least two levels of walks and their generally shorter path lengths. With respect to the angular data, all but one of the Residents' samples again show no significant concentration of values while the other two classes show a clear concentration towards  $0^{\circ}$ . As with the earlier findings, the Residents differ significantly from the other two and there appear to be no important

**TABLE 6.33a. STATISTICS FOR THE ANGLES TURNED BETWEEN DAY-RANGE VECTORS**

Turtle	Day-range Vectors				Form-sites
	n	m <sub>θ</sub>	r <sub>θ</sub>	c <sub>θ</sub>	c <sub>θ</sub>
<b>Residents:</b>					
1	27	12	0.36	0.35**	0.26*
4	28	288	0.39	0.12	0.26
7	33	83	0.13	0.02	0.03
8r	10	43	0.34	0.25	0.55**
9	41	46	0.14	0.10	-0.05
10	35	0	0.17	0.17	0.11
16	27	198	0.09	-0.16	-0.06*
26	21	18	0.27	0.26	0.27*
total	222	7	0.13	0.13	0.11**

Correlation between c<sub>θ</sub> for day-range vectors and for 25-ft steps leading into and out of the form-sites:

Kendall's Tau = 0.71, p = 0.0071

**Transients:**

8tr	16	338	0.31	0.29	0.47**
11	2	310	0.97	0.62	0.62
12	3	1	0.43	0.43	0.67
14	4	330	0.65	0.56	0.52
17	3	62	0.47	0.22	0.58*
23	12	4	0.65	0.65**	0.51**
27	2	42	1.00	0.74	0.08**
total	42	356	0.46	0.46**	0.49**

Correlation between values of c<sub>θ</sub>:

Kendall's Tau = -0.33, n.s.

**Experimentals:**

X2	4	300	0.70	0.35	0.69*
X15	6	342	0.71	0.68**	0.66*
X16	10	14	0.24	0.23	0.29*
X17	8	327	0.60	0.50*	0.46*
X19	5	347	0.73	0.71**	0.28**
total	33	337	0.50	0.46**	0.37**

Correlation between values of c<sub>θ</sub>:

Kendall's Tau = -0.20, n.s.

\* Significant at 0.05 level, V-Test

\*\* Significant at 0.01 level

**TABLE 6.33b. INTER-CLASS COMPARISONS OF  $C_0$  FOR DAY-RANGE VECTORS**

Kruskall-Wallis:  $H = 9.52$ ,  $p < 0.05$

Mann-Whitney:

Residents vs Transients:  $U = 4$ ,  $p = 0.007$

Residents vs Experimentals:  $U = 4$ ,  $p = 0.003$

Transients vs Experimentals:  $U = 17$ , n.s.

**TABLE 6.34 STATISTICS FOR THE LENGTH COMPONENTS OF THE DAY-RANGE VECTORS\***

Turtle	n	$\bar{x}$	s
<b>Residents:</b>			
1	29	118	91.7
4	37	134	121.4
7	40	118	86.9
8r	12	111	107.7
9	54	104	78.6
10	45	94	90.7
16	35	84	57.4
26	25	119	90.8
Total	277	109	90.3
<b>Transients:</b>			
8tr	19	158	215.2
11	3	191	91.5
12	4	319	129.4
14	5	185	107.1
17	4	206	227.5
23	13	126	116.3
27	3	238	93.0
Total	51	175	168.5
<b>Experimentals:</b>			
X2	5	183	103.8
X15	7	302	199.5
X16	11	121	93.1
X17	9	216	260.2
X19	6	304	194.3
Total	38	214	187.5

\* Includes only those segments used in the MSD analysis

**Inter-class comparisons:**

Kruskall-Wallis:  $H = 12.6, p < 0.01$

Mann-Whitney:

Residents vs Transients:  $U = 1, p < 0.001$

Residents vs Experimentals:  $U = 1, p < 0.001$

Transients vs Experimentals:  $U = 13, n.s.$

differences between the Transients and the Experimentals.

Only for the Residents, however, is there a strong correlation among individuals between the values of  $C_0$  for the form-site turns and the turns between the day-range vectors. In the similar comparison of different levels of turns made with respect to the visually determined points of "discontinuity", discussed above, all three classes showed such relationships. Among the Residents the change in direction at the start of the day is evidently of major importance; subsequent changes in target do not alter the overall "straightness" of the day-ranges sufficiently to destroy the angular relationships between the steps at the form-sites themselves. In contrast, even though the day-ranges of the Transients and Experimentals are generally more linear (less deflected) than the Residents', the lack of correspondences among the two types of turns within these groups indicate that other, within-day changes in target are roughly equivalent to the form-site turns in importance. This difference is probably related to the smaller magnitudes of turns at their form-sites compared to the Residents'.

More striking evidence for the importance of the between-day turns for the Residents comes from the results of the MSD analysis of the day-range vectors (Table 6.35 and Figure 6.14). Whereas the dominant pattern within the day-ranges was one of linear orientation, just the opposite is the case for the between-day movements. In all but one Resident, T10, the observed MSD's either reach a horizontal asymptote or fall back towards zero after only a few days' travels (T1 also has one higher point at the end of her curve, as a result of an egg-laying trip, an excursion probably possessing a much lower deflec-

**TABLE 6.35a MEAN SQUARED RESULTANTS FOR SEQUENCES OF DAY-RANGE  
AZIMUTHS: RESIDENTS**

Mean Squared Resultants								
Turtle	n <sub>st</sub> =	2	3	4	5	6	7	8
1	n <sub>sq</sub>	4	4	4	4	4	4	1
	e <sub>mw</sub>	2.63	4.89	7.78	11.30	15.46	20.24	25.65
	o	<b>2.53</b>	<b>5.47</b>	<b>8.43</b>	<b>12.81</b>	<b>12.89</b>	<b>10.34</b>	<b>21.97</b>
	e <sub>cw</sub>	2.63	4.45	6.34	8.24	10.14	12.05	13.95
4	n <sub>sq</sub>	9	7	6	3	3		
	e <sub>mw</sub>	2.24	3.72	5.44	7.40	9.60		
	o	<b>2.10</b>	<b>2.49</b>	<b>4.91</b>	<b>2.15</b>	<b>0.86</b>		
	e <sub>cw</sub>	2.24	3.24	4.14	5.05	5.99		
7	n <sub>sq</sub>	7	6	6	5	4	3	2
	e <sub>mw</sub>	2.03	3.10	4.19	5.32	6.49	7.68	8.91
	o	<b>2.26</b>	<b>2.04</b>	<b>2.43</b>	<b>4.48</b>	<b>4.66</b>	<b>5.71</b>	<b>4.51</b>
	e <sub>cw</sub>	2.03	3.03	4.03	5.03	6.03	7.03	8.03
8r	n <sub>sq</sub>	2	2	2	2	2		
	e <sub>mw</sub>	2.50	4.49	6.99	9.98	13.47		
	o	<b>2.04</b>	<b>3.62</b>	<b>2.12</b>	<b>3.76</b>	<b>7.84</b>		
	e <sub>cw</sub>	2.50	4.01	5.47	6.91	8.34		
9	n <sub>sq</sub>	12	10	6	4	3	2	2
	e <sub>mw</sub>	2.20	3.60	5.19	6.99	8.98	11.18	13.57
	o	<b>2.30</b>	<b>2.77</b>	<b>2.06</b>	<b>1.44</b>	<b>1.80</b>	<b>1.66</b>	<b>0.37</b>
	e <sub>cw</sub>	2.20	3.40	4.59	5.78	6.97	8.16	9.35
	n <sub>st</sub> =	9	10					
	n <sub>sq</sub>	1	1					
	e <sub>mw</sub>	16.16	18.95					
	o	<b>1.41</b>	<b>0.27</b>					
	e <sub>cw</sub>	10.54	11.73					
10	n <sub>sq</sub>	10	7	5	4	4	2	2
	e <sub>mw</sub>	2.33	3.99	5.99	8.31	10.97	13.96	17.28
	o	<b>2.86</b>	<b>3.30</b>	<b>4.80</b>	<b>7.69</b>	<b>8.90</b>	<b>18.69</b>	<b>25.18</b>
	e <sub>cw</sub>	2.33	3.72	5.11	6.51	7.91	9.30	10.70
	n <sub>st</sub> =	9						
	n <sub>sq</sub>	1						
	e <sub>mw</sub>	20.93						
	o	<b>11.19</b>						
	e <sub>cw</sub>	12.10						

TABLE 6.35a. CONTINUED

		Mean Squared Resultants							
		$n_{st} =$	2	3	4	5	6	7	8
16	$n_{sq}$	8	6	5	3	3	2		
	$e_{mw}$	-	-	-	-	-	-		
	$c_o$	1.95	1.82	3.69	1.02	2.59	2.10		
	$e_{cw}$	1.83	2.68	3.53	4.37	5.22	6.07		
26	$n_{sq}$	4	3	3	2	2	2	2	
	$e_{mw}$	2.52	4.56	7.12	10.21	13.81	17.94	22.58	
	$c_o$	2.49	3.51	6.63	9.40	6.29	6.26	2.86	
	$e_{cw}$	2.52	4.16	5.83	7.50	9.17	10.83	12.50	
		$n_{st} =$	9	10					
		$n_{sq}$	2						
		$e_{mw}$	27.75	33.43					
		$c_o$	6.02	6.94					
		$e_{cw}$	14.17	15.84					
total	$n_{sq}$	56	45	37	27	25	15	9	
	$e_{mw}$	2.25	3.75	5.49	7.49	9.73	12.23	14.97	
	$c_o$	2.33	2.91	4.24	5.41	5.99	7.73	9.76	
	$e_{cw}$	2.25	3.53	4.81	6.10	7.38	8.66	9.95	
		$n_{st} =$	9	10					
		$n_{sq}$	4	2					
		$e_{mw}$	17.98	21.22					
		$c_o$	4.48	3.60					
		$e_{cw}$	11.23	12.51					

\*  $c_\theta$  was negative in violation of menotactic model

**TABLE 6.35b MEAN SQUARED DISTANCES OF TRAVEL DIVIDED BY MEAN SQUARED STEP LENGTHS FOR SEQUENCES OF DAY-RANGE VECTORS: RESIDENTS**

		M (D <sup>2</sup> ) / M (S <sup>2</sup> )						
Turtle	n <sub>st</sub> =	1	2	3	4	5	6	7
1	n <sub>sq</sub>	4	4	4	4	4	4	4
	e <sub>mw</sub>	1.00	2.40	4.20	6.40	8.99	11.99	15.39
	o	1.26	1.32	4.41	7.49	7.26	6.55	6.15
	e <sub>cw</sub>	1.00	2.40	3.92	5.48	7.05	8.62	10.20
	n <sub>st</sub> =	8						
	n <sub>sq</sub>	1						
	e <sub>mw</sub>	19.18						
	o	21.03						
	e <sub>cw</sub>	11.77						
4	n <sub>sq</sub>	9	9	7	6	3	3	
	e <sub>mw</sub>	1.00	2.13	3.40	4.80	6.33	7.99	
	o	0.57	1.90	2.18	3.50	4.61	2.87	
	e <sub>cw</sub>	1.00	2.13	3.13	4.08	5.03	5.99	
7	n <sub>sq</sub>	7	7	6	6	5	4	3
	e <sub>mw</sub>	1.00	2.02	3.06	4.13	5.21	6.32	7.45
	o	0.72	3.59	2.02	2.01	1.21	1.95	0.29
	e <sub>cw</sub>	1.00	2.02	3.02	4.02	5.02	6.02	7.03
	n <sub>st</sub> =	8						
	n <sub>sq</sub>	2						
	e <sub>mw</sub>	8.59						
	o	0.19						
	e <sub>cw</sub>	8.02						
8r	n <sub>sq</sub>	2	2	2	2	2	2	
	e <sub>mw</sub>	1.00	2.27	3.80	5.60	7.66	10.00	
	o	2.79	4.64	4.41	4.39	4.49	4.35	
	e <sub>cw</sub>	1.00	2.27	3.54	4.79	6.02	7.25	
9	n <sub>sq</sub>	12	12	10	6	4	3	2
	e <sub>mw</sub>	1.00	2.13	3.38	4.76	6.27	7.91	9.67
	o	0.86	1.98	4.32	3.55	0.96	1.02	0.14
	e <sub>cw</sub>	1.00	2.13	3.25	4.38	5.50	6.62	7.74
	n <sub>st</sub> =	8	9	10				
	n <sub>sq</sub>	2	1	1				
	e <sub>mw</sub>	11.56	13.58	15.72				
	o	1.22	2.42	0.26				
	e <sub>cw</sub>	8.86	9.99	11.11				



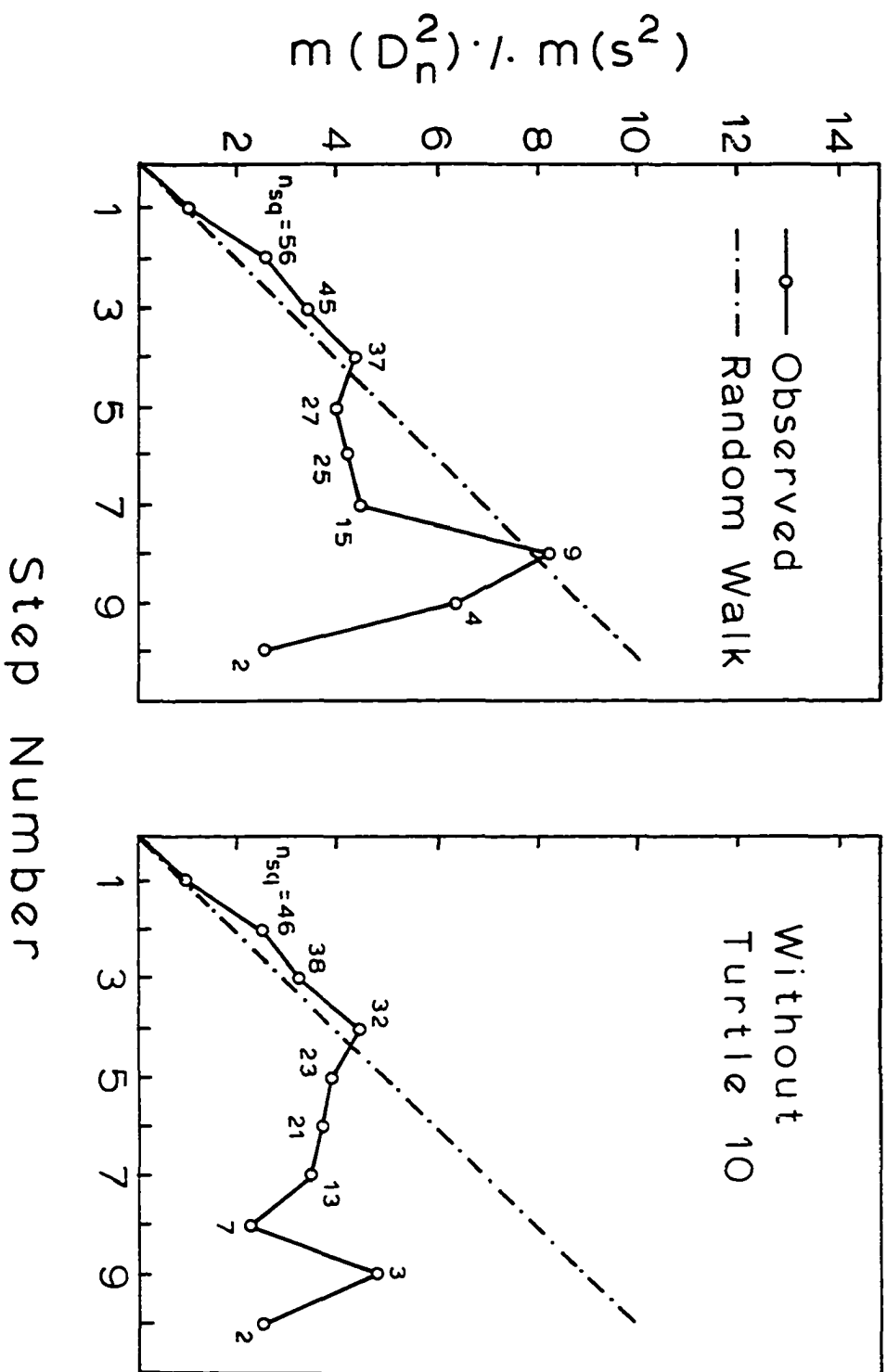
TABLE 6.35b. CONTINUED

		M (D <sup>2</sup> ) / M (S <sup>2</sup> )						
		n <sub>st</sub> = 1	2	3	4	5	6	7
10	n <sub>sq</sub>	10	10	7	5	4	4	2
	e <sub>mw</sub>	1.00	2.17	3.52	5.04	6.73	8.60	10.63
	o	1.52	3.17	3.77	3.71	4.72	7.51	12.54
	e <sub>cw</sub>	1.00	2.17	3.38	4.58	5.79	7.00	8.20
	n <sub>st</sub> =	8	9					
	n <sub>sq</sub>	2	1					
	e <sub>mw</sub>	12.85	15.24					
	o	21.79	12.95					
	e <sub>cw</sub>	9.41	10.62					
	n <sub>st</sub> =	8	9					
16	n <sub>sq*</sub>	8	8	6	5	3	3	2
	e <sub>mw</sub>	-	-	-	-	-	-	-
	o	1.00	2.65	3.74	7.24	1.95	2.48	3.06
	e <sub>cw</sub>	1.00	1.89	2.78	3.68	4.57	5.47	6.36
	n <sub>st</sub> =	8	9					
26	n <sub>sq</sub>	4	4	3	3	2	2	2
	e <sub>mw</sub>	1.00	2.33	4.00	6.01	8.35	11.02	14.02
	o	1.81	3.93	4.14	6.89	7.18	6.23	7.11
	e <sub>cw</sub>	1.00	2.33	3.75	5.17	6.60	8.03	9.46
	n <sub>st</sub> =	8	9	10				
	n <sub>sq</sub>	2	2	1				
	e <sub>mw</sub>	17.37	21.04	25.05				
	o	5.53	5.83	4.50				
	e <sub>cw</sub>	10.89	12.32	13.75				
	n <sub>st</sub> =	8	9	10				
total	n <sub>sq</sub>	56	56	45	37	27	25	15
	e <sub>mw</sub>	1.00	2.15	3.44	4.89	6.48	8.21	10.10
	o	1.06	2.60	3.35	4.45	4.04	4.27	4.56
	e <sub>cw</sub>	1.00	2.15	3.31	4.48	5.65	6.82	7.99
	n <sub>st</sub> =	8	9	10				
	n <sub>sq</sub>	9	4	2				
	e <sub>mw</sub>	12.13	14.31	16.64				
	o	8.31	6.47	2.60				
	e <sub>cw</sub>	9.15	10.32	11.49				

\* c<sub>θ</sub> was negative in violation of menotactic model

**FIGURE 6.14** Residents' sequences of day-range vectors, with and without the contribution of Turtle 10. The curves for the mean squared resultants ( $R_n$ ) are ignored here since they do not contribute anything to the picture given by the actual mean squared distances of travel — no significant klinotactic effects show up in these samples.

# Residents: Day Range Vectors



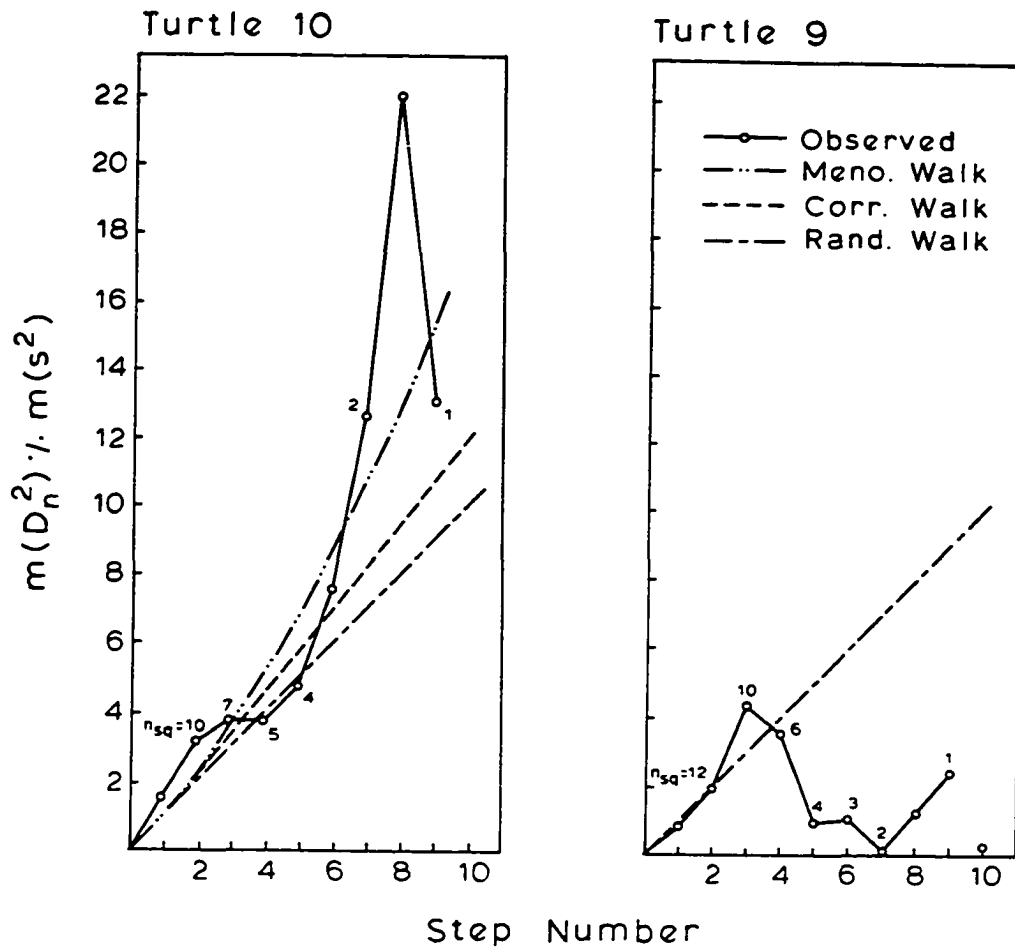
tivity than the rest of her sample; when her "resident" routes are treated separately, an asymptote is clearly reached).

These results do not appear to be produced by a biased correlated walk; the predictions derived from the turn distributions generally indicate an onward-going tendency (this interpretation assumes, of course, that the turns do not represent a mixture of different populations, with different mean headings). Most likely, these curves represent the action of true spatial constraints on the movements of this class of turtles, as was proposed by Waser (1976) for similar curves obtained from the movements of mangabey monkeys.

But what about Turtle 10, who in all other respects discussed so far appears to be a typical Resident? This turtle shows no evidence for between-day constraints (Figure 6.15) despite the fact that he was found on the study area during large parts of four consecutive years and was observed hibernating there once. The answer probably lies partly in the relatively large range he covered (Figure 2.5g). Perhaps the series of day-range vectors were simply too short to demonstrate any boundary effects. On the other hand, Turtle 9, a male whose range overlapped T10's extensively, shows very strong constraints over series of similar length, despite the fact that his apparent range was nearly as big as T10's. A more important difference lies in the way T10 patterned his movements within his range. More than any other Resident, he made long sweeping movements across his range and interspersed among these journeys several days of more spatially concentrated activity. Turtle 9, in comparison, was more prone to loop back to areas he had visited only a few days before. Whether this is a sufficient explanation for the differences between

**FIGURE 6.15** A comparison of the day-range sequences belonging to Turtle 10 with those of Turtle 9, another male whose pattern is more typical of the residents as a whole.

# Day Range Vectors



T10 and the rest of the Residents, however, cannot be judged using these data. The question of T10's residency status will be taken up again in the next section.

Similar in appearance to T10's curve are those of the Transients (Table 6.36 and Figure 6.16). Unlike the Residents, which typically show a dramatic shift in pattern from within-days to between-days, no major change in route behavior occurs in this class. In fact, the curves here are quite similar to those presented in the previous section for the "discontinuity" steps. The dominant pattern once again involves active orientation, as seen in the position of the observed MSD's above the expectations for a correlated walk. As found in the inter-"discontinuity" series, there also appears to be some evidence for a correlation between step length and direction. This effect shows up most clearly when the routes are divided into as many series of at least four steps as possible to obtain a more uniform set of averages. It is also well-exemplified within just the routes of T8tr (Figure 6.17). Despite an extremely low value for  $c_0$  — not significantly different from zero — her overall routes were very straight (Figure 2.6b), perhaps in part because of the klinotactic-like effects apparent within her day-range vectors.

The data for the Experimentals also show signs of this sort of correlation, but Table 6.37 and Figure 6.18 indicate there could also be the kind of klinokinetic non-stationarity that was discussed in the preceding section on the "discontinuity" steps. The strong downward bowing seen in the MSD curve as compared to the azimuthal MSR curve suggests that the day-ranges were initially short and more deflected and their paths became longer and narrower as the turtle moved away

**TABLE 6.36a MEAN SQUARED RESULTANTS FOR SEQUENCES OF DAY-RANGE  
AZIMUTHS: TRANSIENTS**

		Mean Squared Resultants						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
8tr	$n_{sq}$	3	2	2	2	2	1	1
	$e_{mw}$	2.57	4.71	7.42	10.70	14.55	18.97	23.96
	$o$	2.40	2.51	4.65	8.55	9.18	6.86	12.34
	$e_{cw}$	2.57	4.28	6.01	7.74	9.46	11.19	12.92
	$n_{st} =$	9	10	11				
	$n_{sq}$	1	1	1				
	$e_{mw}$	29.51	35.64	42.34				
	$o$	19.61	26.06	36.92				
	$e_{cw}$	14.65	16.37	18.10				
11	$n_{sq}$	1	1					
	$e_{mw}$	3.26	6.79					
	$o$	3.62	5.21					
	$e_{cw}$	3.26	5.23					
12	$n_{sq}$	1	1	1				
	$e_{mw}$	2.87	5.60	9.21				
	$o$	1.03	3.66	8.41				
	$e_{cw}$	2.87	5.11	7.52				
14	$n_{sq}$	1	1	1	1			
	$e_{mw}$	3.12	6.37	10.74	16.24			
	$o$	1.09	2.26	6.13	11.28			
	$e_{cw}$	3.12	5.67	8.23	10.62			
17	$n_{sq}$	1	1	1				
	$e_{mw}$	2.43	4.30	6.59				
	$o$	0.42	0.54	2.86				
	$e_{cw}$	2.43	3.62	4.60				
23	$n_{sq}$	1	1	1	1	1	1	1
	$e_{mw}$	3.29	6.88	11.76	17.94	25.40	34.16	44.22
	$o$	3.66	1.64	5.14	10.35	16.97	26.18	37.39
	$e_{cw}$	3.29	6.42	10.07	14.07	18.27	22.61	27.03
	$n_{st} =$	9	10	11	12	13		
	$n_{sq}$	1	1	1	1	1		
	$e_{mw}$	55.57	68.21	82.14	97.37	113.89		
	$o$	50.51	64.54	79.95	92.11	112.17		
	$e_{cw}$	31.50	36.00	40.53	45.06	49.60		



**TABLE 6.36a CONTINUED**

		Mean Squared Resultants						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
27	$n_{sq}$	1	1					
	$e_{mw}$	3.47	7.42					
	$\sigma$	3.51	6.12					
	$e_{cw}$	3.47	6.12					
total	$n_{sq}$	9	8	6	4	3	2	2
	$e_{mw}$	2.92	5.75	9.50	14.17	19.75	26.25	33.67
	$\sigma$	2.28	3.06	5.31	9.68	11.78	16.52	24.86
	$e_{cw}$	2.92	5.25	7.78	10.39	13.04	15.70	18.38
		$n_{st} =$	9	10	11	12	13	
		$n_{sq}$	2	2	2	1	1	
		$e_{mw}$	42.01	51.26	61.43	72.51	84.52	
		$\sigma$	35.06	45.30	58.44	92.11	112.17	
		$e_{cw}$	21.05	23.73	26.41	29.09	31.77	

**TABLE 6.36b MEAN SQUARED DISTANCES OF TRAVEL DIVIDED BY MEAN SQUARED STEP LENGTHS FOR SEQUENCES OF DAY-RANGE VECTORS: TRANSIENTS**

		M (D <sup>2</sup> ) / M (S <sup>2</sup> )						
Turtle	n <sub>st</sub> =	1	2	3	4	5	6	7
8tr	n <sub>sq</sub>	3	3	2	2	2	2	1
	e <sub>mw</sub>	1.00	2.21	3.62	5.24	7.07	9.10	11.34
	o	0.36	5.88	3.80	7.52	8.56	8.53	15.26
	e <sub>cw</sub>	1.00	2.21	3.46	4.73	5.99	7.26	8.52
	n <sub>st</sub> =	8	9	10	11			
	n <sub>sq</sub>	1	1	1	1			
	e <sub>mw</sub>	13.78	16.44	19.29	22.36			
	o	18.31	22.58	23.08	26.92			
	e <sub>cw</sub>	9.78	11.05	12.31	13.57			
	n <sub>st</sub> =	8	9	10	11			
11	n <sub>sq</sub>	1	1	1				
	e <sub>mw</sub>	1.00	3.09	6.28				
	o	1.75	2.90	3.94				
12	e <sub>cw</sub>	1.00	3.09	4.93				
	n <sub>sq</sub>	1	1	1	1			
	e <sub>mw</sub>	1.00	2.89	5.66	9.32			
14	o	0.26	1.03	3.14	9.18			
	e <sub>cw</sub>	1.00	2.77	4.88	7.13			
	n <sub>sq</sub>	1	1	1	1	1		
17	e <sub>mw</sub>	1.00	2.89	5.66	9.32	13.87		
	o	2.32	2.16	1.06	2.31	4.66		
	e <sub>cw</sub>	1.00	2.89	5.08	7.29	9.36		
23	n <sub>sq</sub>	1	1	1	1	1	1	1
	e <sub>mw</sub>	1.00	2.72	5.16	8.33	12.22	16.82	22.15
	o	0.01	3.06	2.96	3.48	6.11	10.62	18.39
	e <sub>cw</sub>	1.00	2.72	4.91	7.39	10.06	12.85	15.71
	n <sub>st</sub> =	8	9	10	11	12	13	
	n <sub>sq</sub>	1	1	1	1	1	1	
	e <sub>mw</sub>	28.20	34.98	42.47	50.69	59.62	69.28	
	o	29.17	30.93	31.23	36.11	57.63	78.89	
	e <sub>cw</sub>	18.62	21.55	24.51	27.47	30.44	33.42	

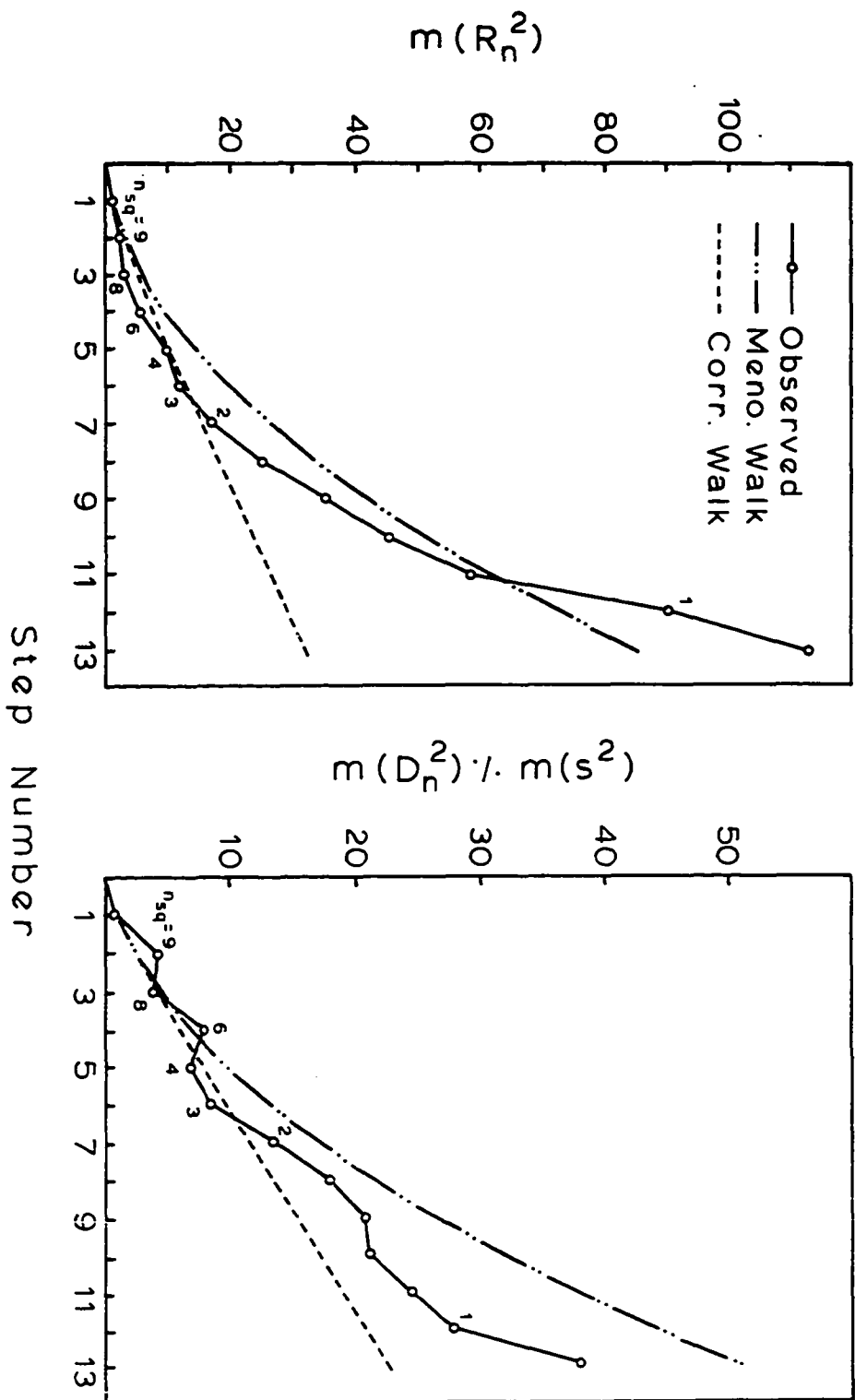
**TABLE 6.36b CONTINUED**

		M (D <sup>2</sup> ) / M (S <sup>2</sup> )						
Turtle	n <sub>st</sub> =	1	2	3	4	5	6	7
27	n <sub>sq</sub>	1	1	1				
	e <sub>mw</sub>	1.00	3.34	7.01				
	o	1.75	4.57	5.84				
	e <sub>cw</sub>	1.00	3.34	5.83				
total	n <sub>sq</sub>	9	9	8	6	4	3	2
	e <sub>mw</sub>	1.00	2.48	4.44	6.89	9.81	13.22	17.11
	o	0.74	4.12	3.88	7.81	6.63	8.39	13.39
	e <sub>cw</sub>	1.00	2.48	4.18	5.98	7.83	9.69	11.57
		n <sub>st</sub> =	8	9	10	11	12	13
		n <sub>sq</sub>	2	2	2	2	1	1
		e <sub>mw</sub>	21.48	26.33	31.67	37.48	43.78	50.55
		o	17.78	20.71	21.08	24.51	27.76	38.00
		e <sub>cw</sub>	13.45	15.33	17.21	19.09	20.97	22.86

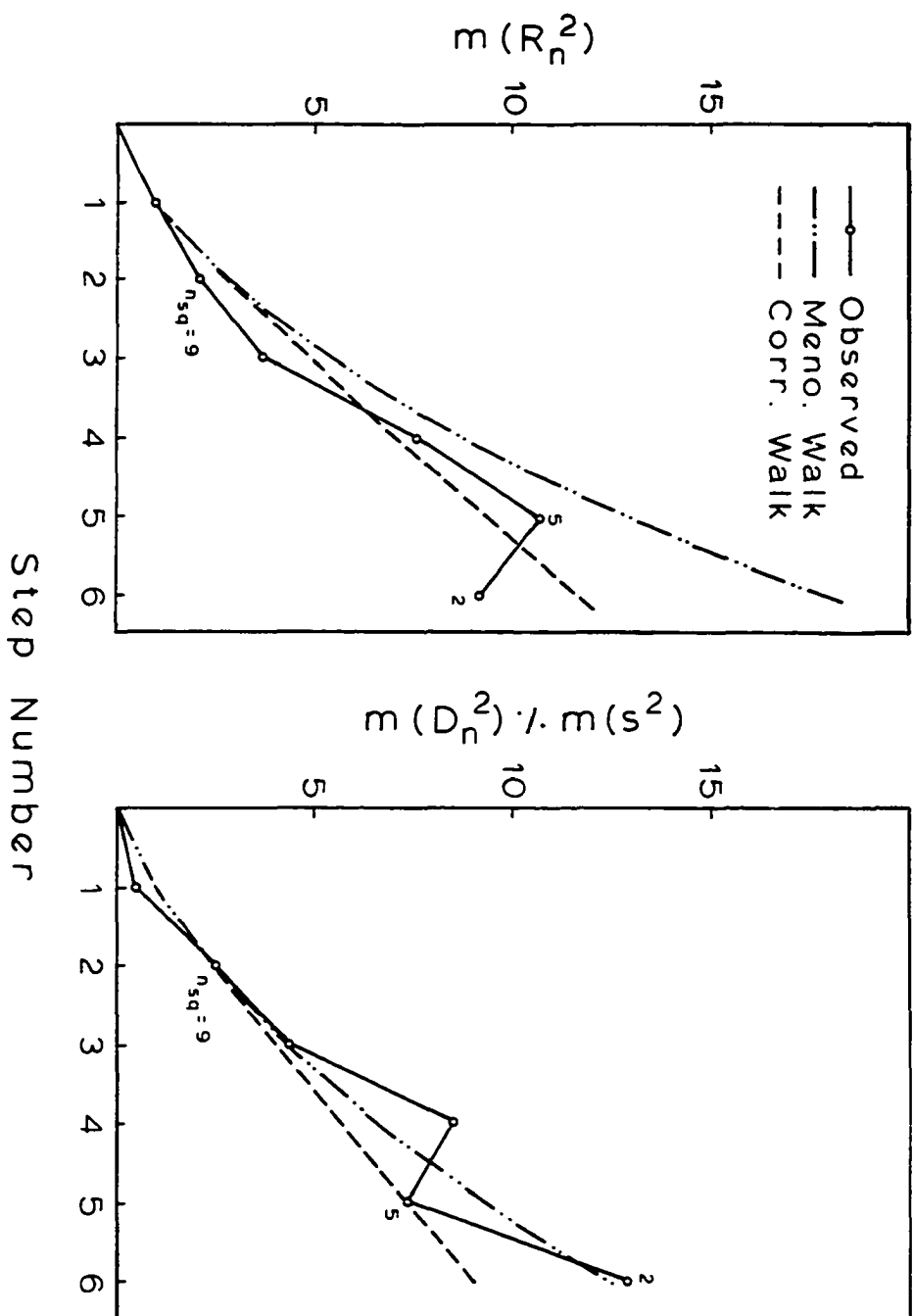
**FIGURE 6.16** Transients' sequences of day-range vectors.

- a. Partitioned according to the seven-step-minimum rule.
- b. Partitioned into four-step-minimum sequences.

# Transients: Day Range Vectors

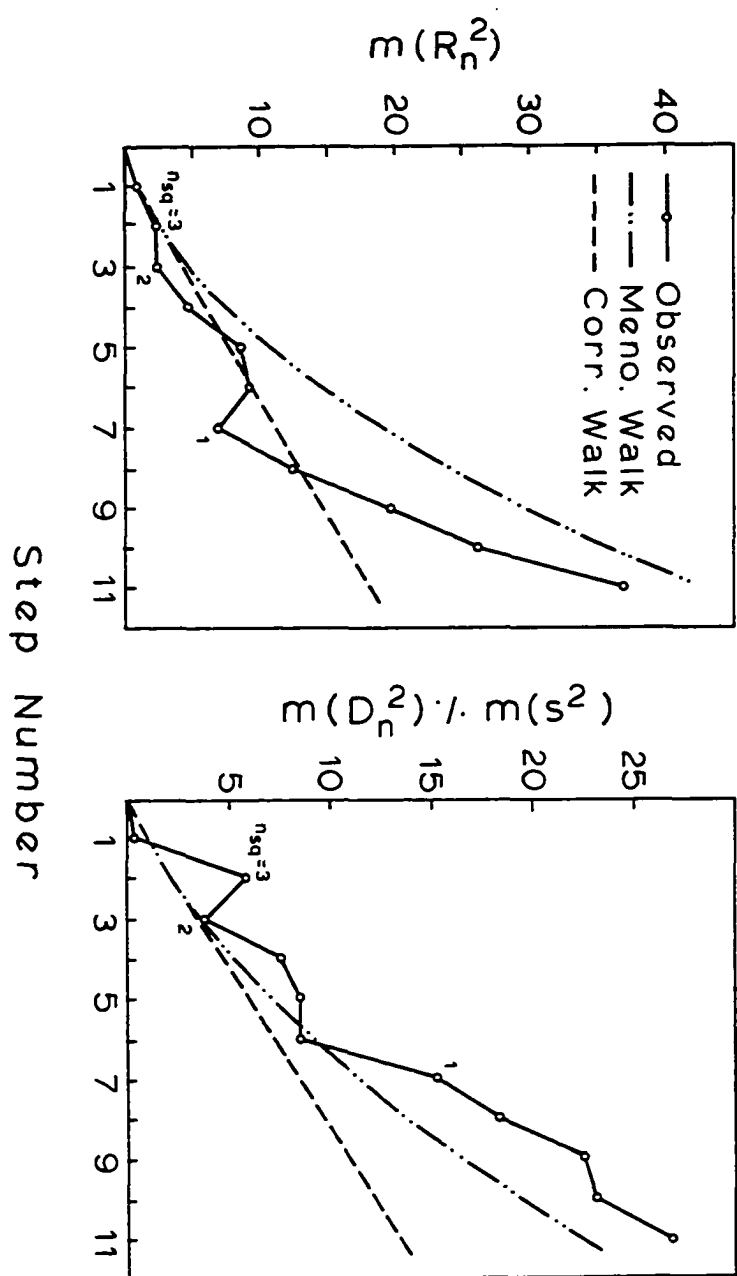


# Transients: D.R.V.'s in Series of 4-7 Steps



**FIGURE 6.17** Turtle 8's off-range series of day-range vectors.

# Turtle 8<sub>tr</sub>: Day Range Vectors





**TABLE 6.37a MEAN SQUARED RESULTANTS FOR SEQUENCES OF DAY-RANGE  
AZIMUTHS: EXPERIMENTALS**

Turtle	Mean Squared Resultants							
	$n_{st} =$	2	3	4	5	6	7	8
X2	$n_{sq}$	1	1	1	1			
	$e_{mw}$	2.70	5.11	8.22	12.04			
	$o$	1.00	2.58	1.63	1.88			
	$e_{cw}$	2.70	3.94	4.49	4.81			
X15	$n_{sq}$	1	1	1	1	1	1	
	$e_{mw}$	3.36	7.07	12.14	18.57	26.36	35.50	
	$o$	2.38	4.61	9.16	9.37	15.02	23.65	
	$e_{cw}$	3.36	6.54	10.16	13.95	17.75	21.47	
X16	$n_{sq}$	1	1	1	1	1	1	1
	$e_{mw}$	2.46	4.37	6.74	9.57	12.85	16.59	20.78
	$o$	3.68	4.98	10.27	17.42	26.46	33.11	43.69
	$e_{cw}$	2.46	4.01	5.58	7.16	8.74	10.31	11.89
	$n_{st} =$	9	10	11				
	$n_{sq}$	1	1	1				
	$e_{mw}$	25.44	30.55	36.11				
	$o$	31.49	43.26	39.58				
	$e_{cw}$	13.47	15.05	16.62				
X17	$n_{sq}$	1	1	1	1	1	1	1
	$e_{mw}$	3.00	6.00	10.01	15.01	21.02	28.02	36.03
	$o$	0.10	1.70	2.38	3.44	5.32	10.03	16.37
	$e_{cw}$	3.00	5.30	7.53	9.59	11.52	13.35	15.16
	$n_{st} =$	9						
	$n_{sq}$	1						
	$e_{mw}$	45.04						
	$o$	23.48						
	$e_{cw}$	16.96						
X19	$n_{sq}$	1	1	1	1	1		
	$e_{mw}$	3.42	7.27	12.54	19.23	27.34		
	$o$	3.75	7.98	11.95	19.74	27.30		
	$e_{cw}$	3.42	6.81	10.80	15.15	19.68		

**TABLE 6.37a CONTINUED**

		Mean Squared Resultants						
Turtle	n <sub>st</sub> =	2	3	4	5	6	7	8
total	n <sub>sq</sub>	5	5	5	5	4	3	2
	e <sub>mw</sub>	2.93	5.79	9.57	14.29	19.93	26.50	34.00
	o	2.18	4.37	7.08	10.37	18.52	22.26	30.03
	e <sub>cw</sub>	2.93	5.21	7.58	9.95	12.30	14.61	16.92
	n <sub>st</sub> =	9	10	11				
	n <sub>sq</sub>	2	1	1				
	e <sub>mw</sub>	42.43	51.79	62.07				
	o	27.48	43.26	39.58				
	e <sub>cw</sub>	19.21	21.50	23.79				

**TABLE 6.37b MEAN SQUARED DISTANCES OF TRAVEL DIVIDED BY MEAN SQUARED STEP LENGTHS FOR SEQUENCES OF DAY-RANGE VECTORS: EXPERIMENTALS**

		M (D <sup>2</sup> ) / M (S <sup>2</sup> )						
Turtle	n <sub>st</sub> =	1	2	3	4	5	6	7
X2	n <sub>sq</sub>	1	1	1	1	1		
	e <sub>mw</sub>	1.00	2.56	4.68	7.36	10.60		
	o	<b>0.48</b>	<b>0.43</b>	<b>1.02</b>	<b>1.21</b>	<b>3.56</b>		
	e <sub>cw</sub>	1.00	2.56	3.74	4.39	4.85		
X15	n <sub>sq</sub>	1	1	1	1	1	1	1
	e <sub>mw</sub>	1.00	2.99	5.97	9.93	14.88	20.83	27.76
	o	<b>0.78</b>	<b>1.28</b>	<b>1.75</b>	<b>4.49</b>	<b>4.47</b>	<b>10.63</b>	<b>20.66</b>
	e <sub>cw</sub>	1.00	2.99	5.58	8.49	11.52	14.55	17.54
X16	n <sub>sq</sub>	1	1	1	1	1	1	1
	e <sub>mw</sub>	1.00	2.30	3.89	5.78	7.97	10.46	13.25
	o	<b>0.24</b>	<b>0.66</b>	<b>0.93</b>	<b>2.37</b>	<b>13.88</b>	<b>26.84</b>	<b>28.91</b>
	e <sub>cw</sub>	1.00	2.30	3.66	5.03	6.41	7.78	9.16
	n <sub>st</sub> =	8	9	10	11			
	n <sub>sq</sub>	1	1	1	1			
	e <sub>mw</sub>	16.33	19.71	23.38	27.36			
	o	<b>43.45</b>	<b>39.17</b>	<b>44.10</b>	<b>42.04</b>			
	e <sub>cw</sub>	10.53	11.91	13.29	14.66			
X17	n <sub>sq</sub>	1	1	1	1	1	1	1
	e <sub>mw</sub>	1.00	2.44	4.31	6.62	9.37	12.55	16.17
	o	<b>0.48</b>	<b>0.39</b>	<b>0.38</b>	<b>0.84</b>	<b>10.80</b>	<b>19.97</b>	<b>22.06</b>
	e <sub>cw</sub>	1.00	2.44	4.00	5.54	7.00	8.41	9.77
	n <sub>st</sub> =	8	9					
	n <sub>sq</sub>	1	1					
	e <sub>mw</sub>	20.23	24.72					
	o	<b>27.15</b>	<b>29.68</b>					
	e <sub>cw</sub>	11.12	12.47					
X19	n <sub>sq</sub>	1	1	1	1	1	1	
	e <sub>mw</sub>	1.00	3.06	6.18	10.36	15.61	21.91	
	o	<b>1.45</b>	<b>1.63</b>	<b>4.38</b>	<b>10.84</b>	<b>12.94</b>	<b>22.06</b>	
	e <sub>cw</sub>	1.00	3.06	5.84	9.07	12.57	16.20	

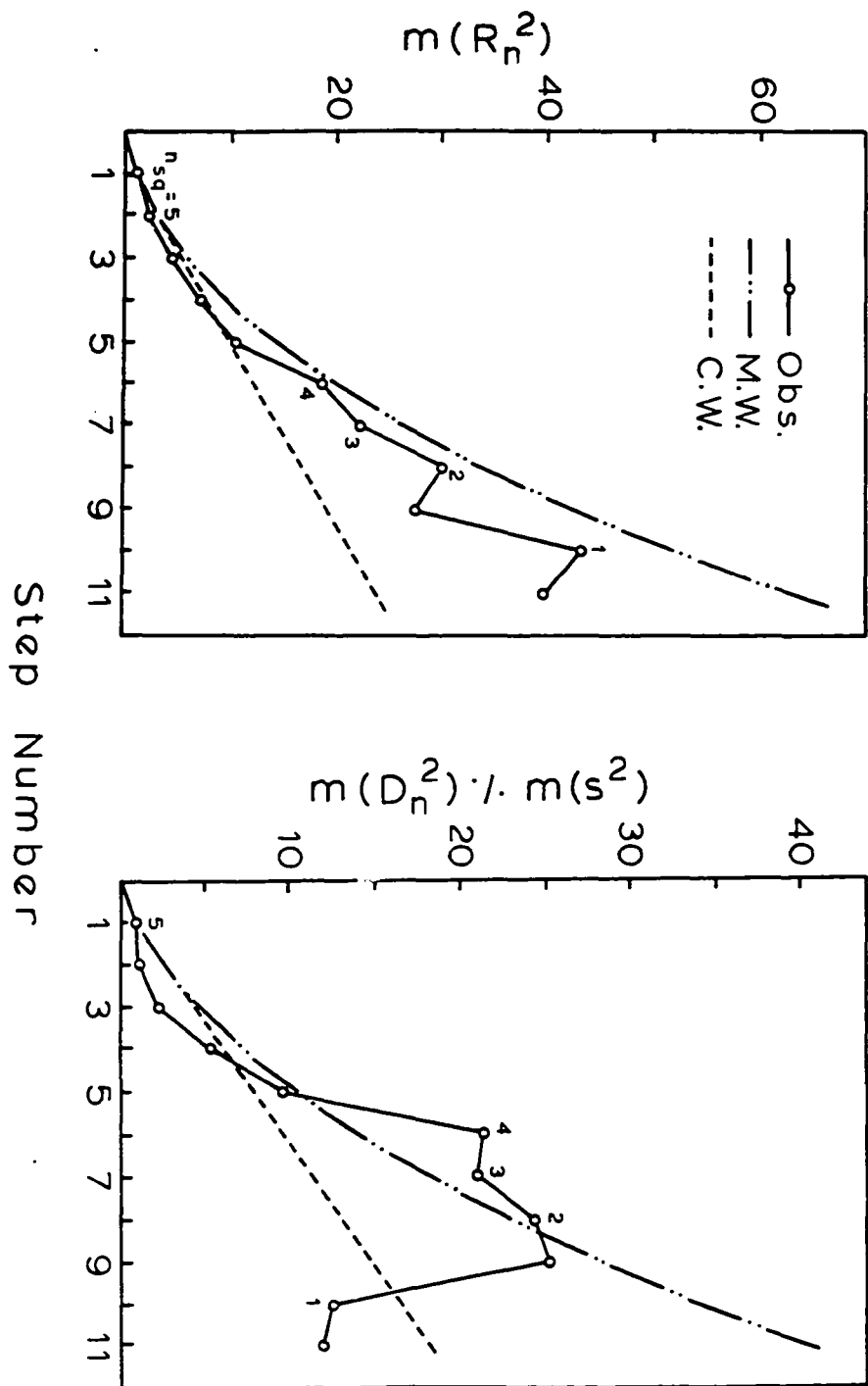
**TABLE 6.37b CONTINUED**

Turtle	$n_{st} =$	$M (D^2) / M (S^2)$						
		1	2	3	4	5	6	7
total	$n_{sq}$	5	5	5	5	5	4	3
	$e_{mw}$	1.00	2.53	4.59	7.19	10.31	13.97	18.16
	$o$	0.88	1.09	2.16	5.24	9.45	21.25	20.88
	$e_{cw}$	1.00	2.53	4.26	6.05	7.83	9.60	11.36
	$n_{st} =$	8	9	10	11			
	$n_{sq}$	2	2	1	1			
	$e_{mw}$	22.88	28.13	33.91	40.22			
	$o$	24.24	25.32	12.45	11.87			
	$e_{cw}$	13.10	14.41	16.58	18.32			

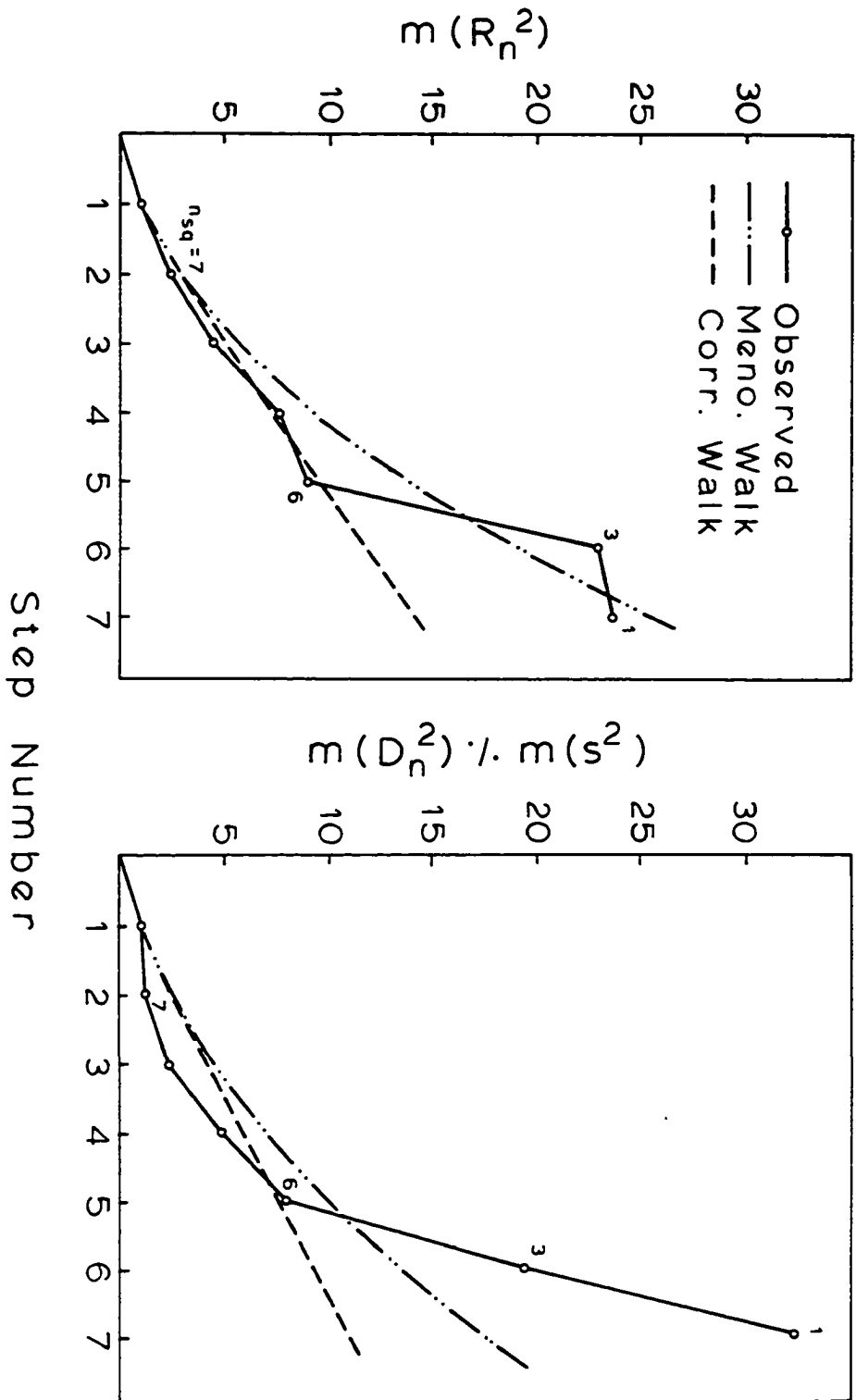
**FIGURE 6.18** Experimentals' sequences of day-range vectors.

- a. Partitioned according to the seven-step-minimum rule.
- b. Partitioned into four-step-minimum sequences.

# Experimentals: Day Range Vectors



# Experimentals: D.R.V.'s in Series of 4-7 Steps



from the release point. The ragged decline seen at the end of the curve further suggests another change in route behavior, possibly a shift to exploration following a period of more direct flight away from a source of disturbance (the release into unfamiliar surroundings).

Analysis of Higher-order, Uniform Partitions. Between the form-sites and the hibernacula (of which I have too few records), no points along the routes stand out as natural places at which to divide the routes into steps larger in scale than the day-ranges. Any attempt at higher-order analysis, thus, requires an arbitrary partitioning scheme. Rather than continue to use the visual approach of hunting for discontinuities, with all its uncertainties, I chose here to make use only of uniform partitions.

The method I used to produce a series of larger scale, uniform steps was a computerized version of applying a pair of dividers to a map. Starting at the origin of a route, successive points at equal distances apart are simply "walked" off. The computer program accomplished this by determining the point of intersection between a circle whose center fell at the origin of the new step and the line-segment of the basic survey that crossed the perimeter of this circle (only the x-y coordinates of the survey points were thus considered). Although the points of intersection will not necessarily mark places in space that the subject actually visited, the error this creates will become negligible as larger and larger steps are considered (see Figure 5.3).

The smallest step I employed in this analysis was 100 feet. This approximates the average net distances of travel for the Residents'



day-ranges. Walks composed of such steps should thus reflect mainly between-day patterns of movement and can reasonably be compared to the results obtained from analysis of the actual day-range vectors. It should be noted, however, that I made use of all available sections of the routes for this partition, including segments for which the form-sites were missing. Furthermore, I ignored small gaps in the routes (100 ft or less) if the endpoints of the break fell within the same day, or thereabouts if the day-range endpoints were not known exactly. In walking off the higher-level steps, I treated such gaps just like straight connections between the points.

In addition to the 100-ft steps, I also employed 250- , 500- , and 1000-ft steps, although beyond the 250-ft level the data becomes rather sparse. The main thing I was interested in at this level of analysis was to see whether any changes occurred from the patterns already described at the more meaningful level of the day-range vectors. For this purpose, I believe this set was adequate.

For the Residents, increases in the scale of partition accentuate the patterns observed at the level of the day-ranges. The general flattening of the MSD curves observed previously is reached over ever fewer steps with each increase in the scale of measurement (Tables 6.38 and 6.39; Figure 6.19). Now even Turtle 10 is included in this pattern, at least at the 250-ft scale and above, linking him firmly with the rest of the Residents.

The only anomaly occurring in this analysis was Turtle 16, a female that actually had the tightest home-range observed. Instead of reaching a horizontal asymptote most quickly at the higher scales of measurement, her observed MSD's at both the 100- and 250-ft scales

**TABLE 6.38 STATISTICS FOR THE TURN ANGLES OCCURRING WITHIN THE HIGHER LEVEL UNIFORM PARTITIONS: RESIDENTS**

Turtle	Scale	n	m	r	c
1	100 ft	37	8	0.64	0.64
	250 ft	8	48	0.62	0.42
	500 ft	2	136	0.80	-0.57
4	100 ft	67	347	0.56	0.54
	250 ft	15	340	0.32	0.31
	500 ft	3	219	0.70	-0.55
7	100 ft	92	10	0.32	0.32
	250 ft	17	182	0.47	-0.47
	500 ft	1	142	1.00	-0.79
8r	100 ft	21	12	0.54	0.52
	250 ft	4	99	0.26	-0.04
	500 ft	0	-	-	-
9	100 ft	70	10	0.48	0.47
	250 ft	13	100	0.38	-0.06
	500 ft	1	155	1.00	-0.91
10	100 ft	99	345	0.34	0.33
	250 ft	18	344	0.34	0.32
	500 ft	3	291	0.37	0.12
16	100 ft	41	350	0.16	0.16
	250 ft	7	320	0.11	0.08
	500 ft	1	0	1.00	1.00
26	100 ft	63	3	0.49	0.48
	250 ft	11	63	0.09	0.04
	500 ft	0	-	-	-
total	100 ft	490	0	0.41	0.41
	250 ft	93	47	0.09	0.06
	500 ft	11	184	0.28	-0.28

**TABLE 6.39 MEAN SQUARED DISTANCES OF TRAVEL FOR SEQUENCES OF HIGHER ORDER UNIFORM STEPS: RESIDENTS\***

		Mean Squared Distances						
Turtle	n <sub>st</sub> =	2	3	4	5	6	7	8
1	100 ft	n <sub>sq</sub>	5	4	4	4	4	4
		e <sub>mw</sub>	3.27	6.80	11.59	17.65	24.98	33.57
		o	<b>3.56</b>	<b>7.43</b>	<b>8.93</b>	<b>12.72</b>	<b>18.62</b>	<b>23.12</b>
		e <sub>cw</sub>	3.27	6.31	9.84	13.64	17.60	21.64
		n <sub>st</sub> =	9	10	11	12	13	
		n <sub>sq</sub>	2	1	1	1	1	
		e <sub>mw</sub>	54.56	66.95	80.60	95.52	111.71	
		o	<b>34.78</b>	<b>37.78</b>	<b>36.52</b>	<b>39.57</b>	<b>52.52</b>	
		e <sub>cw</sub>	29.85	33.97	38.10	42.23	46.35	
	250 ft	n <sub>sq</sub>	2	2	2	1	1	
		e <sub>mw</sub>	2.83	5.50	9.00	13.34	18.50	
		o	<b>3.31</b>	<b>6.20</b>	<b>4.85</b>	<b>0.92</b>	<b>0.003</b>	
		e <sub>cw</sub>	2.83	4.60	6.00	7.10	8.12	
	500 ft	n <sub>sq</sub>	2					
		e <sub>mw</sub>	-					
		o	<b>0.85</b>					
		e <sub>cw</sub>	0.85					
4	100 ft	n <sub>sq</sub>	9	9	9	9	9	3
		e <sub>mw</sub>	3.04	6.11	10.22	15.37	21.55	28.77
		o	<b>2.95</b>	<b>4.78</b>	<b>6.77</b>	<b>10.09</b>	<b>13.02</b>	<b>15.77</b>
		e <sub>cw</sub>	3.04	5.59	8.38	11.27	14.21	17.16
		n <sub>st</sub> =	9	10	11	12		
		n <sub>sq</sub>	2	1	1	1		
		e <sub>mw</sub>	46.33	56.66	68.03	80.43		
		o	<b>1.06</b>	<b>0.58</b>	<b>3.10</b>	<b>7.58</b>		
		e <sub>cw</sub>	23.06	26.01	28.95	31.90		
	250 ft	n <sub>sq</sub>	4	3	2	2	2	1
		e <sub>mw</sub>	2.78	5.34	8.70	12.84	17.75	23.46
		o	<b>2.43</b>	<b>3.57</b>	<b>6.15</b>	<b>7.20</b>	<b>6.75</b>	<b>5.74</b>
		e <sub>cw</sub>	2.78	4.88	7.03	9.24	11.46	13.68
	500 ft	n <sub>sq</sub>	1	1	1			
		e <sub>mw</sub>	-	-	-			
		o	<b>0.09</b>	<b>0.56</b>	<b>0.07</b>			
		e <sub>cw</sub>	0.90	1.02	1.44			

\* Long sequences at the 100-ft level were subdivided into sections 7 or more steps in length; at the 250-ft level 6 or more steps

TABLE 6.39 CONTINUED

		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
7	100 ft	$n_{sq}$	12	12	12	12	12	4
		$e_{mw}$	2.69	5.08	8.15	11.92	16.38	27.37
		$\sigma$	<b>2.46</b>	<b>3.81</b>	<b>5.01</b>	<b>5.48</b>	<b>5.64</b>	<b>3.27</b>
		$e_{cw}$	2.69	4.61	6.61	8.63	10.66	14.71
	250 ft	$n_{sq}$	4	3	2	2	2	1
		$e_{mw}$	-	-	-	-	-	-
		$\sigma$	<b>1.07</b>	<b>1.50</b>	<b>3.78</b>	<b>2.48</b>	<b>1.60</b>	<b>2.00</b>
		$e_{cw}$	1.07	1.57	1.87	2.26	2.61	3.34
	500 ft	$n_{sq}$	1					
		$e_{mw}$	-					
		$\sigma$	<b>0.42</b>					
		$e_{cw}$	0.42					
8r	100 ft	$n_{sq}$	3	3	2	2	2	2
		$e_{mw}$	3.05	6.14	10.28	15.47	21.70	37.31
		$\sigma$	<b>2.67</b>	<b>6.42</b>	<b>7.93</b>	<b>12.06</b>	<b>15.68</b>	<b>23.39</b>
		$e_{cw}$	3.05	5.62	8.43	11.35	14.32	20.28
		$n_{st}$	9	10	11	12	13	
		$n_{sq}$	1	1	1	1	1	
		$e_{mw}$	46.48	57.10	68.57	81.08	94.64	
		$\sigma$	<b>26.44</b>	<b>33.72</b>	<b>26.86</b>	<b>19.97</b>	<b>13.21</b>	
		$e_{cw}$	23.66	26.24	29.22	32.19	35.16	
	250 ft	$n_{sq}$	2	1	1			
		$e_{mw}$	-	-	-			
		$\sigma$	<b>2.94</b>	<b>4.49</b>	<b>1.28</b>			
		$e_{cw}$	1.92	2.71	3.52			
9	100 ft	$n_{sq}$	11	11	10	10	9	4
		$e_{mw}$	2.95	5.86	9.73	14.54	20.31	34.72
		$\sigma$	<b>3.14</b>	<b>5.39</b>	<b>6.92</b>	<b>8.49</b>	<b>9.44</b>	<b>8.09</b>
		$e_{cw}$	2.95	5.36	7.97	10.67	13.41	18.94
		$n_{st} =$	9	10	11			
		$n_{sq}$	2	2	2			
		$e_{mw}$	43.35	52.94	63.48			
		$\sigma$	<b>4.32</b>	<b>3.97</b>	<b>7.34</b>			
		$e_{cw}$	21.72	24.49	27.27			

TABLE 6.39 CONTINUED

		Mean Squared Distances						
Turtle	$n_{st}$	2	3	4	5	6	7	8
9								
250 ft	$n_{sq}$	6	4	3				
	$e_{mw}$	-	-	-				
	$\sigma$	2.66	2.89	2.71				
	$e_{cw}$	1.87	2.74	3.61				
500 ft	$n_{sq}$	1						
	$e_{mw}$	-						
	$\sigma$	0.17						
	$e_{cw}$	0.19						
10								
100 ft	$n_{sq}$	14	14	14	14	13	13	4
	$e_{mw}$	2.57	4.71	7.42	10.70	14.55	18.98	23.97
	$\sigma$	2.25	4.10	6.00	8.54	7.92	9.57	22.19
	$e_{cw}$	2.57	4.30	6.07	7.85	9.63	11.42	13.20
	$n_{st}$	9	10	11				
	$n_{sq}$	1	1	1				
	$e_{mw}$	29.53	35.66	42.36				
	$\sigma$	37.64	44.72	50.32				
	$e_{cw}$	14.98	16.77	18.55				
250 ft	$n_{sq}$	4	3	3	2	2	1	1
	$e_{mw}$	2.65	4.94	7.87	11.45	15.68	20.55	26.07
	$\sigma$	2.29	2.93	4.29	1.05	1.20	2.44	2.03
	$e_{cw}$	2.65	4.48	6.37	8.26	10.16	12.06	13.96
	$n_{st}$	9	10					
	$n_{sq}$	1	1					
	$e_{mw}$	32.23	29.04					
	$\sigma$	2.30	6.28					
	$e_{cw}$	15.85	17.75					
500 ft	$n_{sq}$	2	1					
	$e_{mw}$	2.26	3.78					
	$\sigma$	1.51	1.56					
	$e_{cw}$	2.26	3.32					
16								
100 ft	$n_{sq}$	6	6	6	5	5	5	4
	$e_{mw}$	2.36	4.07	6.14	8.57	11.35	14.49	17.99
	$\sigma$	2.85	5.09	6.32	7.22	11.41	13.32	20.45
	$e_{cw}$	2.36	3.78	5.21	6.64	8.07	9.50	10.93

TABLE 6.39 CONTINUED

		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
16	250 ft	$n_{sq}$	1	1	1	1	1	1
		$e_{mw}$	2.17	3.50	5.00	6.67	8.51	10.51
		$o$	<b>3.62</b>	<b>8.35</b>	<b>14.56</b>	<b>23.16</b>	<b>14.70</b>	<b>22.83</b>
		$e_{cw}$	2.17	3.34	4.51	5.68	6.85	9.19
	500 ft	$n_{sq}$	1					
		$e_{mw}$	4.00					
		$o$	<b>4.00</b>					
		$e_{cw}$	4.00					
26	100 ft	$n_{sq}$	6	6	6	6	6	3
		$e_{mw}$	2.99	5.98	9.97	14.94	20.92	35.84
		$o$	<b>3.23</b>	<b>5.31</b>	<b>8.06</b>	<b>11.51</b>	<b>17.21</b>	<b>15.13</b>
		$e_{cw}$	2.99	5.48	8.22	11.07	13.99	19.90
		$n_{st} =$	9	10	11	12		
		$n_{sq}$	1	1	1	1		
		$e_{mw}$	44.80	54.75	65.69	77.63		
		$o$	<b>19.25</b>	<b>12.55</b>	<b>11.17</b>	<b>18.32</b>		
		$e_{cw}$	22.87	25.84	28.82	31.79		
	250 ft	$n_{sq}$	2	2	2	1	1	1
		$e_{mw}$	2.08	3.24	4.48	5.81	7.21	10.26
		$o$	<b>1.92</b>	<b>2.34</b>	<b>1.50</b>	<b>1.40</b>	<b>0.51</b>	<b>0.09</b>
		$e_{cw}$	2.08	3.15	4.22	5.29	6.36	8.50
		$n_{st} =$	9					
		$n_{sq}$	1					
		$e_{mw}$	11.90					
		$o$	<b>3.66</b>					
		$e_{cw}$	9.57					

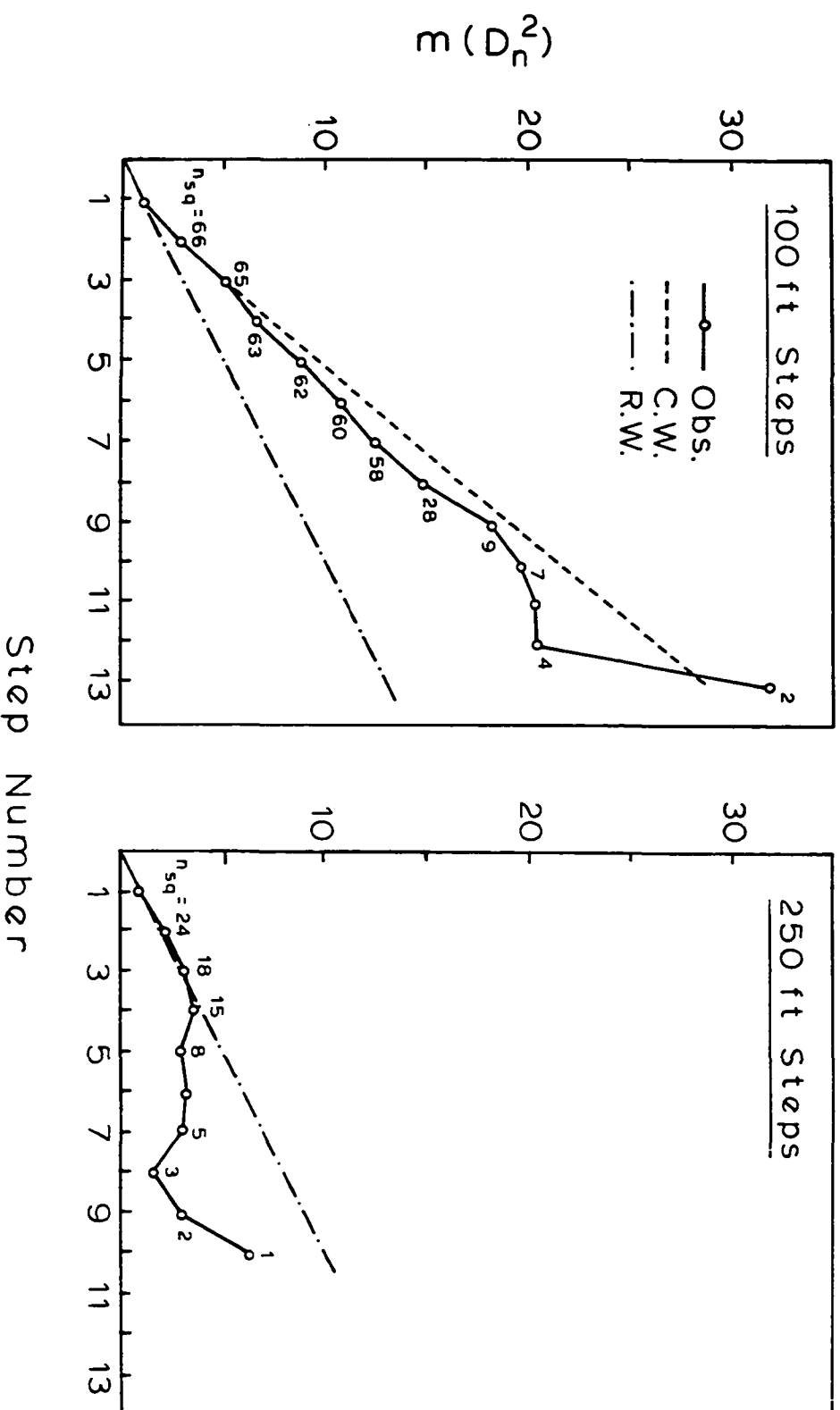
TABLE 6.39 CONTINUED

		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
total								
100 ft	$n_{sq}$	66	65	63	62	60	58	28
	$e_{mw}$	2.83	5.48	8.96	13.27	18.41	24.38	31.17
	$o$	<b>2.79</b>	<b>4.87</b>	<b>6.54</b>	<b>8.73</b>	<b>10.65</b>	<b>12.38</b>	<b>14.78</b>
	$e_{cw}$	2.83	5.00	7.31	9.68	12.07	14.48	16.88
	$n_{st} =$	9	10	11	12	13		
	$n_{sq}$	9	7	7	4	2		
	$e_{mw}$	38.79	47.23	56.51	66.61	77.54		
	$o$	<b>18.18</b>	<b>19.61</b>	<b>20.38</b>	<b>21.36</b>	<b>32.87</b>		
	$e_{cw}$	19.29	21.70	24.11	26.53	28.94		
250 ft	$n_{sq}$	25	19	16	9	9	6	4
	$e_{mw}$	2.15	3.44	4.88	6.46	8.19	10.07	12.10
	$o$	<b>2.36</b>	<b>3.45</b>	<b>4.34</b>	<b>5.22</b>	<b>4.48</b>	<b>6.35</b>	<b>4.81</b>
	$e_{cw}$	2.15	3.29	4.44	5.58	6.73	7.87	9.02
	$n_{st} =$	9	10					
	$n_{sq}$	2	1					
	$e_{mw}$	14.27	16.58					
	$o$	<b>2.98</b>	<b>6.28</b>					
	$e_{cw}$	10.16	11.30					
500 ft	$n_{sq}$	8	2	1				
	$e_{mw}$	-	-	-				
	$o$	<b>1.18</b>	<b>1.06</b>	<b>0.07</b>				
	$e_{cw}$	1.44	2.03	2.58				

**FIGURE 6.19** Residents' sequences of higher-order uniform steps. Note that only  $m(D_n^2)$  needs to be shown since it is identical to  $m(R_n^2)$  in this case.



# Residents: Higher-order Uniform Steps



actually lie above the predictions for menotaxis. The explanation, however, is immediately apparent in the map of her movements (Figure 2.5h): before settling down into a very convoluted ranging pattern, she spent several days traveling from a distant hibernaculum by means of a very straight series of movements. Whereas the smaller scale analyses gave far more weight to the convoluted part of her overall route, over greater scales of measurement her entire home-range became spanned by only one or two steps. In contrast, the long, linear part of her route leading to her eventual range provides several steps even at the 250-ft level of analysis. Obviously, there is a big discontinuity separating the two parts of T16's movements; the correct way to treat her data probably would have been to handle the two parts of her routes separately, the same way I treated the data for T8.

One other apparent discrepancy worth pointing out in the combined sample for the Residents is that at the 100-ft scale of measurement the observed curve shows less sign of spatial constraints than did the curve for the day-range vectors; the curve, in fact, lies between the expectations for the correlated and truly random walks. Again there is a fairly simple explanation: some of the 100-ft steps fall within the limits of single day-ranges and would reflect the dominant influence of orientation present at that level of analysis, while others bridge two or more different day-ranges and should show the influence of the spatial constraints dominant at that level. If this is the case, then it clearly illustrates the problems involved in choosing steps artificially: they will cut unpredictably across the true steps at one or more levels in the route hierarchy. Nonetheless, the overall effects of spatial constraints becomes more and more evident

when larger scales of measurement are employed.

A very different but equally clear trend is seen in the Transients' data (Tables 6.40 and 6.41 and Figure 6.20). As the scale of measurement increased, the concentration parameters for the distributions of both first- and second-order turns showed a marked tendency to increase in value, and the relationships between these parameters became more like those expected under menotaxis. Correspondingly, the observed MSD curves showed a strong convergence on the predictions for a menotactic walk. Together these trends towards increasing sequential homogeneity indicate that single target headings were maintained over the great lengths of the Transients' routes, at least at the top of the route hierarchy.

This pattern is dramatically illustrated just within the routes traveled by Turtle 8<sub>tr</sub> (Figure 6.21). Recall first of all that this individual showed almost no sign of orientation among the azimuthal MSR's for her day-ranges, but showed marked orientation when the actual MSD's were considered (which treated step length as a variable). Similarly, there is a general lack of fit to the menotactic model in her steps at the 100-ft level of analysis but an almost exact fit at the 250-ft level and beyond. This smoothing-out of the curves either represents a declining influence of klinotaxis at higher scales of measurement or a shift to a more tropotactic mechanism (where step lengths would be actually independent of their directions). In any case, these data represent my best evidence for the ability of box turtles to maintain single target headings for prolonged periods of time, over long distances, and through varied and presumably unfamiliar terrain.

**TABLE 6.40 STATISTICS FOR THE TURN ANGLES OCCURRING WITHIN THE HIGHER  
LEVEL UNIFORM PARTITIONS: TRANSIENTS**

Turtle	Scale	$n_{\theta 1}$	$m_{\theta 1}$	$r_{\theta 1}$	$c_{\theta 1}$	$c_{\theta 2}$
8tr	100 ft	65	0	0.90	0.90	0.83
	250 ft	24	359	0.91	0.91	0.87
	500 ft	10	1	0.90	0.90	0.91
	1000 ft	4	3	0.98	0.98	0.99
11	100 ft	9	1	0.55	0.55	0.34
	250 ft	2	344	0.43	0.41	0.57
12	100 ft	15	355	0.77	0.77	0.56
	250 ft	4	15	0.86	0.83	0.57
	500 ft	1	9	1.00	0.99	-
14	100 ft	7	350	0.80	0.79	0.54
	250 ft	1	310	1.00	0.64	-
17	100 ft	11	345	0.79	0.76	0.53
	250 ft	3	348	0.66	0.65	0.92
	500 ft	1	29	1.00	0.87	-
23	100 ft	15	1	0.92	0.92	0.87
	250 ft	5	2	0.89	0.89	0.87
	500 ft	2	17	0.95	0.91	0.83
27	100 ft	7	8	0.92	0.91	0.87
	250 ft	2	31	0.98	0.84	0.45
	500 ft	1	53	1.00	0.60	-
total	100 ft	129	358	0.85	0.85	0.73
	250 ft	41	0	0.84	0.84	0.83
	500 ft	15	10	0.90	0.88	0.90
	1000 ft	4	3	0.98	0.98	0.99
total - T8 <sub>tr</sub>	100 ft	64	357	0.79	0.79	0.63
	250 ft	17	3	0.76	0.76	0.76
	500 ft	5	25	0.94	0.86	0.83

**TABLE 6.41 MEAN SQUARED DISTANCES OF TRAVEL IN SEQUENCES OF HIGHER ORDER UNIFORM STEPS: TRANSIENTS\***

		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
$8_{tr}$	100 ft	$n_{sq}$	8	8	8	8	8	8
		$e_{mw}$	3.81	8.44	14.89	23.15	33.22	45.11
		$o$	3.93	8.34	14.28	21.96	31.42	42.59
		$e_{cw}$	3.81	8.28	14.23	21.53	30.06	39.70
		$e_{cw}$	50.34					
	250 ft	$n_{st} =$	9					
		$n_{sq}$	3					
		$e_{mw}$	74.53					
		$o$	69.53					
		$e_{cw}$	61.89					
	500 ft	$n_{sq}$	4	4	4	4	2	
		$e_{mw}$	3.82	8.45	14.89	23.15	33.23	45.11
		$o$	3.75	8.26	14.73	22.54	32.01	44.81
		$e_{cw}$	3.82	8.28	14.23	21.53	30.06	39.69
		$e_{cw}$						
	1000 ft	$n_{sq}$	2	2	2	2		
		$e_{mw}$	3.79	8.38	14.76	22.93	32.90	
		$o$	3.74	8.51	14.79	23.40	33.34	
		$e_{cw}$	3.79	8.19	14.03	21.16	29.44	
		$e_{cw}$						
11	100 ft	$n_{sq}$	2	2				
		$e_{mw}$	3.96	8.88				
		$o$	3.99	8.89				
		$e_{cw}$	3.96	8.84				
		$e_{cw}$						
	250 ft	$n_{st} =$	9	10				
		$n_{sq}$	1	1				
		$e_{mw}$	48.53	59.42				
		$o$	39.68	52.98				
		$e_{cw}$	25.54	28.96				
	500 ft	$n_{sq}$	1	1				
		$e_{mw}$	2.83	5.48				
		$o$	2.35	6.38				
		$e_{cw}$	2.83	4.97				
		$e_{cw}$						

\* Long sequences at the 100-ft level were subdivided into sections 7 or more steps in length; at the 250-ft level 6 or more steps

**TABLE 6.41 CONTINUED**

		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
<b>12</b>								
100 ft	$n_{sq}$	2	2	2	2	2	2	2
	$e_{mw}$	3.54	7.62	13.25	20.42	29.12	39.37	51.16
	$o$	<b>3.22</b>	<b>5.56</b>	<b>8.74</b>	<b>11.70</b>	<b>14.82</b>	<b>21.33</b>	<b>27.40</b>
	$e_{cw}$	3.54	7.27	11.91	17.25	23.12	29.40	36.00
250 ft	$n_{sq}$	1	1	1	1			
	$e_{mw}$	3.67	8.00	14.00	21.66			
	$o$	<b>3.95</b>	<b>8.59</b>	<b>14.32</b>	<b>18.60</b>			
	$e_{cw}$	3.67	7.62	12.48	17.90			
500 ft	$n_{sq}$	1						
	$e_{mw}$	3.98						
	$o$	<b>3.98</b>						
	$e_{cw}$	3.98						
<b>14</b>								
100 ft	$n_{sq}$	1	1	1	1	1	1	1
	$e_{mw}$	3.57	7.71	13.42	20.71	29.56	39.99	51.98
	$o$	<b>3.93</b>	<b>3.81</b>	<b>5.14</b>	<b>8.06</b>	<b>13.51</b>	<b>19.83</b>	<b>28.40</b>
	$e_{cw}$	3.57	7.34	11.98	17.25	22.93	28.86	34.94
250 ft	$n_{sq}$	1						
	$e_{mw}$	3.29						
	$o$	<b>3.31</b>						
	$e_{cw}$	3.29						
<b>17</b>								
100 ft	$n_{sq}$	2	2	2	2	2		
	$e_{mw}$	3.51	7.52	13.03	20.06	28.58		
	$o$	<b>2.69</b>	<b>4.62</b>	<b>8.55</b>	<b>13.80</b>	<b>19.86</b>		
	$e_{cw}$	3.51	7.00	11.00	15.16	19.21		
250 ft	$n_{sq}$	1	1	1				
	$e_{mw}$	3.29	6.87	11.74				
	$o$	<b>3.71</b>	<b>7.37</b>	<b>13.44</b>				
	$e_{cw}$	3.29	6.38	9.93				
500 ft	$n_{sq}$	1						
	$e_{mw}$	3.75						
	$o$	<b>3.77</b>						
	$e_{cw}$	3.75						

TABLE 6.41 CONTINUED

		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
23								
100 ft	$n_{sq}$	2	2	2	2	2	2	2
	$e_{mw}$	3.84	8.53	15.06	23.44	33.66	45.72	59.63
	$o$	<b>4.00</b>	<b>8.37</b>	<b>14.61</b>	<b>22.39</b>	<b>32.31</b>	<b>43.32</b>	<b>57.23</b>
	$e_{cw}$	3.84	8.39	14.50	22.05	30.93	41.03	52.25
250 ft	$n_{sq}$	1	1	1	1	1		
	$e_{mw}$	3.79	8.36	14.73	22.88	44.55		
	$o$	<b>3.99</b>	<b>8.95</b>	<b>15.92</b>	<b>21.77</b>	<b>32.00</b>		
	$e_{cw}$	3.79	8.17	13.98	21.06	29.27		
500 ft	$n_{sq}$	1	1					
	$e_{mw}$	3.81	8.44					
	$o$	<b>4.00</b>	<b>8.30</b>					
	$e_{cw}$	3.81	8.12					
27								
100 ft	$n_{sq}$	1	1	1	1	1	1	1
	$e_{mw}$	3.81	8.44	14.87	23.12	33.19	45.06	58.75
	$o$	<b>4.00</b>	<b>8.64</b>	<b>15.48</b>	<b>22.59</b>	<b>30.49</b>	<b>37.13</b>	<b>49.33</b>
	$e_{cw}$	3.81	8.23	14.06	21.07	29.07	37.85	47.23
250 ft	$n_{sq}$	1	1					
	$e_{mw}$	3.68	8.03					
	$o$	<b>3.89</b>	<b>7.24</b>					
	$e_{cw}$	3.68	7.25					
500 ft	$n_{sq}$	1						
	$e_{mw}$	3.20						
	$o$	<b>3.20</b>						
	$e_{cw}$	3.20						
total								
100 ft	$n_{sq}$	17	17	17	17	17	15	15
	$e_{mw}$	3.69	8.08	14.16	21.94	31.40	42.57	55.42
	$o$	<b>3.71</b>	<b>7.35</b>	<b>12.07</b>	<b>18.24</b>	<b>26.11</b>	<b>36.66</b>	<b>47.44</b>
	$e_{cw}$	3.69	7.82	13.16	19.53	26.76	34.73	43.32
	$n_{st} =$	9	10					
	$n_{sq}$	4	1					
	$e_{mw}$	69.97	86.21					
	$o$	<b>62.07</b>	<b>52.98</b>					
	$e_{cw}$	52.44	62.00					

TABLE 6.41 CONTINUED

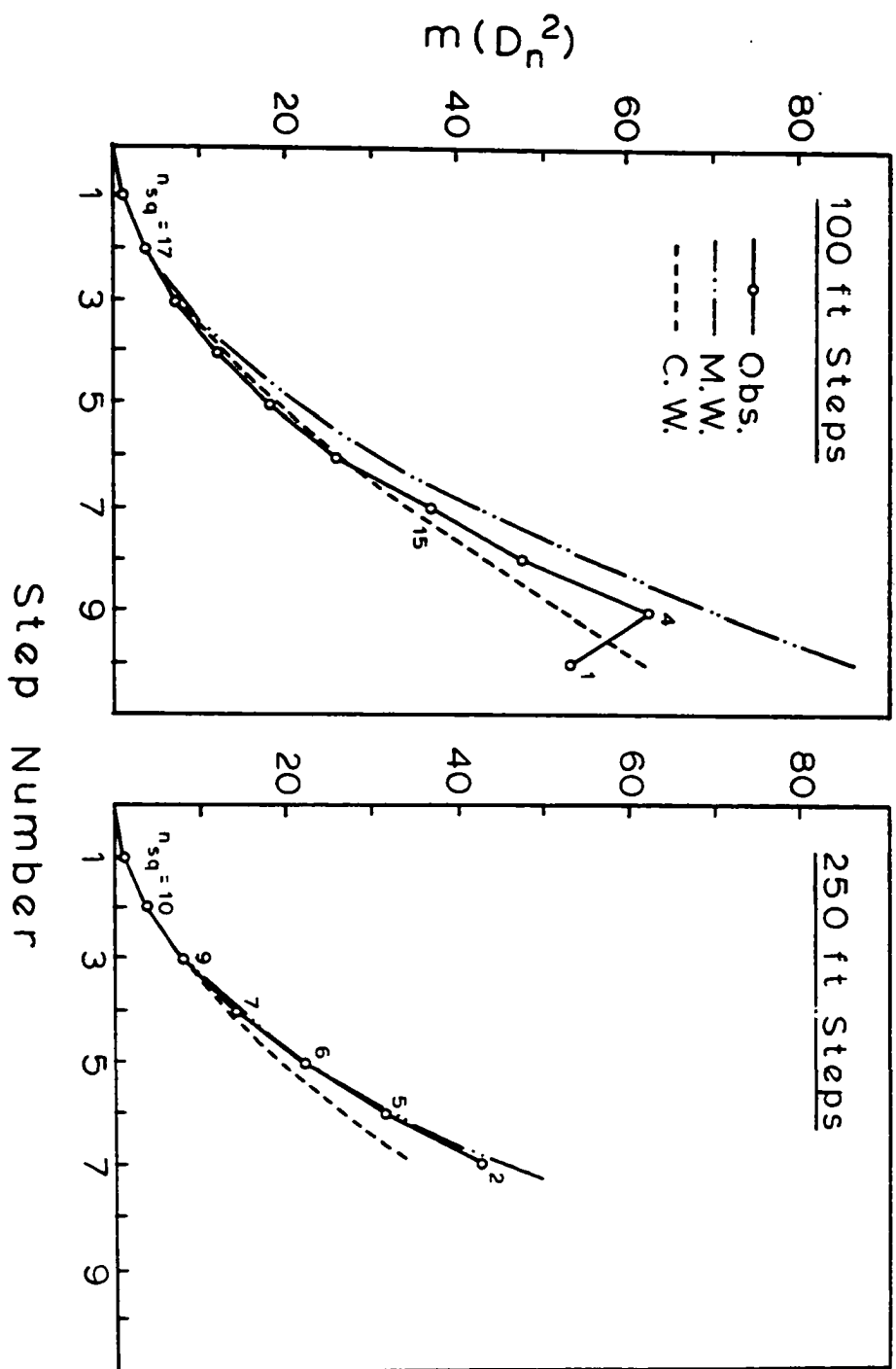
		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
total								
250 ft	$n_{sq}$	10	9	7	6	5	2	
	$e_{mw}$	3.68	8.05	14.11	21.85	31.27	42.38	
	$o$	<b>3.62</b>	<b>7.95</b>	<b>14.66</b>	<b>21.76</b>	<b>32.01</b>	<b>44.81</b>	
	$e_{cw}$	3.68	7.79	13.09	19.39	26.54	34.41	
500 ft*	$n_{sq}$	8	5					
	$e_{mw}$	3.78	8.33					
	$o$	<b>3.76</b>	<b>8.35</b>					
	$e_{cw}$	3.78	8.04					
total -								
$T8_{tr}$								
100 ft	$n_{sq}$	9	9	9	9	9	7	7
	$e_{mw}$	3.58	7.74	13.47	20.78	29.68	40.15	52.20
	$o$	<b>3.51</b>	<b>6.47</b>	<b>10.11</b>	<b>14.93</b>	<b>21.39</b>	<b>29.88</b>	<b>39.67</b>
	$e_{cw}$	3.58	7.40	12.19	17.74	23.89	30.49	37.44
	$n_{st} =$	9	10					
	$n_{sq}$	1	1					
	$e_{mw}$	65.82	81.03					
	$o$	<b>39.69</b>	<b>52.98</b>					
	$e_{cw}$	44.66	52.10					
250 ft	$n_{sq}$	6	5	3	2	1		
	$e_{mw}$	3.52	7.55	13.09	20.16	28.73		
	$o$	<b>3.53</b>	<b>7.70</b>	<b>14.57</b>	<b>20.20</b>	<b>32.00</b>		
	$e_{cw}$	3.52	7.18	11.70	16.88	22.54		
500 ft	$n_{sq}$	4	1					
	$e_{mw}$	3.71	8.12					
	$o$	<b>3.73</b>	<b>8.31</b>					
	$e_{cw}$	3.71	7.55					

\* Turtle  $8_{tr}$ 's sequences at the 500-ft level were subdivided into sections of three steps each in order to match up with the rest of the samples



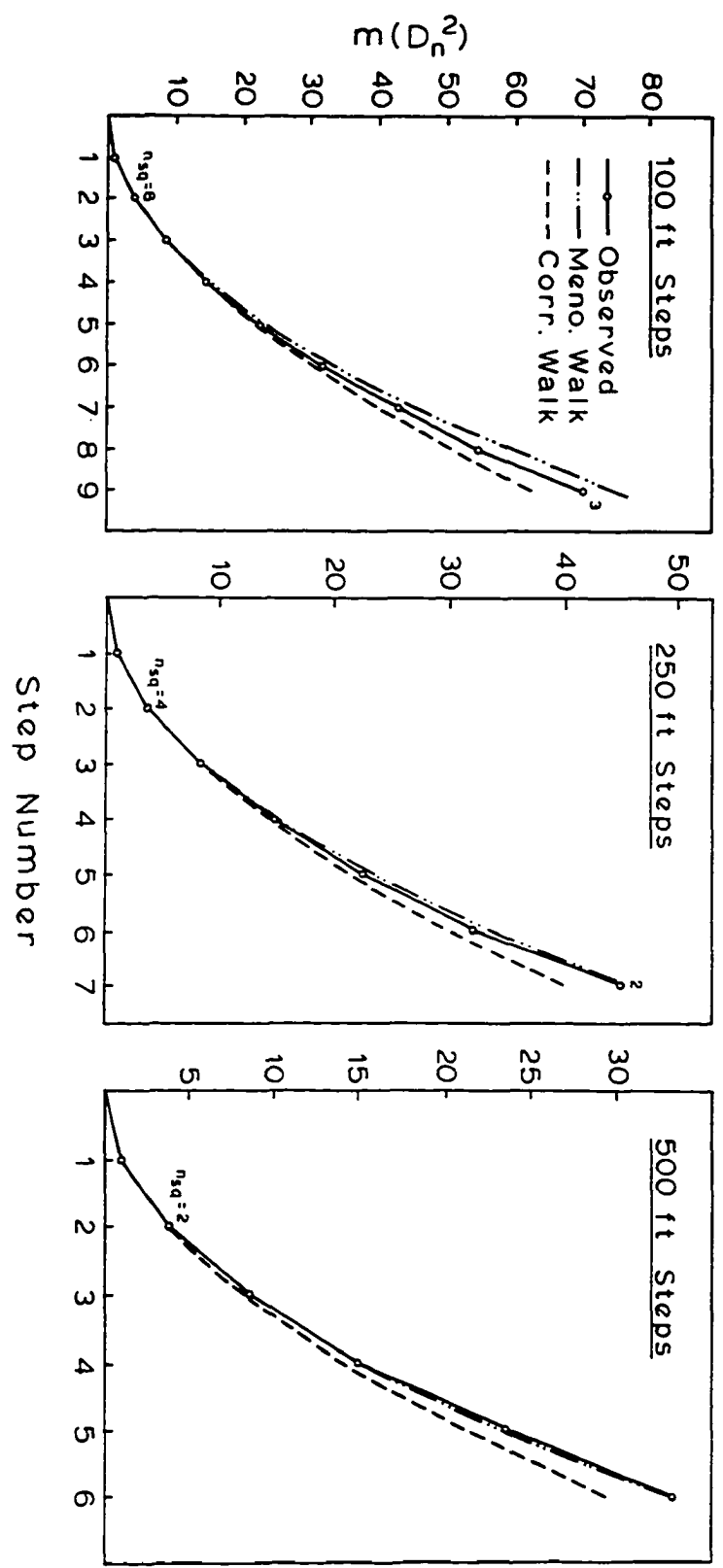
**FIGURE 6.20** Transients' sequences of higher-order uniform steps.

# Transients: Higher-order Uniform Steps



**FIGURE 6.21** Turtle 8tr's sequences of higher-order uniform steps.

# Turtle 8<sub>tr</sub>: Higher-order Uniform Steps



The other Transients behaved similarly to  $T8_{tr}$ , but not all to the same degree (Tables 6.40 and 6.41). There were, for instance, individual departures from the trend towards increasing values among the concentration parameters and various degrees of discrepancy in the observed MSD's from those predicted under menotaxis. These variations might reflect simply the small sample sizes available, or that some of the Transients were not as single-minded in heading towards a particular goal as  $T8_{tr}$ , who was apparently on egg-laying excursions both times she was followed off-range. At least some of the Transients were probably a lot closer to their destinations when first found than  $T8_{tr}$ ; several were considered to be "neighbors" based on the number of visits they made to the study area over the years (see Section II.E). Nonetheless, the pooled data for the Transients, even without the inclusion of  $T8_{tr}$ , still show the same trends described above.

In contrast, the Experimentals no longer show the qualitative similarity to the Transients that was seen at lower levels of analysis (Tables 6.42 and 6.43; Figure 6.22). Although they do continue to show the effects of active orientation up to at least the 250-ft scale of measurement, they do not demonstrate the same kind of convergence with the menotactic model as did the Transients. To the contrary, both their MSD curves and the relationships between  $c_{\theta 1}$  and  $c_{\theta 2}$  indicate a decline towards the correlated walk model at the 500-ft level of analysis.

Also note that despite the fact that the Experimentals show a higher value of  $c_{\theta 1}$  than the Transients for the first time at that scale of measurement, it is the Transients that still travel further

**TABLE 6.42 STATISTICS FOR THE TURN ANGLES OCCURRING WITHIN THE HIGHER LEVEL, UNIFORM PARTITIONS: EXPERIMENTALS**

Turtle	Scale	$n_{\theta 1}$	$m_{\theta 1}$	$r_{\theta 1}$	$c_{\theta 1}$	$c_{\theta 2}$
X1	100 ft	4	8	0.90	0.89	0.84
	250 ft	1	359	1.00	1.00	-
X2	100 ft	17	342	0.76	0.72	0.38
	250 ft	3	309	0.50	0.32	-0.09
X15	100 ft	27	356	0.77	0.77	0.72
	250 ft	9	346	0.86	0.83	0.73
	500 ft	3	341	0.95	0.90	0.71
	1000 ft	1	323	1.00	0.80	-
X16	100 ft	11	9	0.80	0.79	0.63
	250 ft	3	5	1.00	1.00	0.97
	500 ft	1	13	1.00	0.97	-
X17	100 ft	19	355	0.91	0.91	0.88
	250 ft	7	349	0.96	0.94	0.93
	500 ft	3	350	0.97	0.96	0.87
	1000 ft	1	331	1.00	0.87	-
X18	100 ft	5	3	0.89	0.89	0.83
	250 ft	1	327	1.00	0.84	-
X19	100 ft	19	355	0.85	0.84	0.78
	250 ft	6	347	0.88	0.86	0.87
	500 ft	3	340	0.96	0.90	0.84
	1000 ft	1	333	1.00	0.89	-
total	100 ft	102	356	0.82	0.81	0.70
	250 ft	30	347	0.85	0.83	0.64
	500 ft	10	347	0.95	0.92	0.80
	1000 ft	3	329	1.00	0.85	-

**TABLE 6.43 MEAN SQUARED DISTANCES OF TRAVEL IN SEQUENCES OF HIGHER ORDER UNIFORM STEPS: EXPERIMENTALS\***

		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
<b>X1</b>								
100 ft	$n_{sq}$	1	1	1	1			
	$e_{mw}$	3.78	8.34	14.68	22.79			
	$\sigma$	3.31	7.57	14.03	22.51			
	$e_{cw}$	3.78	8.11	13.77	20.53			
250 ft	$n_{sq}$	1						
	$e_{mw}$	2.63						
	$\sigma$	2.65						
	$e_{cw}$	2.63						
<b>X2</b>								
100 ft	$n_{sq}$	2	2	2	2	2	2	2
	$e_{mw}$	3.42	7.26	12.53	19.21	27.31	36.84	47.79
	$\sigma$	2.97	4.59	5.90	8.13	11.54	14.99	16.52
	$e_{cw}$	3.42	6.76	10.62	14.71	18.85	22.93	26.90
	$n_{st} =$	9						
	$n_{sq}$	2						
	$e_{mw}$	60.15						
	$\sigma$	20.84						
250 ft	$e_{cw}$	30.73						
	$n_{sq}$	1	1	1				
	$e_{mw}$	2.63	4.90	7.80				
	$\sigma$	2.65	1.76	4.89				
	$e_{cw}$	2.63	4.16	5.46				
<b>X15</b>								
100 ft	$n_{sq}$	4	4	4	4	4	4	
	$e_{mw}$	3.52	7.56	13.11	20.19	28.78	38.89	
	$\sigma$	3.61	7.96	12.83	19.13	26.48	34.59	
	$e_{cw}$	3.52	7.19	11.74	16.95	22.66	28.76	
250 ft	$n_{sq}$	1	1	1	1	1	1	1
	$e_{mw}$	3.66	7.99	13.99	21.65	30.97	41.96	54.62
	$\sigma$	2.65	3.96	8.56	13.47	18.64	27.17	38.52
	$e_{cw}$	3.66	7.63	12.53	18.04	23.87	29.78	41.19
	$n_{st} =$	9	10					
	$n_{sq}$	1	1					
	$e_{mw}$	68.94	84.92					
	$\sigma$	50.49	64.66					
	$e_{cw}$	41.19	46.49					

\* Long sequences at the 100-ft level were subdivided into sections of 7 or more steps in length; at the 250-ft level 6 or more steps

TABLE 6.43 CONTINUED

		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
X15								
500 ft	$n_{sq}$	1	1	1				
	$e_{mw}$	3.79	8.37	14.75				
	$o$	3.51	7.27	13.24				
	$e_{cw}$	3.79	8.00	13.13				
X16								
100 ft	$n_{sq}$	1	1	1	1	1	1	1
	$e_{mw}$	3.59	7.77	13.54	20.89	29.84	40.37	52.50
	$o$	3.31	7.57	13.90	21.79	26.31	37.24	50.28
	$e_{cw}$	3.59	7.41	12.16	17.58	23.49	29.71	36.13
	$n_{st} =$	9	10	11	12			
	$n_{sq}$	1	1	1	1			
	$e_{mw}$	66.21	81.51	98.40	116.89			
	$o$	64.92	81.49	99.97	97.51			
	$e_{cw}$	42.65	49.23	55.80	62.34			
250 ft	$n_{sq}$	1	1	1				
	$e_{mw}$	3.99	8.96	15.91				
	$o$	3.99	8.88	15.79				
	$e_{cw}$	3.99	8.93	15.78				
500 ft	$n_{sq}$	1						
	$e_{mw}$	3.95						
	$o$	3.95						
	$e_{cw}$	3.95						
X17								
100 ft	$n_{sq}$	2	2	2	2	2	2	2
	$e_{mw}$	3.91	8.73	15.47	24.11	34.66	47.13	61.61
	$o$	3.43	7.92	14.11	21.92	29.94	41.52	54.67
	$e_{cw}$	3.91	8.61	14.94	22.73	31.77	41.86	52.78
	$n_{st} =$	9	10					
	$n_{sq}$	2	2					
	$e_{mw}$	77.79	95.99					
	$o$	69.78	86.97					
	$e_{cw}$	64.30	76.21					
250 ft	$n_{sq}$	1	1	1	1	1	1	1
	$e_{mw}$	3.88	8.64	15.28	23.80	34.19	46.47	60.63
	$o$	3.49	7.97	14.52	22.32	32.11	44.25	56.00
	$e_{cw}$	3.88	8.46	14.51	21.77	29.95	38.76	47.90



**TABLE 6.43 CONTINUED**

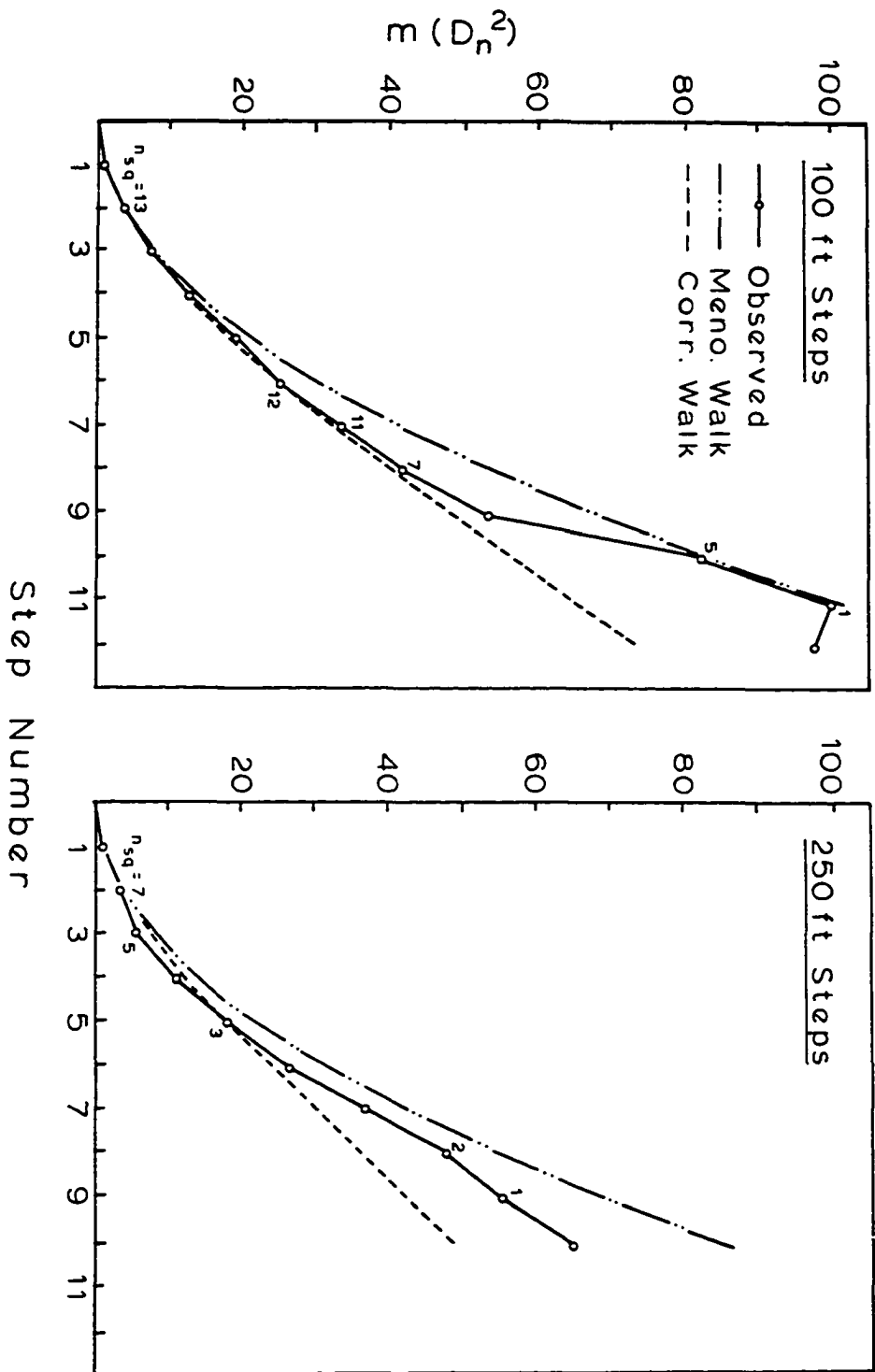
		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
<b>X17</b>								
500 ft	$n_{sq}$	1	1	1				
	$e_{mw}$	3.92	8.76	15.52				
	$o$	<b>3.99</b>	<b>8.41</b>	<b>14.97</b>				
	$e_{cw}$	3.92	8.62	14.93				
<b>X18</b>								
100 ft	$n_{sq}$	1	1	1	1	1		
	$e_{mw}$	3.78	8.33	14.67	22.78	32.67		
	$o$	<b>3.99</b>	<b>8.96</b>	<b>15.21</b>	<b>23.36</b>	<b>32.67</b>		
	$e_{cw}$	3.78	8.13	13.88	20.86	28.92		
250 ft	$n_{sq}$	1						
	$e_{mw}$	3.68						
	$o$	<b>3.68</b>						
	$e_{cw}$	3.68						
<b>X19</b>								
100 ft	$n_{sq}$	2	2	2	2	2	2	2
	$e_{mw}$	3.67	8.02	14.05	21.74	31.12	42.16	54.88
	$o$	<b>3.86</b>	<b>8.61</b>	<b>13.90</b>	<b>17.95</b>	<b>26.54</b>	<b>37.51</b>	<b>48.60</b>
	$e_{cw}$	3.67	7.74	12.96	19.13	26.08	33.66	41.74
	$n_{st} =$	9	10					
	$n_{sq}$	2	2					
	$e_{mw}$	69.28	85.35					
	$o$	<b>61.96</b>	<b>77.46</b>					
	$e_{cw}$	50.24	59.05					
250 ft	$n_{sq}$	1	1	1	1	1	1	
	$e_{mw}$	3.71	8.14	14.27	22.12	31.68	42.95	
	$o$	<b>2.45</b>	<b>6.28</b>	<b>11.59</b>	<b>18.65</b>	<b>28.00</b>	<b>38.50</b>	
	$e_{cw}$	3.71	7.81	12.96	18.85	25.17	31.69	
500 ft	$n_{sq}$	1	1	1				
	$e_{mw}$	3.80	8.41	14.81				
	$o$	<b>3.49</b>	<b>7.95</b>	<b>13.71</b>				
	$e_{cw}$	3.80	8.01	13.11				

**TABLE 6.43 CONTINUED**

		Mean Squared Distances						
Turtle	$n_{st} =$	2	3	4	5	6	7	8
total								
100 ft	$n_{sq}$	13	13	13	13	12	11	7
	$e_{mw}$	3.64	7.91	13.83	21.38	30.56	41.39	53.85
	$o$	<b>3.51</b>	<b>7.55</b>	<b>12.48</b>	<b>18.48</b>	<b>25.02</b>	<b>33.06</b>	<b>41.41</b>
	$e_{cw}$	3.64	7.61	12.67	18.61	25.25	32.47	40.14
	$n_{st} =$	9	10	11	12			
	$n_{sq}$	7	5	1	1			
	$e_{mw}$	67.95	83.69	101.06	120.08			
	$o$	<b>52.87</b>	<b>82.07</b>	<b>99.97</b>	<b>97.51</b>			
	$e_{cw}$	48.17	56.49	65.03	73.75			
250 ft	$n_{sq}$	7	5	5	3	3	3	2
	$e_{mw}$	3.66	7.99	13.99	21.65	30.97	41.96	54.61
	$o$	<b>3.27</b>	<b>5.77</b>	<b>11.07</b>	<b>18.15</b>	<b>26.25</b>	<b>36.64</b>	<b>47.26</b>
	$e_{cw}$	3.66	7.64	12.58	18.17	24.14	30.27	36.37
	$n_{st} =$	9	10					
	$n_{sq}$	1	1					
	$e_{mw}$	68.93	84.91					
	$o$	<b>50.49</b>	<b>64.66</b>					
	$e_{cw}$	42.33	48.06					
500 ft	$n_{sq}$	4	3	3				
	$e_{mw}$	3.85	8.55	15.09				
	$o$	<b>3.74</b>	<b>7.88</b>	<b>13.97</b>				
	$e_{cw}$	3.85	8.31	14.09				

**FIGURE 6.22** Experimentals' sequences of higher-order uniform steps.

# Experimentals: Higher-order Uniform Steps



over at least the first three steps. This result again indicates a difference in control processes at the highest observable level: the value of  $c_{\theta 1}$  equal to 0.92 for the Experimentals might reflect the actual deflectivity displayed by a correlated walk, whereas the value of  $c_{\theta 1}$  equal to 0.88 for the Transients might reflect a true deflectivity for menotaxis equal to  $0.88^2$ , or 0.94. Despite the appearances indicated by the turn angles, the Transients once again appear to possess the narrowest deflectivities, just as they did at all lower levels of analysis!

While the sequences are too short to demonstrate conclusively the absence in the Experimentals' of an ability to control for deflections at the highest levels, discontinuities continue to play an important role just as they did at lower scales of measurement. Perhaps that is still the only real difference separating the two groups of non-residents.

## **CHAPTER VII. DISCUSSION**

#### **VII.A. Evidence for the Discrete, Hierarchical Nature of Box Turtles' Routes of Travel.**

The model for organismal movements presented in Chapter III represents an extreme, comprising those features of an animal's behavior that would most clearly distinguish movements based on discrete decisions from those produced by random impacts. It seems likely, however, that there can be some continuous aspects to organismal movements and that higher-order patterns can occasionally be generated by processes observed at a lower scale of measurement. The fact that a walk model, based on discrete steps, can serve as a useful approximation to an animal's route, perhaps revealing much about its behavior, is not in itself any proof that movement decisions are actually made at discrete intervals. What is the actual evidence then that the routes of box turtles display any of the characteristics proposed by this theory?

The most concrete evidence for the occurrence of abrupt changes in direction are the turns that take place at the form sites. Bounded as they are by within-day turns of much smaller magnitude, these changes in direction do not appear to represent simple detours. Instead they are consistent with what would be expected for true changes in target heading at discrete points in space. Even the finding among the Residents that the final and initial turns of a day-range also show more scatter than the rest of within-day turns does not obscure this picture. The dominance of the between-day turns is clearly seen

in the similarity of the form-site turns between the 25-ft vectors to those between entire day-range vectors. Among the Transients and Experimentals, furthermore, there is no suggestion whatsoever that between-day changes in orientation extend over more than one point in space.

Apart from the form-site turns, other point-like discontinuities are apparent in the routes; these discontinuities formed the basis for my visual partitioning scheme. In the analysis of such "discontinuities", isolated points of change predominated. Most of these apparent changes in target resembled the changes at the form-sites: in both cases, sharp changes in direction were bounded by first- and often second-order turns of lesser magnitude.

The few runs of "discontinuities" that did occur offer little support for the hypothesis that directional changes happen gradually, spread out over space. While there were a few more curves (sequences of turns with the same sign) than expected from chance alone, there were still few enough so that the possibility of their representing surveying artifacts seems high. The only probable exceptions were the curves over five steps in length, and these, again, were really too few in number to indicate they played any major role within the routes.

The overall MSD plots for runs of "discontinuities", furthermore, showed evidence for ongoing orientation, a finding inconsistent with the hypothesis that changes in target are spread out over space and time. However, it does indicate that my identification of "discontinuities" based on the "tangle" criterion was not very accurate. This criterion was, after all, based on the absolute magnitude of the



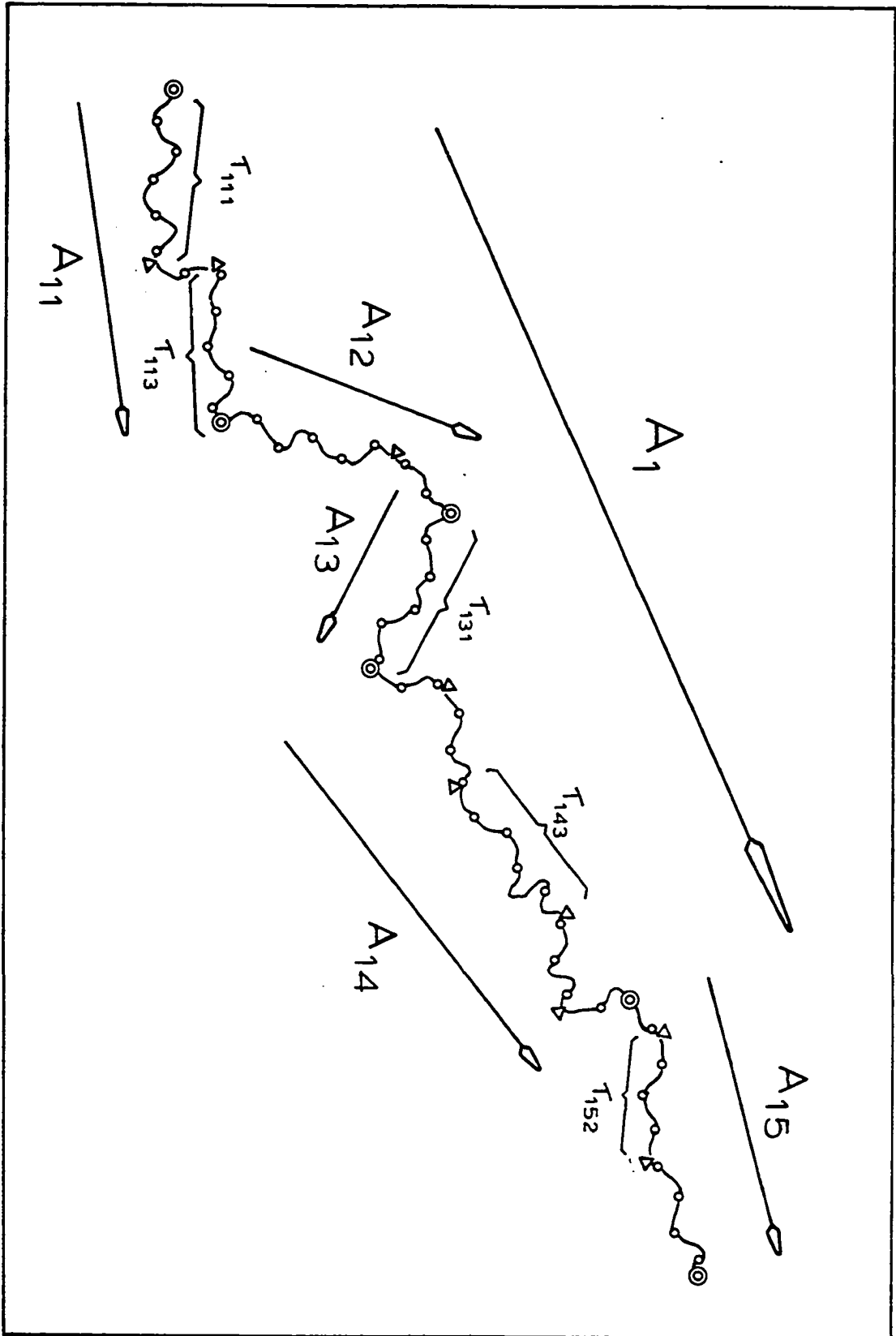
changes in direction, rather than on the relative changes used in identifying the "form-like discontinuities". In summary, any true curves or periods of randomness that possibly existed did not have any substantial influence on movements.

The general absence of longer curves or random turning was also evident in the more arbitrary samples of seven-step, within-day sequences. Only 1% of all such samples showed any bias towards one side or the other. The more frequent samples of apparently "random" steps found among the Residents failed to match the behavior expected of a truly random walk. Their MSD curve (Figure 6.3) probably reflects points of discontinuity occurring within oriented walks: the curve initially rises above that for a random walk and then falls off toward the end, an indication of some sort of heterogeneity, but not any gradual change in orientation.

In addition to the evidence that changes in orientation occur at discrete points in space, the presence of an hierarchical structure within the routes further supports the theory that organismal walks are produced by discrete movement decisions. Evidence for hierarchical patterning is found in the emergence of at least two and possibly three different patterns of movements at the highest scale of measurement from the basic orientational pattern that all turtles seemed to share at the lowest level. More important for the volitional model is evidence that all three classes show a nesting of orientational processes within days.

Figure 7.1 illustrates what I believe is going on within the routes. Over some substantial section of a route, a single orientational target ( $A_1$ ) prevails. Within each such section, however, there

**FIGURE 7.1** An example of a route demonstrating a hierarchy of taxes. Over a period of several days (endpoints indicated by the double circles), a menotactic target,  $A_i$ , holds sway. The steps within this walk additionally show evidence for klinotaxis, i.e., their length and directional components are correlated. Within each day-range, another taxis, indicated by the  $A_{ij}$ 's, appears to operate, but the presence of discontinuities (shown by the triangles) obscures its nature, as well as hints at processes at still a lower level. The steps formed between the triangles again show some sign of klinotaxis. Finally, within each of these steps are the segments representing the route survey. Although they only roughly approximate the actual path, they clearly indicate the action of yet one more lower-level taxis.



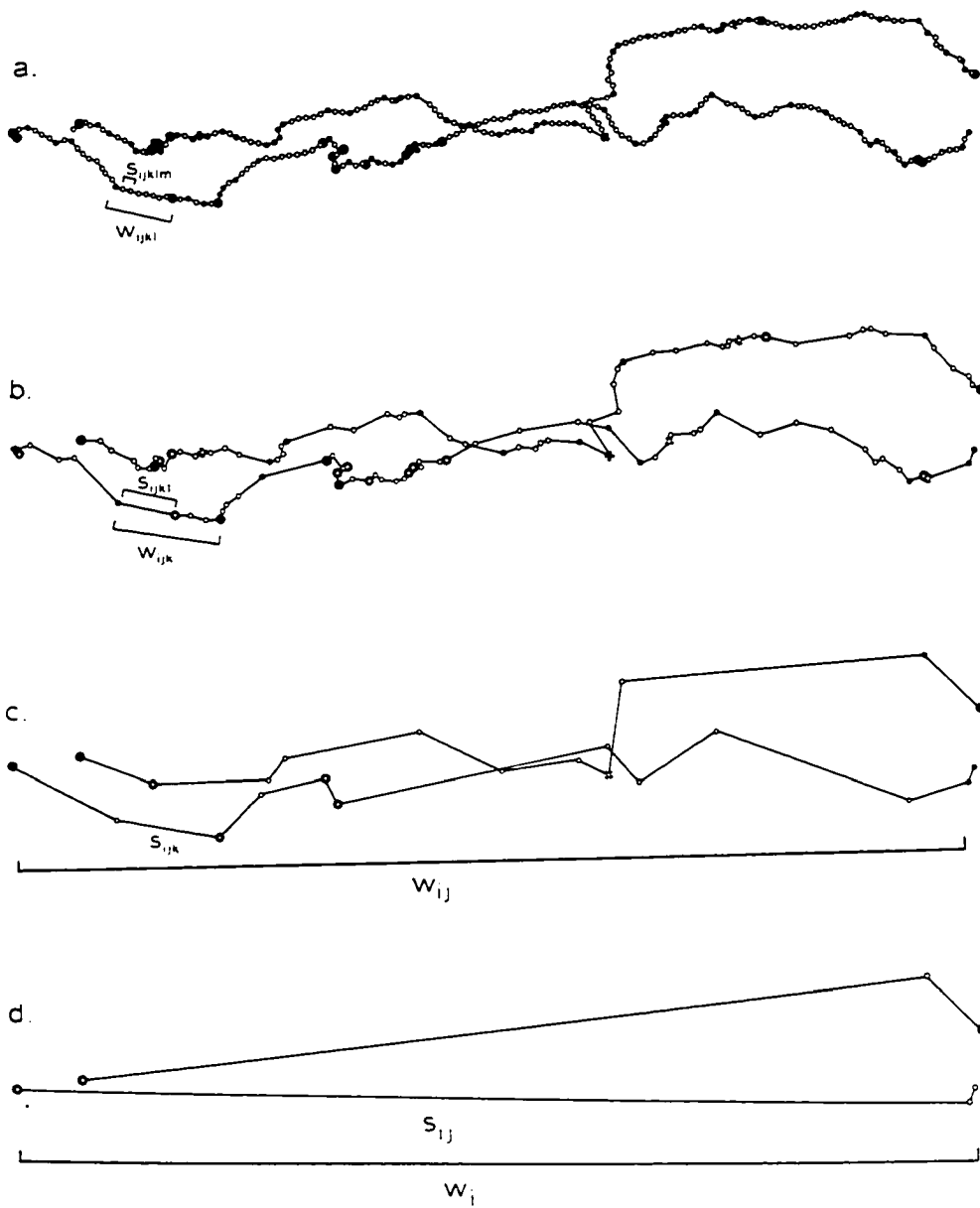
can exist sub-targets, each denoted by two subscripts. Each of these targets corresponds to a single deflectional event within the section of the route dominated by  $A_i$ . They are denoted as targets, however, because each of the  $A_{ij}$ 's itself controls a subset of steps, each one of which corresponds to a still lower order deflectional event. The important aspect of this model is that it implies that active control over movement is switched down through several subsidiary levels and passed back upwards after a lower-level step has been completed, just like the execution of subroutines within a computer program.

This pattern is best seen among the Transients, who carry the nesting of orientational control beyond the level of the day-ranges. The clearest example is shown by Turtle 8<sub>tr</sub>, whose different levels of orientation are illustrated in Figure 7.2. The steps at the lowest level are, naturally, those produced by the survey of 25-ft segments. In 7.2.a these are indicated as  $s_{ijkl}$  (the fourth subscript implies that this series is not homogeneous over its entire length but is divided into a series of distinct walks on three different levels). The visual partitioning supplied the endpoints for the first level of walks, and the MSD analysis indicated that each such walk represented a tactic process, governed by a target,  $A_{ijk}$ .

Each one of these targets themselves represents a single step in a higher-order walk. Again the MSD analysis of these steps indicated the action of a taxis, but also the presence of further points of discontinuity. An attempt to divide these steps into homogeneous walks is illustrated in 7.2.c. Each step now corresponds to a target, indicated by the  $A_{ij}$ , of the steps that were shown in 7.2.b. It should be noted that these steps cross the limits of single day-

**FIGURE 7.2** Visual partitions of the routes of Turtle 8<sub>tr</sub> illustrating a hierarchy of orientational control. Within any sequence, discontinuities are indicated by the solid circles. They correspond to walk endpoints at the level shown and to step endpoints at the next level up.

- a. Sequences of the original survey steps. The discontinuities at this level correspond either to form sites (double circles) or to the visually-determined points used in previous analyses. The walks indicated ( $w_{ijkl}$ ) fit the menotactic model quite well but may represent a taxis other than menotaxis itself (I will present evidence later on that suggests the process may be telotaxis).
- b. The walks at this level ( $w_{ijk}$ ) also appear to be tactic and some of the steps seem to show a correlation between their length and directional components (as was suggested by the analysis of the steps between the visually-determined "discontinuities"). Note that in this partition I have allowed some of the steps to span different day-ranges, as seems reasonable, although I did not do so in the actual analyses presented in Chapter VI.
- c. Even clearer evidence for klinotaxis is shown in this series, as was also discovered in the MSD analyses of the Transients' day-range vectors.
- d. The overall walks shown here probably represent movement towards a particular goal, a nest site, but might be divided into an initial component governed by vector navigation and a terminal step representing direct telotaxis.



ranges. In some cases form-sites provide endpoints for these steps, but there are also instances where a target's influence carried over from one day to the next.

At this level of analysis there is still some heterogeneity evident, as indicated by arrows showing some possible points of discontinuity. The departure from menotaxis here, as reflected in the analysis of the day-range vectors (which include a few additional divisions into steps than are shown in Figure 7.2.c) involves mainly steps of shorter length. The clusters of form-sites in both years probably represent a shift from an oriented, sequential process to one that is spatially constrained. There is also one upward jag in the route that appears to reflect a single, aberrant target heading. In both these cases the departures are short-lived and bounded by steps that appear to obey a yet higher level target,  $A_i$ . This is clearly indicated in the larger-scale, uniform partitions, which suggest that a single ultimate target operated over both entire routes of travel.

As implied by the variable subscript, this highest order target itself defines a single step. In  $T8_{tr}$ 's case, it probably represents the single event, "nesting". The second step in this walk would correspond to the subsequent event, "return to the home range". An MSD plot of this two-step walk would rise to one at the first step and then return to zero at the second, illustrating very precise spatial constraints on the movements.

The other Transients, of course, may not show any spatial constraints at the highest level, depending on whether or not they were true dispersers rather than excursionists like  $T8_{tr}$ . They could also differ in the number of levels through which orientational control is

switched. Indeed, I cannot place too much confidence on the four or five levels deduced for Turtle 8<sub>tr</sub>. It should be clear by now how easy it is to confound the steps of one walk with those of another, even when they represent different levels in the hierarchy or even entirely different sorts of control processes. Nevertheless, all the Transients appear to be distinguished by a high-level tactic process that operates over a period of days. Below that level other tactic processes are evident, but these lower-level processes are shared with other classes of turtles.

The expression of a unique tactic process at the very highest level among the Transients together with their very low deflectivities at all levels raises another question about the validity of the theory proposed in Chapter III: could there be incomplete switching of control between the various levels of the hierarchy, allowing the influence of higher level processes to supplement those at lower levels? While that would not actually sink the general theory of decisive movements, it would certainly complicate the analysis of the routes.

But the evidence for such incomplete switching between levels is not strong. For one thing, the deflectivities seen at various levels within the routes of the Transients seem to vary in a complex way: the values of  $\tau_0$  for the various within-day partitions are all higher than for the day-range vectors, but they increase again in the still higher-order uniform partitions. While this finding does not actually negate the hypothesis of orientational interaction between the levels, it seems more consistent with the theory that the control processes as well as the deflectional influences within any one level are more or less independent of those operating at other levels.



In a much more significant departure from the expectations of an interaction hypothesis, the fit to menotaxis is very good within-days once the "discontinuities" have been removed from the series. If there were any between-day influences at work at the level of the 25-ft survey steps, then there should still have been some residual correlation between the steps, which would lower the observed curves relative to the expected. Instead, the close fit to the model implies at least a fairly high degree of independence between the steps (if not an actual case of menotaxis). Within a single target's regime, represented by the walk between two points of "discontinuity", the steps obey only that heading determined by the immediately next higher process within the hierarchy.

There are, moreover, other explanations for the differences in deflectivity seen among the various classes that do not call for modification of the simpler theory involving complete switches in control from one level to the next. Indeed, some such other explanation seems likely to account for the Residents' comparatively high deflectivities seen at all levels within the route hierarchy. While in their case control processes at the highest level seem to involve spatial constraints rather than an ongoing taxis, these constraints themselves bespeak no less control over the directions of travel than that of the Transients. If the interactional hypothesis were correct, in fact, it might be necessary to ask why the Residents do not show even less deflectivity at the lower levels than do the Transients.

The hypothesis of orientational interactions between the levels also seems difficult to apply to the Experimentals. If there was any group that appears to show no taxis at the highest level, it was this

one. Although they appeared to show an oriented pattern of movement similar to the Transients over the lowest three levels examined, beyond the level approximately equivalent to the day-ranges, their movements approached the expectations for a correlated walk. Nevertheless, even without a strong, ultimate target heading, their lower-order steps showed a level of deflectivity similar, if slightly lower, to that of the Transients.

While the arguments just presented seem to rule out a significant role for orientational interactions between levels, there is still another sort of interaction that more successfully demonstrates an incomplete switch between levels: the correlations between step lengths and directions observed nearly everywhere they were possible to detect. That more radical directional departures from the menotactic model appeared to be associated with shorter-than-average step lengths implies that a deflectional event within a particular target's regime is not completely independent of the field's effect. A deflection appears to be terminated more quickly the further off target it is (contrast this with the definition of deflectional events given in Section III.D).

Even if this were the case, however, it would still be consistent with a theory of organismal movements based on decisions. The orientational independence between levels still argues for a complete switching of guidance, but the organism appears to retain an ability to decide at what point to switch back to the more dominant process. If anything, this sort of behavior argues even more strongly for the existence of endogenous controls over movement that can supercede any exogenous influences.

On the whole, the evidence supports the theory presented in Chapter III. There do appear to be definite hierarchies of control processes, and each process is manifested as a series of relatively clearly defined steps that are bounded by sharply defined endpoints.

The results, furthermore, appear to show that all three classes of turtles are similar at the lowest level of control. Their significant differences emerge only on roughly the third level in the hierarchy. Residents display strong spatial constraints at that level, while the Transients and Experimentals continue to show a strong ongoing tendency. At approximately the fourth level in the hierarchy, the latter two groups diverge. The Transients display a high-order taxis and the Experimentals an absence of higher-order control.

While the abstract model for volitional movements appears to account well for box turtle routes of travel, what might the actual behavioral processes be that correspond to the various levels of control? Although the answer cannot be ascertained directly from my data — there is too little contextual information for that — nonetheless, the complex interplay of orientation, klinokinesis, and spatial constraints does prompt certain speculations.

In the following sections, I show that a single model can yet explain the apparent divergences between the classes, as well as their similarities. The hypothesis of vector-navigation, developed notably by Jander (1957), the Wiltschko's (1975a; 1978; Wiltschko, Wiltschko, and Keeton, 1978), and Wehner (Wehner and Srinivasan, 1981), involves both orientational and positional control over movements. As such, it is compatible with the findings of spatial constraints among the Residents as well as the directional movements of all three classes.

Furthermore, it suggests a role for nested hierarchies of route decisions.

In making a case for this behavioral model of box turtle movements, I will consider evidence related to each of the traditional paradigms of movement study. Although I will follow the conventional separations, it will be obvious that this theory of vector-navigation links these disciplines firmly together; each contributes a complement to the overall model. Furthermore, the model that emerges accounts even better for the various aspects of the movement patterns than can each of the respective paradigms devoted to their study.

## **VII. B. Hypotheses Concerning the Orientational Structure of the Routes**

The predominant pattern that emerges from all analyses is one of active orientation. Within days for all three classes of turtles, and between days for at least the Transients, there is indisputable evidence that the turtles compensate in some way for deflections; as a result, they travel farther in a number of steps than would a first-order correlated walker. Even where the Residents show a leveling-off of distances traveled below that expected for a randomly moving organism, the implied spatial constraints themselves bespeak some orientational process. Only in the Experimentals, and only at the very highest scale of measurement is there the slightest suggestion of a lapse in active orientation.

The evidence further indicates that the orientational processes are what I have termed tactic: the influence of an orientational target is represented by a field that remains constant in space despite the organism's changes in position within it. After a given deflection, the turtle refers back to this field, and by so doing prevents effects of the deflections from accumulating. Among the Transients, the tactic nature of at least the highest apparent process was demonstrated by the increasingly good fit to the menotactic predictions with increases in the scale of measurement. It was also implied in the lowest level analyses for all three classes by the very close fit to the menotactic model that was obtained when the visual "discontinuities" were removed from the series of survey steps.

Conversely, the usual expectation that box turtles do, in fact, travel in a tactic manner supports the hypothesis that the "discon-

tinuities" were indeed real. As mentioned in section I.G, there are several experimental studies that document various taxes for box turtles. Gould (1957, 1959) and DeRosa and Taylor (1982) presented evidence for the use of a sun-compass. The latter study also demonstrated that time-compensation is involved, since the compass can be clock-shifted. Recently Mathis and Moore (1985) presented evidence for the use of magnetic information by box turtles. In addition to these two forms or menotaxis, telotaxis towards objects can be assumed, and Madden (1975) suggested that olfactory guidance (a form of telotaxis) is employed in homing. The presence of this orientational repertory in any vertebrate should no longer seem surprising.

While my data support the hypothesis of tactic orientation, the lack of contextual information as well as methods for distinguishing even telotaxis from true menotaxis, make further progress difficult. Furthermore, even if telotaxis or menotaxis could actually be pinned down as the correct form of taxis, it still would be impossible using route data alone to distinguish among the various physiological processes that underlie it.

There is, nevertheless, at least enough circumstantial evidence upon which to build some speculations. There are two main categories of questions I would like to consider: 1) How well do my data agree with various proposals for the way different orientational processes interact with one another? and 2) How do the three classes of turtles differ with respect to orientation? Are there differences that could correspond to Watson and Lashley's (1915) "near" and "far" types of orientation or to Griffin's (1952) types I, II, or III navigation? I will argue that all three classes show the same basic pattern of

orientation, one whose hierarchical complexity is due the turtles' primary use of indirect cues to travel towards particular headings or goals.

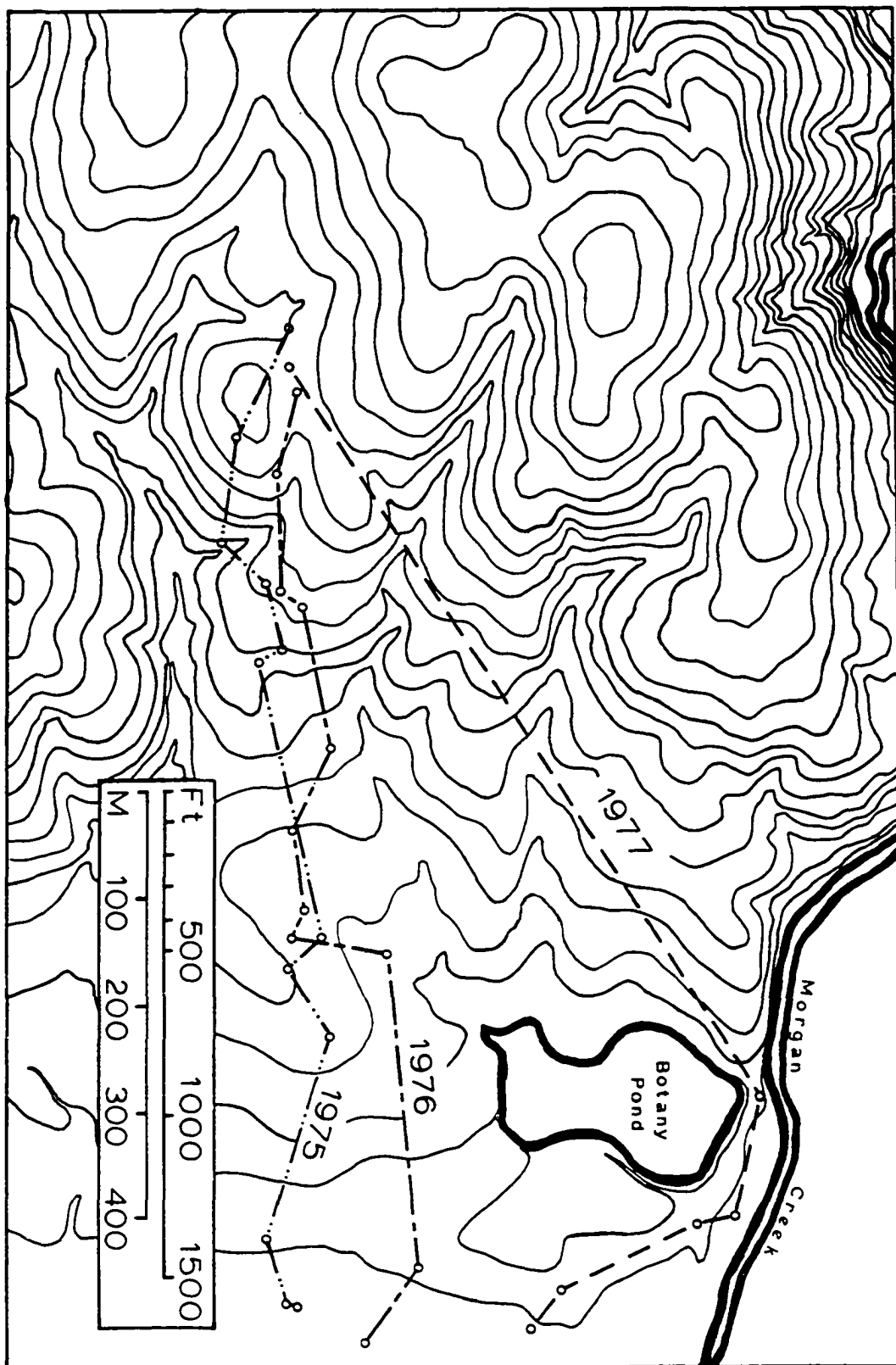
Long distance orientation by the Transients: the vector-navigation hypothesis. Turtle 8<sub>tr</sub> offers the best contextual information regarding long-distance orientation. The two trips surveyed (Figure 2.6b and c) almost certainly represent egg-laying excursions. From the close coincidence of the routes between years, it appears, moreover, that the goal area of the movements was the same in both years. The orientation displayed at the higher scales of measurement was not only very precise, as indicated by the high values of  $r_{\alpha}$  but had virtually the same heading both years. At the 250 ft scale of measurement the mean vector for 1975 was:  $\mu_{\alpha} = 90^{\circ}$ ,  $r_{\alpha} = 0.95$ ; and for 1976 it was:  $\mu_{\alpha} = 88^{\circ}$ ,  $r_{\alpha} = 0.94$ . The difference between these vectors is insignificant.

These findings strongly suggest that long-term memory plays an important role in box turtle orientation, but is this a memory for places or directions or both? While the routes start at roughly the same place on the study area and end in the same overgrown field, the third and lower level steps apparent in the routes do not line up very well (Figures 7.2 and 7.3). This finding suggests that, though the overall routes are possibly learned in some fashion, they are not guided by a succession of intermediate, remembered landmarks (similar arguments were made in the case of pigeon homing by Michener and Walcott, 1967). Further support for this hypothesis is the observation (see Figure 7.3) that the turtle crossed between two different watersheds en route but not at the same points in different years; she

**FIGURE 7.3** Offrange excursions of Turtle 8. The routes for 1975 and 1976 are represented by the same points as shown in Figure 7.2 c. Note that neither shows any obvious following of watersheds or other topographic leading lines. It is also worth mentioning that the point where they diverge just west of Botany Pond is where they cross a dike of diabase, an igneous rock formation rich in iron.

The route for 1977 was not surveyed in detail. However, the lines shown are fairly representative — the initial long section ran obliquely across the ridge slope as shown and did not show any deflecting influence by the pond. The point where the turtle emerged from the woods at the end of this section and began to turn more towards the east is accurately depicted, just above the bluff along Morgan Creek.





was not just following a single leading line.

While this finding would seem to rule out pilotage as a major factor in the overall orientation of the two routes, it does not conflict with direct telotaxis towards the ultimate goal. If the entire thicket-covered field was her target, then perhaps some odor of blackberry or rose blossoms guided her to it. Another possibility would be her use of some form of dead reckoning, depending on memory for the starting and ending points, but allowing a great deal of variability in between.

The behavior this turtle displayed in 1977 sheds some more light on this question. Although I was unfortunately unable to survey that year's egg-trip before a large part of her thread trace was bulldozed, I was still able to plot a few points at what appeared to be significant sites along its course (Figure 7.3).

As in the two previous years, she began moving away from the study site in early June, departing from nearly the same point as before. This time, however, her initial series of movements diverged  $30^{\circ}$  to the northward from her earlier routes. Following a path that appeared similar in straightness to the first two, she cut obliquely across several watersheds and was eventually deflected from this course only when she reached Morgan Creek, a large perennial stream. After traveling along the streambank for five days, she turned inland, whereupon her path became extremely convoluted. After another week, her path straightened out quite abruptly as she headed directly toward the old field that had been her apparent destination the two years before. Even at the point where she resumed her linear travels, however, the field was not directly visible; she first crossed over a

grassy area she had been skirting for several days and then had to move through a small stand of pines.

While the final leg of the journey suggests that the goal of the entire trip was the same as in the previous years, the initial series implies that direct perception of that goal had not been the guiding factor, at least at first. Rather, it appears more likely that she had been relying on memory for the direction to the goal area from some starting point on her home range, a memory that had served her reliably in the first two years but which had gone awry in the third.

If that hypothesis is correct, then furthermore some form of compass orientation (menotaxis) must have served as the process whereby the learned heading was carried out. Such uses of menotaxes to achieve orientation to a goal have been categorized as Type II orientation (Griffin, 1952) or vector-navigation (Jander, 1957; Schmidt-Koenig, 1973; Wehner and Srinivasan, 1981). These models are distinguished from true navigation, which also involves a "compass" in steering towards a goal (Kramer, 1953), in that the direction is set by learning rather than with reference to a spatially-generalized "map", one that can be read at any point in space whether in familiar territory or not. This learning could involve memory for places, like the specific starting and stopping points I suggested for the routes of T8tr, or it could involve the recording of all the twists and turns over a path in order to calculate a more direct return trip (Wolf, 1927; Marais, cf. Schone, 1984; von Frisch, 1965; Barlowe, 1964). Ferguson's (1967) hypothesis of y-axis orientation, which involves homing towards a target with essentially an infinitely broad face, is similar, but only one target heading need be remembered irrespective

of starting point: simply the reverse of whatever heading the animal had originally taken in moving orthogonally away from "home".

As is implied in the use of the term "vector" navigation in the strict sense, there could also be memory (or calculated expectation) for the distance to the goal. When a distance has been traversed that the animal expects to have brought it home but has failed to do so, searching is often initiated (Wehner and Srinivasan, 1981; Hoffman, 1983a, b). There is some suggestion, in fact, that memory for distances influenced T8<sub>tr</sub>'s excursion in 1977: her trail became extremely convoluted at a distance from the starting point that was roughly equivalent to the travel distances of her two more successful trips. On the other hand, this search, if that was what it really was, could have been triggered by her encountering the creek or some other environmental conditions she had not met with in other journeys.

These arguments for vector-navigation in Turtle 8<sub>tr</sub>'s excursions, while anecdotal, are at least in general accordance with other studies of chelonian orientation, and of the box turtle's in particular.

Gibbons and Smith (1968) displaced individuals of Gopherus polyphemus, Chrysemys floridana, and Chelydra serpentina and watched them follow the same headings they had been traveling before the displacement, an indication of some form of Type II orientation. Gourley (1974) further tested the homing ability of Gopherus polyphemus and also found they could indeed maintain a compass heading for significant periods of time, but that their directions bore no relationship to the home-ward bearing. Tests with clock-shifted individuals demonstrated the use of a time-compensated sun-compass in this species, and similar time-compensated sun-compasses were discovered in Terrapene carolina,

as well as Chrysemys and Trionyx by DeRosa and Taylor (1982).

The findings of both DeRosa and Taylor and Mathis and Moore (1985) further indicate that some form of menotaxis actually is employed by box turtles in true vector navigation, although, as will be discussed below, these studies are in disagreement about the cues involved. Other studies have also found only a short-range homing ability in the box turtle (Lemkau, 1970; Metcalf and Metcalf, 1970, 1978; Madden, 1975). While these studies do not absolutely rule out the use of a spatially-generalized "map", they are far more consistent with the use of vector-navigation or direct telotaxis towards a goal. This ability is expected in animals such as the box turtle that are seldom naturally displaced over any great distances from their homes (Emlen, 1969; Carroll and Ehrenfeld, 1978).

The role of multimodal orientational systems in vector-navigation. If some form of menotaxis operates at least over the highest level in the route hierarchy of Turtle 8<sub>tr</sub> and other Transients, then what is going on at levels lower down? While a single orientational mechanism, such as sun-compass, could conceivably be operating at several different levels, this hypothesis does not seem very likely, especially in view of the variety of different orientational mechanisms that the box turtles are known to possess. Surely to some extent the different levels correspond to the use of different sorts of orientational processes.

The existence of a multitude of different orientational modes, on the other hand, does not in itself imply a nested hierarchical structure for the routes. In fact the most prevalent hypotheses for the way different sources of directional information interact argue

against nested sub-routines for orientational control.

(1) The integration hypothesis: all available information is pooled in some manner to produce a single target heading, for instance in the way gravity and incident light cues interact in the well-known dorsal-light orientation in fish (see Schone, 1984, for an extensive review of this and other integration theories).

(2) The substitution hypothesis: switching occurs between alternative orientation processes depending on the quality or quantity of the information available to the various orienting modes, for instance in the way a homing pigeon substitutes a magnetic compass for a sun compass in overcast conditions (Keeton, 1971), or in the way Cataglyphis bicolor, a desert ant, switches from direct sun-compass to polarotaxis to landmark pilotage or to anemotaxis, depending on the relative strengths of the available cues (Wehner, 1972; see also Able, 1980, for additional examples of orientational substitutions).

Although both of these hypotheses usually also involve a preference hierarchy of cues or modes — some may be given more weight in integration or be preferred over alternatives in substitution — neither provides an answer for the nested hierarchy of walks that I observed in the box turtles. Rather, they both imply that only a single target heading is maintained over an entire route of travel, which allows perhaps for some variation in the degree of deflectivity as a response to changes in the quality or quantity of directional information, but not any role for subsidiary targets.

The calibration hypothesis. One prominent theory that could involve a walk hierarchy is the Wiltschkos' hypothesis (they credit Vleugel, 1953, with the original idea) for the interaction between magnetic and stellar compasses in night-migrating birds (Wiltschko and Wiltschko, 1975a, b; 1976). In this model, there is also a hierarchy of preferred orientational processes, but the significant feature is that the subordinant mechanisms receive their target headings from the more dominant processes. The primary, or highest level process (in the Wiltschkos' example, the magnetic compass) is the most reliable over long distances or time periods, but is often not the most efficient over shorter intervals. The secondary process (in the Wiltschkos' example, the stellar compass) is the more precise or easier to maintain over shorter term movements and thus allows straighter courses to be traveled, but it is not as accurate as the primary mechanism over the long run. The two mechanisms interact by the primary process "calibrating" the secondary one at periodic intervals; the subsidiary target heading is re-set every so often to the dominant target. The Wiltschkos additionally suggest that in night-migrating birds recalibration is a function of time, but it is actually a function of the drift in the secondary process which can be related to the distance traveled just as easily as to time.

Recent evidence indicates that the situation for night migrants is probably more complicated than suggested by the Wiltschkos' earlier models, by involving still other forms of calibration or the integration or substitution of cues (Able, 1980; Able and Bingman, 1987). However, the Wiltschko's general proposal of primary, secondary, and even tertiary mechanisms (Wiltschko and Wiltschko, 1976) does seem to

fit well with the sort of nested walk hierarchies I found in the box turtles' routes. Furthermore, their reasons for the differentiation of roles in a complex, interactive compass system seems to explain yet other aspects of the box turtles' movements.

For example, the correlation seen between step length and direction in the box turtles' walks, especially at the higher levels, strongly suggests some form of klinotaxis. In this mode of orientation, as in any other form of taxis, there is an orientational field of some sort, but in case of klinotaxis it is difficult to "read" at any point in space; its directional features can only be picked up as the organism moves through the field. The more divergent a heading is with respect to the target direction set by the field, the more quickly the error is detected and adjusted for. Headings that depart less from the target are correspondingly followed for greater distances before being checked.

Such behavior would therefore seem one indication of a primary field that is difficult to use and results in less efficient paths in terms of straightness. The routes of at least some night-migrating birds indeed display these features. Emlen and DeMong (1978), for instance, found that white-throated sparrows released from balloons under nocturnal overcast showed strongly zig-zagging tracks along with relatively slow flight speeds (similar results were observed by Griffin, 1972, in radar tracks of nocturnal migrants). Under clear skies, in contrast, the paths showed only an initial zig-zagging before more direct and rapid flights were obtained.

Like the Wiltschkos, Emlen and DeMong hypothesized that the birds used some more difficult-to-use orientational system under cloudy



conditions, where better cues were presumably unavailable. But the initial ziz-zags in the clear-sky conditions also suggest a role for that system in calibrating a secondary, more precise one. Significantly, zig-zagging has often been associated with klinotaxis in other organisms, for instance ants or pit-vipers following odor trails or sharks locating prey in an odor-gradient (see Schone, 1984, for a review).

A klinotactic primary system and a calibrated, tropotactic secondary system could explain still other features of the box turtles' routes. The initial "uncertainty" seen in the movements of the Experimentals, for instance, could provide more evidence for klinotaxis. Following a series of shorter, more deflected "steps", their paths straightened out, just as did those of Emlen and DeMong's sparrows released under clear conditions. Eventually, the paths of the Experimentals came to resemble those of the Transients in their extremely low deflectivities. Perhaps the dislocation of the Experimentals in time and space from the sites with which they were familiar disrupted their memory for prior directions of travel. Perhaps they needed to first establish a primary heading before they could calibrate their more precise secondary system. In this view, the "uncertainty" of the Experimentals would be due only to their use of the less precise primary cues rather than the secondary cues such as possibly used by the Transients right from the start. This leaves unexplained why their highest level patterns approach the expectations for a correlated walk, but perhaps if they had been followed further the effects of their initial wobbliness would have become swamped by an increasingly tactic pattern of movements.

A similar pattern of initial uncertainty was also present in the movements of all three classes of turtles, but at a level below that of the day-ranges: all individuals seemed to need to re-establish their primary headings at the outset of each day. In the Transients and the Experimentals, this process is implied by their ability to correct the discontinuities observed at the form-sites. While their between-day patterns suggested that a target heading was carried over from one day to the next, the smaller-scale, form-site turns suggested just the opposite (exactly where the correction occurs, however, is unclear since the initial within-day turns were not significantly larger than normal in these two classes).

A vector-navigation hypothesis for the Residents' day-ranges

In contrast to the Transients and Experimentals, Residents frequently made a larger than normal turn at the outset of a day's travels. While this deviation could again indicate the calibration of some more precise tropotactic system by means of a klinotactic one, here it appears to represent the establishment of an entirely new target heading, not the re-establishment of a previous one. But is there any other evidence for the existence of a two-tiered hierarchy of taxes at the highest levels within the Residents' routes of travel as there appeared to be at least for the Transients? In particular, is there any suggestion that they would even need a vector-navigation mechanism such as the klinotaxis possibly observed among the Transients? In traveling their much shorter distances between major changes in target, why could they not be using much more direct forms of perception, and, if so, why would they need a calibratory system at all?

There is, in fact, some evidence that the Residents might be more truly telotactic than the other two classes. Their day-ranges tend to be much shorter and the deflectivities indicated by the turn angles for the steps between "discontinuities" much larger, a negative association expected for telotaxis but not for menotaxis (nor, by extension, for vector-navigation). This sort of association would hold true, furthermore, even if the Transients and Experimentals were not directly telotactic, as hypothesized above; for a given level of true deflectivity, a telotactic walker will still show a much greater degree of turning between steps than will a menotactic one.

There are, on the other hand, other possible explanations for the greater amounts of deflectivity seen among the Residents, as will be discussed in Section VII.C. The fact that the day-range termini are in some way related to spatial constraints also need not indicate that they represent actual target points guiding the entire day's travels. Again, a vector-navigation system could be employed for the same end, to bring the animal to a particular site without its being able to perceive it directly from any distance. The spatial constraints could simply act to terminate a route, no matter how it is guided, once some kind of boundary or limit has been reached. In that kind of system, the termini would not represent targets at all, whether of a telotactic system or one employing vector-navigation. The large turns occurring at the end of the day's travels indeed suggest that the form-sites themselves are not chosen until the very last minute.

That the Residents show evidence of a tactic hierarchy within days supports the hypothesis that they do not differ qualitatively from the other two classes. The within-day patterns of movements for

all three classes appear to be more similar to one another than would be expected if they were all using radically different mechanisms. If the Transients and Experimentals really are employing some form of lower-level tropotaxis simply as an adjunct to vector-navigation, then so might the Residents. The weight of the evidence suggests that the Residents, as well as the other two classes, employ the same sort of calibratory processes, probably in the service of indirect, vector-navigation (although the functions of this process need not be the same for all classes, as will be discussed below).

Magnetic-celestial orientation hypotheses for vector-navigation.

The next question to consider is what might the actual physiological processes be that make up this system. The first hypothesis to take up is the Wiltschkos' model for an calibratory interaction between a primary, magnetic-based system and a secondary system making use of celestial cues. Since the box turtles are strictly diurnal, however, the star compass of the Wiltschkos' model needs to be replaced with a sun compass.

As mentioned earlier, the use of magnetic cues by box turtles has recently been demonstrated experimentally by Mathis and Moore (1985). Their subjects were trained to orient towards one direction within a circular arena, and then tested wearing either bar magnets or brass bars. Since only the animals wearing the brass could still orient, the addition of the magnets did indeed seem to disrupt their orientational capabilities. Similar uses of magnetic cues over short distances have been demonstrated in red-spotted newts by Phillips (1986), and such findings suggest that even the Residents could display magneto-klinotaxis as a primary system within the limits of their day-

ranges.

On the other hand, the results of DeRosa and Taylor's study conflict with those of Mathis and Moore and seem to rule out the calibration model generally. In their experiments, a sun-compass alone seems to provide box turtles their menotactic headings. Under sunny conditions, turtles could be trained to swim towards land within a water-filled circular arena. Under overcast skies this ability is lost, suggesting that magnetic cues do not provide even a back-up system. Furthermore, the findings that clock-shifted animals misread the sun compass could also be interpreted as meaning that this system is not initially calibrated by some more constant set of orientational cues (but see the discussion below).

While some of the discrepancies between these studies could be due to the widely different conditions in the test arenas, the results, conflicts and all, are otherwise very similar to those obtained from birds, particularly pigeons. Even if detected, the use of magnetic information is typically much harder to verify than the use of solar cues. Often it requires second-order analysis to demonstrate: testing the significance of the mean vector of several individual mean vectors (e.g., Wiltschko and Wiltschko, 1975a, b; 1976; Batschelet, 1981, also provides a detailed description of the methods involved).

One current explanation for the relative insensitivity of the magnetic detector is that the subjects need more freedom of movement than is required for the sun compass (Bookman, 1978). The poor showing in laboratory settings could simply be an artifact of too tight a confinement; klinotaxis might be needed in the detection of magnetic information (although sharks and other aquatic organisms

possibly create an induced magnetic field as they travel through the earth's field; Kalmijn, 1978; Walcott, 1982, however, doubts the importance of this mechanism in terrestrial species).

Further confirmation for this hypothesis for pigeon homing is the well-known circling behavior seen in birds released in unfamiliar surroundings (Elsener, 1978, provides accurate maps of this phenomenon which has been observed since the earliest days of work with homing pigeons). Such circling is at least consistent with the idea that some sort of information needs to be sampled over substantial space before a homeward direction can be established (olfactory klinotaxis could, however, also provide an answer for this behavior).

The "map" and compass hypothesis. But what about the clock-shifting experiments that suggest, both in turtles and in pigeons, that no compass other than the one provided by the sun is consulted upon departure? The answer could be that the primary system functions in some other way than as a simple compass, as was indeed proposed in Kramer's (1953) well-known hypothesis of a separate "map" and compass system involved in the navigation of migrating birds.

This model is conceptually similar to the Wiltschkos' calibration model in that it again is a two-step process, with a primary heading being determined first, in this case from the "map", and transferred to the secondary system, here the compass. The main difference seems to be that the information transferred is more abstract, the heading "south" for example can be read from the "map" without any physical orienting being done by the animal; it may recognize that it has been displaced to the north if it actually remembers the relationship of its current site to its desired destination from previous visits (or

from indirect experience, Papi et al., 1972, 1973) or calculates it from a grid of intersecting gradients (Wallraff, 1974). The directional information is then interpreted by the compass system, and may be done wrongly if that system has been altered. In animals whose clocks have been shifted six hours ahead, for instance, the heading "south" will be interpreted as directly opposite the sun's azimuth at dawn, or 90° clockwise in practice.

The existence of such errors actually imply a more primary system than the sun-compass and in no way invalidates the hypothesis of a higher-level system based on magnetic information. While DeRosa and Taylor's finding of a breakdown in orientation on cloudy days seems difficult to reconcile with the results obtained by Mathis and Moore, the clock-shifting effects by themselves do not present such a problem.

There is mounting evidence, in fact, that the "map" of homing pigeons might be based on magnetic information (Moore, 1980; Gould, 1982; Lednor, 1982; Walcott, 1982). Presumably, this map can be consulted directly to determine the direction home even in the absence of a compass mechanism in the usual sense, by klinotactically comparing information sampled at more than one point in space. That this does not seem to be done in practice, except when the preferred compass proves unreliable, could again indicate that it is more difficult or less efficient to use, just as hypothesized by the Wiltschkos.

An important catch to this hypothesis as far as the box turtles are concerned is that they do not seem to possess a spatially-generalized "map" they can use in determining their directions home, whether or not their compasses are working properly. As mentioned earlier,

box turtles show virtually no homeward orientation if they are displaced too far from their home range, although they do follow very straight courses upon release in unfamiliar surroundings (Lemkau, 1970; Chapter VI).

There are two possible explanations for this failure that still saves the concept of the map. First there is the possibility that the turtles create a "map"-like structure only during the course of an outward journey and again transfer the abstract information acquired in this manner to a compass system that actually interprets the heading. Mathis and Moore, in fact, hypothesized exactly that sort of role for the magnetic system: by recording the twists and turns of an outward path relative to a fixed magnetic reference, the turtles could be calculating a more direct return trip. This sort of vector-navigation implies that the earth's magnetic field supplies only directional cues and that distance information must be acquired through some other means (Wiltschko et al., 1978). If this is the case, however, it might be asked if the magnetic compass serves only as a backup system afterall, working only where a more accurate and easily read sun-compass cannot be employed? The recording of twists and turns over a route would seem to be more efficiently accomplished using cues that can be read at more localized points in time and space than seems to be the case for the magnetic compass.

The hypothesis I favor is that a box turtle's "map" is a long-term, learned structure, representing all the vectors the animal has traveled in the past from one known part of its range to another. Such a map would not be spatially generalized, in accordance with the experimental data for box turtle homing, but would instead be tied to



particular regions in space. It would also be in excellent agreement with the observations of Type II navigation in turtles, the box turtles in particular. In this sort of system, homing abilities are simply extensions of processes that function in more routine activities, another point in its favor when addressing the navigational capabilities of such sedentary species as the box turtle. This theory, in fact, was developed by the Wiltschkos (1978) to explain the evolution of avian migratory abilities from orientational mechanisms used more commonly in everyday life.

I will discuss this hypothesis in more detail when I take up the topic of home range, but here I would like to point out the utility of magnetic information in such a system. Compared to celestial information, which changes with seasonal shifts in the sun's points of rising, setting, and noontime elevation, the magnetic beacons should remain relatively constant over the year (there are, of course, magnetic storms to take into consideration, as well as gradual shifts in declination). Whereas the use of celestial information would seem to require some sort of seasonal calendar, as well as a lot of fancy trigonometry, the use of magnetic information would seem to be much simpler for such long-term tasks. This consideration was, in fact, part of the Wiltschkos' arguments for the use of a primary magnetic compass to calibrate a more variable star compass, although they argued for an innate rather than a learned set of directions and for an actual compass role for magnetic information rather than for its involvement in a more abstract map.

Olfactory orientation hypotheses. There are, however, other cues that could be used to construct a long-term map of remembered headings. These cues, moreover, could equally well explain the higher-level klinotaxis apparent in my subjects' routes of travel. Olfactory cues are the most obvious competitors to magnetic ones in this regard. Indeed, klinotaxis is classically associated with the use of odor cues. As with magnetic information, the cues provided by a wavering odor plume can be difficult to use and require some form of sequential sampling from different positions. At the same time, such information can be relatively stable over long periods of time, especially for animals not needing to home over any great distances (and witness the efficacy of olfactory homing even in such long-distance migrants as salmon, Hasler, 1966, and perhaps sea turtles, Carr, 1972). These features of olfactory guidance make it seem an equally good candidate as magnetic navigation for a primary role within a calibratory model. Madden (1975), in fact, believed olfactory cues to be the primary source of information about the direction of home in displaced box turtles (although he offered no direct evidence).

Olfactory systems could, furthermore, be at work at more than one level, corresponding to a hierarchy of odiferous beacons. This could account for the apparent klinotaxis observed at the level of the steps between the visual "discontinuities" within the day-ranges, as well as at the level of the day-range vectors themselves. In contrast, neither sun-compasses nor magnetic compasses, taken singly, lend themselves to such nesting, as there are no easily identified sub-targets or events associated with their use. Nor does the mixed magnetic-celestial model predict klinotaxis at the lower level; the function of

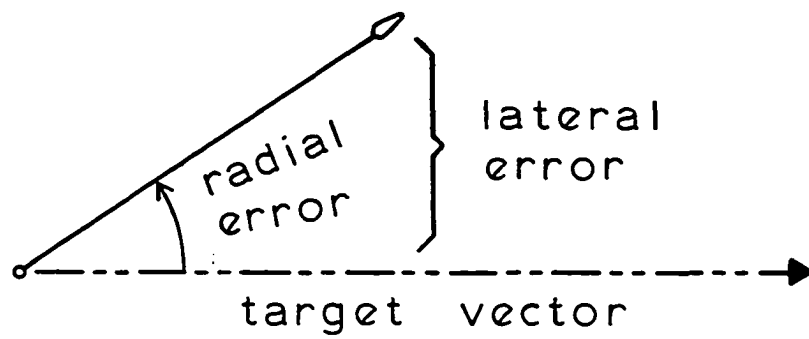
the sun-compass, afterall, would presumably be to provide instantaneously read directions for more efficient routes of travel.

Drift-control hypotheses. An obvious problem with the above argument is that it does not leave any role for the sun-compass at all, a mechanism that is well documented for the box turtle. There are also other forms of visual orientation left to consider, some of which, such as pilotage by visual landmarks, could account for a lower-level klinotaxis as equally well as olfaction, if not better.

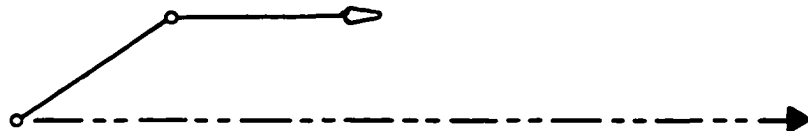
I would next like to take up a model for a combined use of visual cues, some provided by a sun-compass, others by local features of the earth's surface. One virtue of this model is that it accommodates both klinotactic and tropotactic elements, all within one sensory modality. Indeed, it indicates how they could act to supplement one another, both forms of orientation playing essential roles. Furthermore, it is an especially appropriate model, once again, for an animal that uses vector-navigation as its primary means of heading towards remembered destinations, where direct perception of the goals to movement is not possible.

The need for such a combined system can be seen in the routes of Turtle 8<sub>tr</sub>, who, as theorized, departed from a particular point within her range and headed towards a distant nesting site by means of a remembered vector connecting the two points. Along the way she would face two sorts of errors (Figure 7.4). Following a given deflection from her chosen line of travel, she would first need to regain her bearings, presumably through the use of some form of menotaxis, the sun-compass being the most likely mechanism within days. Simple menotaxis by itself, however, cannot counteract nor even detect her

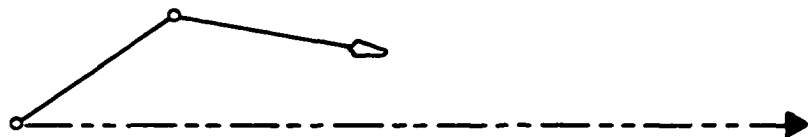
**FIGURE 7.4** The effects of radial and lateral errors in direct and indirect forms of telotaxis. The target vector represents the line connecting the start of the journey and its goal (indicated by the solid triangles) in all three forms of movement shown. Where menotaxis is used as part of vector-navigation towards the goal, only correction for directional departures from the target vector is possible; lateral errors cannot even be detected. Where direct telotaxis guides the route, directional information may be all that is used once again, but in this case there is re-orientation to the actual goal, not simply re-orientation to match the original target heading. In classic klinotaxis, the animal actively seeks to follow the target vector (usually a chemical trail). Following any displacement, it seeks to correct both directional and lateral errors relative to the original line of travel.



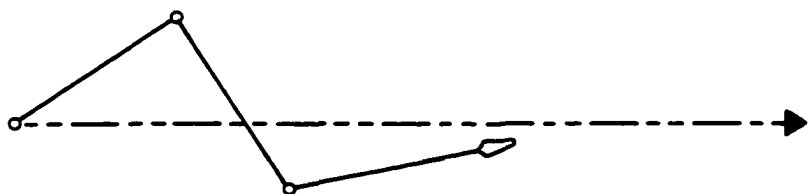
menotactic correction



telotactic correction



klinotactic correction



lateral departure from the chosen line of travel; there being no observable parallax shift in the sun's position, its azimuth will appear to be the same from all nearby points in space, offering no information about her translational change in position.

While true telotaxis towards the destination would, by definition, permit an ability to re-orient towards the ultimate target, in its absence (as in vector navigation), some auxiliary form of orientation must be used, one that presumably does use the parallax shift as its basis for detection. The effect of such a mechanism would be at least to minimize lateral errors, inducing a klinotactic-like effect by shortening the steps taken off target. It could additionally act to bring the animal back to its original line of travel. Its effects, thus, would stand in marked contrast to pure telotaxis, which would not require any form of klinotaxis, but rather the simple re-adjustment of its target heading following each deflection, of whatever length.

The use of fixed, visual landmarks to correct for lateral drift has, in fact, been proposed for flying or swimming animals confronted with a strong directional bias in deflection, such as wind or water currents coming from a constant but oblique heading relative to the target direction (e.g., Heran and Lindauer, 1963; Emlen, 1975). In a fluid medium, drift cannot be detected kinaesthetically, and to avoid being swept far off course organisms must use one or more fixed, external beacons that either actually mark their preferred line of travel or at least allow the rate of drift to be gauged. Hypothetically speaking, any sensory modality could be used for this purpose, so long as it detects changes in position relative to the fixed bea-

con; olfactory or auditory cues might be feasible under some circumstances.

While wind surely has little effect on box turtle movements, topography could be a significant source of biased deflections. For an animal such as  $T8_{tr}$  that had to travel over several ridges and ravines in order to reach a distant, spatially-restricted goal, the chance of missing it as a result of slope-induced errors seems great. The visual detection of parallax relative to closer, fixed referents could here again allow for the detection of lateral drift and its limitation or ultimately for its complete correction. The effects of these corrections might show up as the klinotaxis seen within days at the level of the steps between "discontinuities".

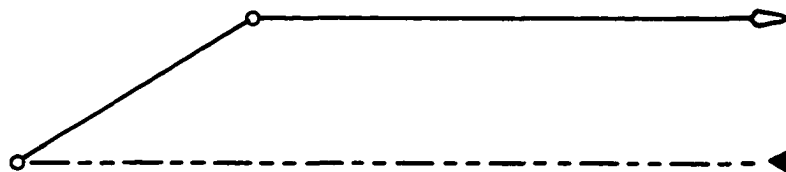
A simple pilotage system, moreover, could theoretically allow an animal to travel along straight lines even in the absence of a true compass system. All that would be necessary would be to use the pathfinder's trick of steering towards a succession of landmarks that fall along a given line of sight. If  $T8_{tr}$  had simply remembered the first couple of landmarks leading to her destination, then she could hypothetically have steered the rest of the way using a non-learned series of cues.

This method, however, runs the risk of radial drift from a given line of travel. As shown in Figure 7.5, this sort of error (assuming the organism does, in fact, wish to follow a particular line through space) can be much more severe than lateral drift. The effects of even a large but single lateral error remain constant over the route, whereas the consequences of a radial error of similar size will continue to grow.

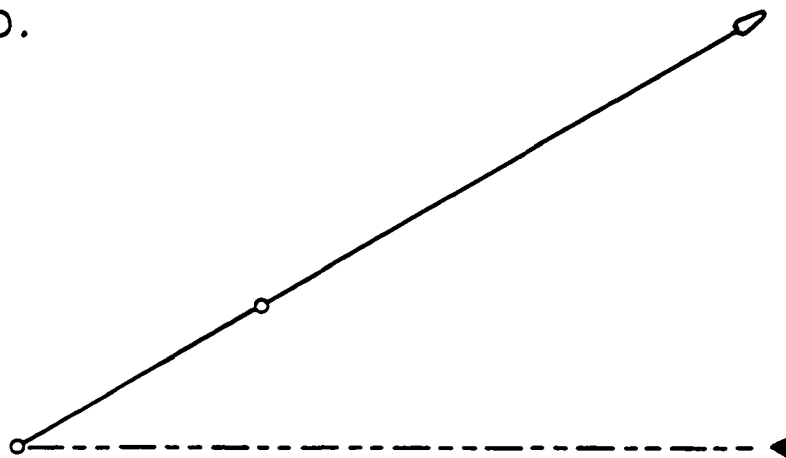
**FIGURE 7.5** An illustration of the relative importance of lateral and radial errors in vector-navigation. As shown in part a, correction of only the radial error following a given deflection will result in a path that is parallel to the target vector; the lateral error will remain constant over the rest of the trip if no further deflections are made. If, on the other hand, the radial error is not corrected, as shown in part b, then the path will continue to diverge away from the target (the lateral error will increase at a fixed rate). The message is that priority must be given to fixing the radial errors in a route; lateral errors are of secondary importance and may be left alone until the end of the journey when direct telotaxis may come into play.



a.



b.



Logically, then, any animal employing a vector-navigation system to head towards a particular goal needs both kinds of control, although possibly it should give priority to its compass system in order to minimize the more serious radial errors. But how do the two components interact? So far I have talked about a combined visual system without really specifying whether I meant an integrated system or yet another nested one. Is there any evidence that a complete switch in control occurs between the two components or, conversely, is there any evidence for only one level of control within days, the presumed point of occurrence of the visual system within the overall route hierarchy?

There do, in fact, appear to be at least two levels of walks within days, which argue against a single integrated system. There are the walks between the points of "discontinuities" and the walks made up of those segments themselves when treated as single steps (a third level might not be truly distinct from the higher, between-day processes).

There is also some evidence to suggest that the lower-level walks correspond to the action of localized telotaxis, which could be involved in some form of pilotage. Although the between-"discontinuity" walks appeared to fit a menotactic process (Figure 6.9), it should be remembered that simple telotaxis would present the same appearance (recall Figure 5.10). What indicates telotaxis is instead the negative correlation observed across the three classes between deflectivity and the length of the walks. As I argued for the day-range vectors, this sort of correlation would be expected either if all turtles were behaving telotactically at this level, but the different classes headed towards targets at consistently different distances

from a point of origin, or if only the Residents were telotactic and the other two classes menotactic.

It also seems to be common sense that this would be the level at which close range orientation, accomplished by telotaxis or pilotage, might be expected to occur. Menotaxis, especially involving a sun compass, would be expected to operate over longer distances, especially if the life-span of a menotactic target were great enough to call for a time-compensated sun compass, as appears to be the case for box turtles.

There is, however, an obstacle that now arises for a strictly nested model for visual orientation: the steps at the next level up, presumably those that would be governed by the sun-compass, appear to be klinotactic, not tropotactic. While I argued that klinotaxis should play a role in vector-navigation, it was at the level controlled by pilotage; it should have appeared within the lowest level walks, not between them (whether or not it was additionally present at that level was obscured by the use of fixed length steps in the basic survey).

One saving explanation could be that an upper level sun-compass switches on whenever large radial errors are detected in the lower-level walks, rather than when lateral errors are discovered, as I proposed earlier. However, a tropotactic mechanism is usually believed to detect such errors immediately, before any movement has taken place, not after some distance has been traversed along the incorrect heading. Another, more plausible explanation could be that the second level up in the hierarchy does, in fact, represent an integrated system, one that makes use of both solar and terrestrial

cues. At the very least, the action of klinotaxis suggests that there is an incomplete switching of control between levels, as argued in Section VII.A. The telotaxis possibly observed at the lowest level could then still fit into a larger scheme involving pilotage, but the overall mechanism would now include compass orientation as well. This sort of combination seems to best able to fulfill all the expectations mentioned above for an animal using vector-navigation to head towards goals remembered but not directly perceived.

One final level in the route hierarchy is left to consider, that indicated by the individual 25-ft survey steps. The results of removing the "discontinuities" from the original series suggests at the very least that the deflections implied by these steps are independent of one another; thus, the fit to menotaxis becomes very good. Even if this independence is due to these steps incorporating the actions of many smaller decisions, that in itself demonstrates that there are still finer processes to be looked for.

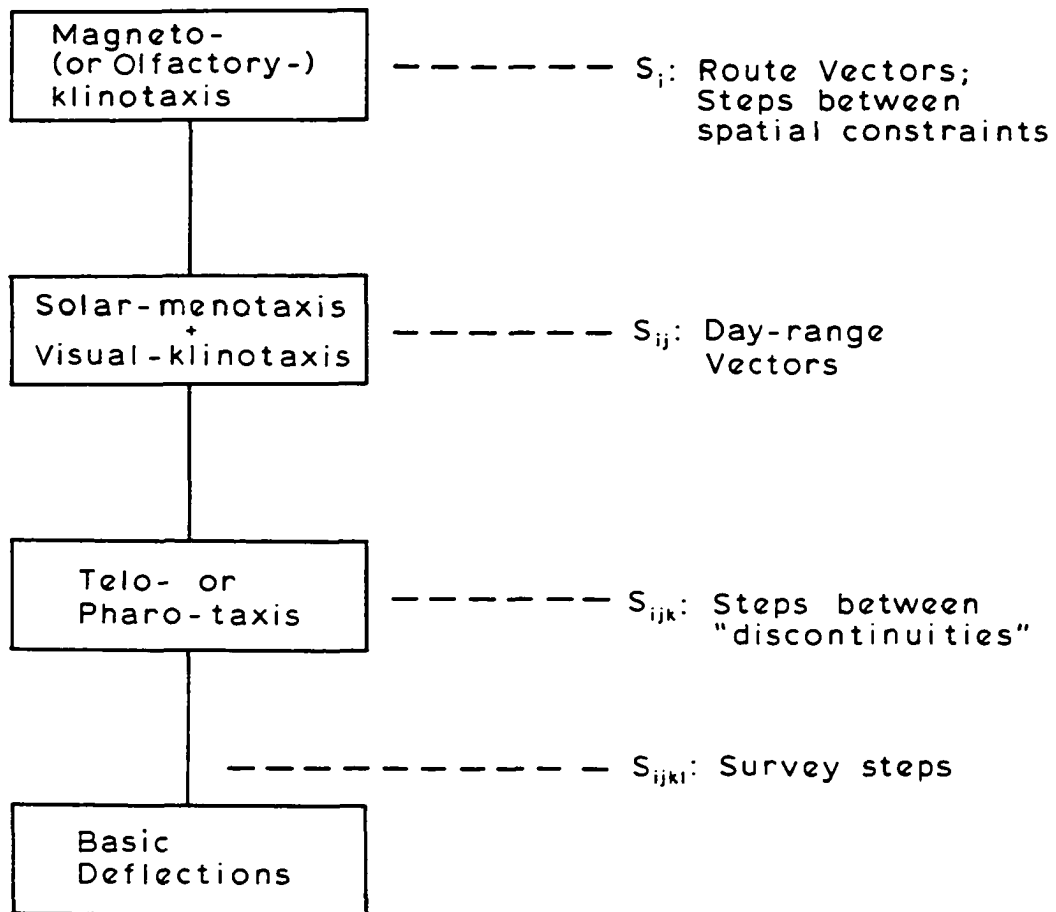
Of course, the unitary nature of these steps, as well as their artificiality, prevents anything more from being discovered about these yet lower-level processes, but here might be the scale of operation for the sort of deflections described in Section III.D: deflections resulting from barriers to movement, attractions to food items or mates, aversions to enemies, or errors from imperfections in gait or perception. However, since each of these events is not represented by a walk of still finer steps, nothing more can be said about the type of processes at work, only that something is causing movements to depart from the straight line towards the targets indicated at the next level in the hierarchy.

Summary of the orientational features of the routes. Despite the rather lengthy explanations above, the overall orientational structure of the routes appears to be remarkably simple, multimodality and hierarchical nesting notwithstanding (Figure 7.6). If the vector-navigation hypothesis is accepted, then the rest of the structure seems to follow necessarily: a control by several nested subroutines seems to be the best way of ensuring travel along one particular line through space. Whether or not all the components of the model turn out to be the ones I have suggested, the simplicity of the overall hypothesis at least indicates that a multileveled route hierarchy is not that hard to imagine.

Whether or not all aspects of the hypothesis prove true, it has one other consequence: it shows that an hypothesis of no qualitative differences in orientation between residents and non-residents is easily sustainable. Simple quantitative differences in the distance to goals could be all that separates the three groups, not any difference with respect to near and far types of orientation or the use of either direct or indirect cues. This sort of model is not far-fetched for a relatively sedentary animal like the box turtle.

Even if true transients do exist, as indicated by the behavior of "Sinbad", studied by Kiestler and the Schwartzes (1981), the only difference in orientation might be the absence of a definite distance component to the navigation "vector". It should be noted that Sinbad also showed evidence for an extremely long-term target heading, one that seemed to persist over two years. As I have suggested, such lengthy adherence to a particular direction of travel might only be possible if the animal is using something like a magnetic-based source

**FIGURE 7.6** A summary of the relationships between the observed levels  
in the route hierarchy and their proposed control mechanisms.



of information at the highest level in a route hierarchy. But if that is right, then other mechanisms must still be employed further down in order to make the routes efficient (one thing, however, that might not be expected for this sort of individual is the strict adherence to a particular line of travel; there would then be no need for klinotactic correction for lateral drift).

If the differences in behavior observed among the three classes are not to be explained in terms of orientational modes, then their basis must be looked for in terms of their functions in the lives of the turtles. Why are the Residents apparently oriented towards closer goals than the other two classes, both within and between days? How does memory for directions and distances operate within normal daily routines as well as more occasional and exceptional journeys? These sorts of questions will be addressed in the next two sections, but it should be recognized that their answers have as much importance in the study of orientational patterns as they do in those of search and home range.



### **VII.C. Hypotheses for the Search Functions of the Routes.**

It is striking that such an epitome of opportunism as the box turtle displays so little evidence of the classic models of searching movements, the random and correlated walks. The absence of such patterns, however, does not necessarily mean that the turtles are not searchers, that they are always guided by direct perception or memory for the location of the goals to their movements. Rather, all that may be inferred from the data is that if search is indeed taking place (which is virtually certain), then it occurs in the context of oriented movements. The questions, then, that this section will address are: 1) to what degree does orientation itself serve the functions of a search strategy? and 2) how do differences in search strategies modulate the common patterns of orientation that were described in the preceding section?

Ironically, the one case of an apparent correlated walk, the movements of the Experimentals over the highest scale of measurement, seems to represent not so much a strategy of search as the failure of normal navigational mechanisms in the face of a situation that box turtles probably rarely, if ever, encounter in nature. This point is best demonstrated by contrasting the movements of the Experimentals with those of the native Transients, which they most closely resemble except for their apparent lack of control at the very highest level. The situation in which the Experimentals find themselves upon release could differ from that of the Transients in any one or all of three ways:

- (1) They could be more disturbed than the Transients as a result of the greater effects of capture, transport, and captiv-

ity before release, or their greater unfamiliarity with the surroundings at the release point.

(2) They could have been true vagrants when captured, whereas the Transients were probably all simple excursionists, with home ranges close to the study site.

(3) Their greater unfamiliarity with the surroundings in itself could have an effect on orientation independent of any effects of disturbance.

No matter which of these factors might be true, it would not be more advantageous for the Experimentals to be less oriented than the Transients. Under the disturbance hypothesis, the expectation would be for the Experimentals to be more motivated to leave the release site as quickly as possible, which, in fact, could explain their generally longer day-ranges. But the most efficient form of orientation for escape would be anti-telotaxis, although if that were too difficult, then menotaxis would still be preferable to a correlated walk (provided more than five steps are involved, which appears to be the case). Furthermore, the paths should be expected to be at least as straight as possible initially, even in a correlated walk, since the greatest amount of disturbance would occur at the release point. But just the opposite is the case, the routes straighten out only after a period of days. The simple disturbance hypothesis thus fails both of two main predictions.

Under the vagrancy hypothesis, there also seems to be no advantage to a correlated walk. The greatest area searched per unit path length will be achieved by traveling in as straight a line as possible. If more than five steps are involved, then menotaxis will be

preferable, once again, to a correlated walk (with anti-telotaxis still being the best choice of all). As discussed in Section I.D, there is no intrinsic value to any pure searcher, such as a vagrant might be presumed to be, in traveling according to some atactic rule of movement.

Only where orientation cannot be maintained would a correlated walk (or some other atactic process) be the next best means for either traveling out of an area as quickly as possible or exploring as much new ground as can be done in a number of steps. Here is where the unfamiliarity with the release site might be expected to play a significant role, but only if pilotage by remembered landmarks is the method box turtles use to steer a straight course.

The Transients, however, also seem to maintain their courses over long distances by means of only distant and indirect cues. Presumably such information would also be available to the Experimentals, if only from neutral (unlearned) navigational beacons. While it would seem reasonable to expect a correlated walk over a succession of such targets if their detection range were limited (not widespread the way the use of magnetic cues would be), the question then would be why the Experimentals are forced to change targets more frequently than the Transients?

There is, in fact, some evidence that true vagrants are capable of maintaining arbitrary courses (using neutral cues) over extremely long distances, as was discovered by Kiester et al. (1981). While their maps provide too few data for me to analyze, it appears as if their subjects maintained single target headings for distances of over a mile before discontinuities occurred. It is even possible that

their turtle 8071 (Sinbad) maintained a single dominant heading over the entire two years he was followed, which corresponded to a travel distance of over 6 miles. Surely the same sort of navigational information would be available to my North Carolina Experimentals as to the Missouri wanderers studied by Kiester and the Schwartzes.

Of course there might be other sorts of behavior expected from an unfamiliarity with the release site. If the Experimentals failed to recognize the magnitude of their displacement, upon release they might use some form of area-restricted search for familiar landmarks, or they could do so after they had traveled some distance along what they believed to be the homeward vector and failed to find what they were looking for (as in Wehner and Srinivasan's ants, 1981; or Hoffman's isopods, 1983a, b). But here again the expectations fail to be met: the movements that were actually shown do not display any tendency for spatial constraints. In this case the observed pattern of ongoing movements, tactic or otherwise, would be especially disadvantageous, since any error in initial heading would continually diminish all subsequent chances of finding the way home (Wehner and Srinivasan, 1981).

That the Experimentals follow linear instead of area-restricted patterns, but do so without the long-distance control seen in the Transients, indicates to me that there has been a breakdown in normal behavior rather than some switch to another form of adaptive search strategy. These turtles could indeed be trying to follow a heading that would have taken them home from their point of original capture, or perhaps they were only attempting to leave the release area by the quickest means possible. But their initial uncertainty, seen in

the greater deflectivities of the first few days of travel, suggests that, even if search is taking place, it might be for directional information rather than familiar landmarks per se (which should require areal restrictions). Under this interpretation, the greater turning tendencies observed initially would be due to the conditions of the displacement rather than the situation occurring at the release point itself. At the very least, the Experimentals appear to need to establish (or re-establish) their bearings before they can proceed.

Under this reasoning, there is then no compelling reason to discard the null hypothesis that the Experimentals are qualitatively similar to the other two classes. Only the magnitude of directional searching (probably klinotactic) is greater in this class, and only initially, at that. The same form of search could be used by all classes in either selecting or maintaining their target headings at the highest level. Once the Experimentals establish such a target (either klinotactically or klinokinetically), their subsequent behavior could become essentially indistinguishable from the native Transients.

In this view, the rather slender evidence for correlated walks at the highest levels of movement would disappear altogether if only longer routes had been surveyed or the initial sections of the Experimentals' routes lopped off (which I did not do for reasons of sample size). As I have mentioned before, there should never be any reason to expect an animal to choose to travel according to a correlated or random walk when other, tactic patterns of movement are available (I leave open the question of whether atactic movements occur at still higher scales of measurement, representing an ultimate inability to

maintain single targets over extremely great spans of time or space). I therefore continue to proceed under the assumption that tactic orientation normally governs the routes at all the levels I examined.

As discussed in the preceding section, such orientation appears to be directed towards particular goals, some of which appear to be located quite far from the starting point of a journey. How, then, can such behavior function as part of a pure search strategy, where the goals of movement, by definition are not known in advance? The answer is perhaps that the goals themselves only have a function as an adjunct to a pure form of search, that the important feature of routes governed by vector-navigation lie in their straightness, not in their arrival at special destinations per se.

As described in Section I.G, much of what a box turtle searches for can only be found opportunistically, not by any special foreknowledge. The turtles' food resources, mating opportunities, and so on are for the most part widely and sparsely scattered over the forest floor and are also probably not quickly renewing; in other words, they are not patchily distributed. The best strategy for utilizing such resources would be the closest approximation to a straight line of travel as possible in the presence of stochastic deflections.

While anti-telotaxis will always be the best choice in this situation, the obvious difficulties in using it over any great distance favors other, more practical solutions. Of these, menotaxis seems the most reasonable alternative: it is universally available to animals; it is always more efficient than positive telotaxis; and it is also more efficient than a correlated walk where resources are not rapidly renewing, i.e., over time periods longer than it takes to

travel at least five steps. This explanation alone might be sufficient to account for the box turtles' use of the sun compass, especially if a single azimuth is maintained over the majority of each day-range, as was suggested in the previous section.

On the other hand, the exploitation of food patches is not totally precluded, and indeed I witnessed the turtles spending days at a time within berry patches or staying within the vicinity of large logs. Such shifts in foraging, however, do not call for a different model of movements; menotaxis and klinokinesis can coexist, after all. Upon encountering a high density of resources, the turtles could simply increase their deflectivity without otherwise altering their form of orientation. More directly, they could employ orientation, particularly vector-navigation, as part of an efficient areally-restricted search. As Kamil (1978) and Olton et al. (1981) have suggested, animals that make several passes through a resource patch could remember their trajectories in order to avoid back-tracking. Here would be one case where the termini of the routes would have no special meaning in themselves, but only serve as markers for the more critical linear sections in between. This hypothesis will be taken up in more detail in the section on home range.

That at least the Residents employ such patch-use strategies is indicated by their "random" seven-step sequences at the 25-ft level of measurement. While these samples proved, in fact, to be non-random, they do seem to represent a mixture of both ongoing and area-restricted patterns of movement, perhaps coupled with greater than normal deflectivities. However, although such features can be reasonably interpreted as indicating some form of convoluted search, not much

more can be said about the nature of the mechanisms; the samples are just too small.

Whatever their precise nature, it seems especially noteworthy that such samples occurred almost exclusively among the Residents' routes of travel. Indeed, all the differences between the Residents and the other two classes seem to reflect different priorities in their search strategies, if not any qualitative differences in the strategies themselves. Perhaps the main distinction between the three groups is motivational. The greater deflectivities of the Residents could indicate less urgency to their movements, more time to feed, look for mates, or simply to explore their habitat. The narrower deflectivities of the Transients and Experimentals could imply the opposite: a greater urgency to return to more familiar surroundings, a lessened interest in exploration for its own sake.

Furthermore, the implications drawn from the deflectivities can be extended to other search-related phenomena, such as area-restricted, or convoluted movement patterns. Thus the Residents might be more object-oriented than the others; recall that they seem to travel shorter distances between changes in targets, which could be telotactic in nature, and that they consequently have more such targets per day-range than the other two classes (the others, in fact, need not be telotactic at all). While that alone could explain the higher deflectivities of the Residents (as argued in the previous section), the two hypotheses are not mutually exclusive; indeed, they would both seem to be indicators of the same sort of tendencies.

Altogether, these differences in quantitative features could indicate that the non-residents are more single-minded in their pur-



suits, placing a greater premium on an ongoing strategy of movements. The Residents could represent the reverse, showing a greater multiplicity in the functions of their movements, and a correspondingly greater diversity of patterning.

But are these the only differences? Is "home range" yet another aspect of a simple search strategy, perhaps functioning the same way as the smaller resource patches mentioned above? While the arguments I have presented in this section seem to indicate little role for learning the features of the environment, other than that which can be accomplished by short-term working memory, there is still other evidence that suggests box turtles are not strictly searchers when it comes to exploiting their resources. Furthermore, even if that were not the case, there would still be the question why any motivational differences should separate the turtles into classes at all. Could a simple continuum of such differences explain the significant dichotomy observed between the animals that were seemingly "at home" compared to those that were not? The next section takes up these questions in more detail, but they are not entirely separate from those considered here or in the preceding section on orientation.

#### VII. D. Hypotheses Concerning the Route Structure of Home Range.

As dominant as the oriented sequences are in the box turtles' routes of travel, sequential rules of movement cannot alone account for all the patterning observed; spatial rules also play a role. Among the Residents at least, route behavior might be ultimately governed by where the turtle is located in space. At the level of the day-ranges (or perhaps over slightly longer or shorter spans), the Residents show a clear imposition of spatial constraints on the lower-order sequential patterns: they move decidedly less far in a series of days than would be predicted given the sequential rules alone.

Such spatially determined behavior is a necessary, if not sufficient, basis for the possession of a home range. That the spatial constraints are also long-term, another criterion for home range (Cooper, 1978), is demonstrated in the analysis of the largest scale partitions of the routes. Less explicitly, it is also evident in the maps, several of which show strong overlap of movements across two or more years (Figures 2.5d, e, h, and i). Given the findings of Stickel (1978) and Schwartz, et al. (1984), these trends for long-term occupancy of ranges can be expected to persist over decades!

That some turtles possess some form of home range can also be argued from the observation that the Residents differ from the Transients in other ways, at least quantitatively. The Residents' routes, as discussed in the preceding section, are consistent with those expected of animals that are "at home" as opposed to "on excursion". Their routes appear to be less hurried, more object-oriented, and otherwise more easily deflected than those of the other two classes, behavior that could easily typify "routine" activities. This be-

havioral dichotomy, moreover, was apparent in the activities of single individuals, such as Turtle 8, for which both home range and excursions were strongly demarcated. Turtle 8 also demonstrated a marked homing ability, yet another form of evidence for the site-faithfulness expected for home range. Given all the evidence, I think it is safe to state that the Residents, at least, have been accurately classified.

Nevertheless, the home ranges of these turtles are still hard to pin down as entities. Well-defined boundaries, such as those supposedly possessed by more territorial animals are nowhere evident in the maps. The spatial constraints, furthermore, appear to operate throughout the areas used by the turtles, as is indicated by the distribution of the form-sites, the points of major changes in target. There is no indication that the constraints operate solely at the peripheries of the ranges.

Statistical approximations of the range limits are also of no help. Not even the most general, non-parametric methods of range estimation avail here. All the problems mentioned in Section I.C regarding probabilistic models of home range are clearly present.

(1) There is not the slightest evidence for a bivariate normal distribution of activity (as also found by Madden, 1975). Nor is there any sign that the range represents a composite of several such distributions (as in the theoretical model of Donn and Rennols, 1983). This virtually rules out any parametric approach to describing the ranges. It also invalidates Dunn and Gipson's (1977) method for dealing with autocorrelation.

(2) As a consequence of orientation, spatial autocorrelation among the points is not the only violation of the provision for random sampling; the azimuths and the turn angles between them are also correlated. Furthermore, longer-term correlations can also be detected in the maps. There appears to be a decided tendency for successive routes through at least some areas to lie parallel to one another, or to bend at roughly the same places.

(3) Contrasting to the trends for the movements to show spatio-temporal predictability, is the dynamic nature of the ranges. While I did not analyze for this dynamism directly, it is quite evident in the maps, particularly where more than one year's data are presented (Figure 2.5d, e, h, and i). Although the same general areas are traversed from one year to the next, the route directions and concentrations are usually completely different, as are any apparent foci of activity. Over shorter time-intervals, similar dynamism can also be observed, as shown in the succession of patches used by Turtle 10 (Figure 2.5i). Such flexibility in route organization severely limits or even prevents the use of the quadrat-transition method of analysis described by Getty (1981), at least as an indicator of the stability of the movement patterns.

(4) As has been discovered by previous investigators of box turtle movements, there is a high diversity in the kinds of ranging patterns among individuals. In my sample of Residents, the movements of Turtle 16 represent one extreme, showing a tightly convoluted pattern, with spatial constraints operating within single day-ranges (Figure 2.5k). At the other extreme are

the movements of Turtle 10, typified by a much more strung-out series of patches, and spatial constraints that appear only over the course of several days. In fact, the continuum of patterns probably does not end with Turtle 10; the movements of the "Transients" appear to be only more exaggerated versions of what the Residents were doing. The egg-laying trips of Turtles 1 and 8<sub>tr</sub> (Figures 2.5c and 2.6f) might differ only in how far they went from the areas that were more heavily used during the rest of the year. The long cross-range movements of Turtle 10 (especially in 1975 and 1976) are quite similar to those of Turtle 12 (Figure 2.6e) who made several visits to the study area over the years but never stayed for very long.

Taken altogether, these findings pose insurmountable obstacles to any attempt to pin down a utilization distribution, even if it were desirable to do so. As I indicated in the Introduction, I feel these methods sacrifice or avoid too much of the information that is central to understanding the patterns of movements, anyway. Although it is intuitively quite clear that the spatially restricted movements of the Residents deserve to be termed a "home range", just as much as a bivariate-normal distribution of activity shown by a Peromyscus, the operational definitions worked out for rodent mark-recapture studies would just as clearly fail to justify this conclusion.

The possibility that there is a continuum of patterns between those of the Residents and the Transients in fact compromises the very concept of home range, at least as it has been customarily formulated. One of the most venerated criteria for home range is Burt's (1943), which excludes all excursions (or dispersals) from consideration and

leaves only "routine" movements as constituting the home range. But there has always been a problem with that definition: how can the routine be distinguished from the extraordinary. My data suggest that there are in fact no qualitative distinctions at all, and that if quantitative differences exist, they vary continuously, making any separation between groups completely arbitrary.

Burt's criterion, however, is eminently reasonable if it is area that is of central concern in the definition of home range. Imagine trying to draw a polygon around all the outermost points of Turtle 8's routes, egg-laying trips included. In terms of area, the result would be ridiculous! Even more meaningless would be the use of polygons to surround one of the Transients' or Experimentals' routes. On the other hand, what about a polygon around all of Turtle 1's movements, egg-laying trip included, or around Turtle 10's or 9's routes, different years included?

The results of such an operation, however, are ridiculous only in terms of area. Take away the polygon (or statistical confidence limits) and there is nothing fanciful at all, just the simple routes of travel. By removing them, the benefit of the doubt is simply being given to the sensible null hypothesis that the "Transients" are not really doing anything different from the Residents. Only when that hypothesis has been disproved, when extraordinary movements can be distinguished both inside and outside the limits of the routine, can such routes be excluded from the sample of movements constituting the home range.

I doubt this will ever prove possible for most animals, for box turtles in particular. Furthermore, such a condition would still not

justify drawing a polygon or any other areal delimitation around the routine movements; it still would need to be shown that area as such means anything to a resident animal. It seems to me more likely that animals do not have any areal concepts at all. Spatial constraints need not be a function of the amount of area the animal has perceived to have "covered" over a particular period of time. Indeed, it is difficult, it not impossible, to imagine how an animal would even measure area (the double-integrator hypothesized by Barlowe, 1964, for inertial navigation could, I suppose, provide the basis for a planimeter). I find it much easier to imagine that spatial constraints are a function of site-fidelity or familiarity, or of memories of previous routes of travel.

In this view of residency, the area of the home range is, at best, an epiphenomenon, perhaps having strong correlates with more vital phenomena, such as distance away from a reference point. At worst, it is only an artifact created by an observer who had nothing better at his disposal to represent his intuitions about spatial constraints.

Even if area were a direct factor in the patterning of an animal's movements, it would still take better methods than traditional areal analyses to prove it. The best way of demonstrating its importance would be to disprove the hypothesis that simpler, non-areal factors can completely account for the observed patterns of movement. In other words, it needs to be shown that areal patterns are truly emergent properties, not just the sum of the behavior present in the routes by themselves. For this, route-based analyses must be employed.

Until forced to conclude otherwise, I will therefore proceed as though area is not critical to the definition of a home range. There are no polygons or analyses of spatial distributions discussed here! The rest of this section will discuss the traditional subject matter of home range studies in terms of route processes. It should be noted that this approach will in no way invalidate the basic concept of the home range, nor even that of routine movements. Only the most cumbersome and disputed aspect, areal analysis of the spatial distribution of points, is discarded.

Hypotheses concerning range familiarity. One immediate result is that it is no longer ironic that my best indications of site-fidelity and familiarity come from the egg-laying trips of Turtle 8<sub>tr</sub>. The fidelity and memory for specifically useful sites, as strongly suggested by these routes, is just what the familiarity theory for home range would call for: an animal is able to exploit its habitat more efficiently if it learns where particular resources are predictably found in time and space. If there is anything extraordinary about these movements, other than the navigational skills required for such long trips, it lies in the extreme site-faithfulness they evidence. From the location of Turtle 1's nest site so close to Turtle 8's range (see Figure 2.5b), it seems as though a simple search strategy for nest selection might have saved Turtle 8 a great deal of trouble.

On the other hand, the faithfulness to such scarce sites (well-drained, sunny spots are hard to find within a forest), no matter how far away, seems a lot less surprising than the apparent fidelity to hibernation sites that is indicated within the "normal" ranges of Turtles 7 and 16. Although it is understandable for the turtles to be



choosy in their selection of hibernacula, why should they be so conservative as to choose virtually the same site from one year to the next? Suitable sites appear to be widely available, and again, a simple form of search would seem to require a lot less effort.

Perhaps the answer is that such feats as returning to nest- or hibernation-sites are no more extraordinary than what the turtles do every day. The evidence I presented earlier for the routine use of vector-navigation would tend to support this idea. At its simplest, this type of navigation presumes only a goal and the use of indirect cues to get there. While it is often coupled in the literature with some form of dead-reckoning used to keep track of the twists and turns of an outward path, it could just as easily involve a memory, perhaps in the form of a cognitive map, for the directions to the goal from particular, recognized starting points (Wiltschko and Wiltschko, 1978). A memory-based navigation system seems especially likely for animals, such as those mentioned above, that need to travel to particular sites only once a year. In contrast, the task for a dead-reckoning system performing the same feats would be formidable; it would need to integrate all the twists and turns over an entire year's worth of movements.

In a negative way, the results for the Experimentals also support this hypothesis: their seeming failure to navigate towards home suggests that recognition for the starting points, as well as points along the way, is crucial for both the initial selection and subsequent maintenance of a particular course of travel (it should be noted that this hypothesis differs somewhat, but is not mutually exclusive with what I suggested earlier, that displacement disrupted their sense

of direction, which needed to be re-established by means of klinotaxis).

Other evidence for learned routes of travel comes from the structuring of movements apparent in the maps. The frequent paralleling of routes through particular areas and the proximity of major turning points indicates that the turtles use similar spatial rules each time they pass through a given site or region. The overall dynamism of patterning that is also evident further indicates that any similarity that does occur between routes is not due simply to topographic influences. It suggests instead that both aspects of the patterning, dynamism as well as stability, must involve experience and learning on the part of the turtles.

While none of this evidence can be considered anywhere near conclusive, the clear evidence for orientational structure within the home ranges is at least more consistent with the familiarity hypothesis for range use than is the case for the more stochastic models of home range now in vogue. Indeed the essentially non-sequential models proposed by Holgate (1971), Yang (1979), Dunn and Gipson (1977) and Siniff and Jessen (1969), if taken literally, actually curtail the role of familiarity. Although the first three of these models posit a central focus to activities, which could represent a landmark, caching point, or home base, the movements away from that site are not directed towards any other place in particular (nor do these models allow for direct movements back to the focal point). Home range in these models is simply the expression of the animal's tendency to stay close to the focal point, perhaps as part of an area-restricted search, but since all other resources are implied to be randomly

distributed in time and space, there is no point in knowing anything else about the features of the range.

Even more extreme is Siniff and Jessen's model. The movements here are not even organized about a central place. Instead they represent nothing more than a correlated walk within a rigid perimeter. Home range, then, represents only a long-term form of spatially constrained search. Nothing need be remembered about sites in particular. The only expectation about resources, and only an implied one at that, is that the chances of encountering them within the perimeter must be higher than outside. How such expectations could be formed without exploration and periodic modifications of the boundaries is, however, hard to imagine.

The search area hypothesis for home range. Still, the idea that home range is at least partly an expression of spatially constrained search deserves further consideration. The evidence for an orientational structure within the ranges need not exclude this hypothesis and in fact could support it, as discussed in the preceding section on search hypotheses. Indeed, orientation, even vector-navigation, need not imply familiarity with localities in the range at all; it might only serve to increase the efficiency of searching for widely scattered and unpredictable resources. Apart from the slight evidence for returns to particular nesting or hibernation sites, a search hypothesis for range usage in some ways seems to fit the box turtles requirements better than does a range model based on familiarity with local and predictable resources.

A basic expectation of this hypothesis is that areas differ with regard to their qualities (although, as mentioned, the turtles prob-

ably do not respond directly to area as such). While resources in the case of the box turtles are indeed likely to be widely scattered, they could also be more abundant in some regions than others, and predictably so through time. Evidence disputing this hypothesis, however, is the fact that turtle ranges were nearly continuously distributed throughout my study area, overlapping one another quite broadly. There seemed to be no concentration of the turtles in any region that might be more favorable than any other.

On the other hand, areas may also differ with regard to negative characteristics, such as the presence of too many conspecifics. Even without territoriality, it might be advantageous to move away from areas with too dense a population to avoid either competition or perhaps the attention of predators (Waser and Wiley, 1980). The box turtle does in fact rely partly on crypticity to escape predation, and Tinbergen, et al. (1967) pointed out the value for such animals to be widely spaced. Another density-dependent mortality factor to consider is disease, such as the Pseudomonas lung infection prevalent in the region around my study site (Albert Harris, personal communication).

If the assessment of range quality is made in terms of sparse and mobile factors (either food items or conspecifics), it could require long time periods or extensive movements to come to a judgement. In short, the animal would have to possess at least a tentative home range just in order to gauge an area's qualities. If a favorable judgement is made, and if the range qualities remain constant over time, then long-term residency could well pay off. Moving into any other area would require more investment of time and movements in order to assess its quality. Searching for unoccupied gaps in the

social matrix might prove especially time-consuming.

Such a model of home range does not preclude exploration, however. The ranges can be dynamic and fluid, constantly changing in order to track a continuing assessment of range quality, especially with reference to the location of conspecifics (Stickel, 1946). This model of home range need not assume the existence of objectionably rigid boundaries (as in the Siniff and Jessen model), nor any particular internal structure whatsoever. Several different range patterns could accomplish the same end.

One such mechanism could involve the elaborate orientational structures that I observed in the box turtles' routes of travel. Vector-navigation, even if dependent on a "map" of remembered points in space, can play a major role in a strategy of search based on range fidelity. There is nothing about that hypothesis that requires the goals for movement to have any more significance than what they would have as neutral landmarks. They need not be sites where limited resources can be obtained, only where spatial information is acquired.

The fact that the orientational capabilities of the turtles appear to be greater than those implied in the usual models of klinokinetic or true area-restricted search could simply be due to the greater area the turtles have to cover, the longer time periods involved, or the more homogeneous nature of their habitats (in terms of orientational information). Single reference beacons might be too hard to use over any great distance, especially in wooded and hilly terrain and for so low and slow an animal as the box turtle. The learning of several reference points, on the other hand, would seem to require a lot less memory and perceptual capability than would learn-

ing the features of an arbitrary boundary (such as in the Siniff and Jessen model). Topographic lines, such as stream beds, ridges, and ecotones could still play a role, but they have the drawback of being arbitrarily positioned. My subjects, at least, did not appear to be constrained by such features.

Given that an animal is motivated to remain within a particular region and has some means of doing so, what might be expected about the nature of the routes within the range? As discussed in the preceding section, tactic movements are the most efficient ones in searching for widely dispersed, unpredictable resources, even for a purely vagrant individual; they cover more new ground per unit path length than do atactic movements (assuming a fairly large number of steps are taken, as would be the case for a vagrant). For an animal that places spatial constraints on its movements, tactic movements become even more important. In a confined space, the probability of backtracking over previously searched ground is increased as a result of the inward turning that occurs whenever the spatial limits are encountered.

Oriental control over the routes could alleviate this problem in two different ways.

- (1) By keeping the paths as straight and narrow as possible, orientation reduces the probability of extensive backtracking on a rebound trip. Exactly parallel or coincident routes would be highly unlikely, and single points of intersection would probably not reduce the efficiency of search very much.

- (2) The probability of intersection can be reduced still further if the travel vectors of previous trips can be remembered. New courses could then be calculated explicitly to avoid

the previous searches.

These two functions of oriented movements further suggest that vector-navigation could be the mechanism of choice, independent of whatever role it might serve in maintaining a heading towards only indirectly perceived goals. The klinotaxis I described as accompanying vector-navigation would act to keep the search swath as narrow as possible by limiting lateral drift. If there are, in fact, no real goals to the movements, indirect or otherwise, then limiting drift could be the sole function of klinotaxis.

In addition, with highly linear search swaths the feasibility of remembering previous search vectors is increased; if the path was wider or more rambling, more information would need to be stored in order to define the area previously searched. A simple vector, in contrast, requires only two pieces of information: the coordinates of the endpoints (either in polar or cartesian form). As demonstrated experimentally by Olton et al. (1981) and observed in a natural situation by Kamil (1978), animals indeed possess such abilities; rodents and birds can recall up to eight previous points of visit. While these authors do not suggest what the orientational structure might be that underlies these abilities, some form of vector-navigation would seem to be ideally suited for this task, especially in the case of Kamil's honeycreepers, who made fairly lengthy sweeps in covering their foraging range.

While this model of search suggests no particular significance for the endpoints of a walk themselves (they could be represented strictly internally as part of an inertial guidance system), tying the search vectors to easily remembered landmarks would provide an

easy way of storing information about previous movements. Possessing a framework of known sites would be especially valuable if the routes through a confined space were particularly extensive. The role of such a framework in long-term range fidelity has already been discussed, and would probably pre-date any specialized use of vector-navigation in search.

A general hypothesis for the route structure of home range. The two hypotheses I have outlined for home range, that of familiarity for the purpose of exploiting predictable resources and that of range fidelity for exploiting widely dispersed, unpredictable resources, are not mutually exclusive. I hoped to have shown that the oriented nature of the routes within the home range, particularly their vectorial character, can fit either hypothesis or both at the same time. The turtles could be using vector navigation to head towards distant but remembered sites in order to exploit patchy resources, to travel narrow and avoidable search swaths, and to stay within a conscribed range all at the same time. Such a combination, in fact, seems to accord well with the picture I presented in Section I.G, of the box turtle as a generalist, opportunistic species. Under that view, places within the range, as well as the routes between them, might very well be expected to have multiple significance.

This hypothesis still leaves the nature of the box turtles' ranges fairly indefinite as compared with the more traditional models of home range. This indefiniteness is in fact parsimonious. I did not go beyond what could be constructed from the basic building materials of the routes: oriented walks that are hierarchically structured and the points of discontinuity implicated in the spatial constraints.



Before evidence is obtained to demonstrate a more definite structure, it seems wise to keep the model as open-ended as possible.

There is, for instance, no need to add boundaries, or indeed any areal factors at all. Nor do the ranges have to include any sort of fixed routine of movements. In fact, there seems to be no reason to rule out the null hypothesis that transients are qualitatively indistinguishable from residents. In a route-based model of home range, excursions need not be excluded from consideration but instead can be used to reveal much about the processes underlying the movement patterns overall, as demonstrated, for example, by the route patterns of Turtle 8.

Even though I have been describing a fairly loose, network-like structure for the ranges, there is no need to restrict it even that much. The box turtles' routes, for instance, seem to show more dynamism than, say, the movement patterns Adams and Davis (1967) found for ground squirrels. In their model for the internal anatomy of home range, a network structure was determined by the distribution of burrow entrances, out from which the squirrels forage and back to which they straightaway dash when threatened. Similar runway networks have also been described for voles and other rodents, which invest much time and energy in creating the highways. Box turtles, in contrast, make no investment of labor in modifying their environment, and so need not stick to the rails of any fixed network.

Indeed, only a relatively unstructured and dynamic ranging pattern would appear to suit the needs of such an opportunistic animal. The box turtle is probably freer than most species to add new sites and routes to its repertory, or equally to discard obsolete ones,

both as consequences of its incessantly tracking environmental circumstances. If more flexible than most, the box turtle movements, I suspect, nonetheless capture the essential features of animals' ranging abilities. The model I have proposed could thus serve as a more basic framework for discussing home range than those that are tied to specific structures, such as a particular utilization distribution or definite foci of activities. Conversely, without a model general enough to include box turtles' ranging patterns, we cannot hope to put the phenomenon of home range on a strong theoretical basis.

## **VII. E. Conclusions: the Prospect for a Unified Study of Animal Movements.**

The main thesis of this study has been amply demonstrated: there is indeed a great deal of information present in animals' routes of travel, far more than has been exploited by traditional methods of analysis. This is information, moreover, that has general significance for the understanding of movement patterns generally. It contributes not only to more complete pictures of orientation, search, and home range, considered as separate phenomena, but also reveals all three to be closely intertwined. It is this unifying perspective that I consider to be the major accomplishment of this study.

That the key to this information is found in walk analysis, particularly menotactic analysis, has also been substantiated. The power of this approach is most apparent in its ability to decipher the processes underlying movements even in the absence of contextual information, the usual bane of telemetric studies. Whereas the three traditional paradigms have had great difficulty in digesting long sequences of route data, even when contextual data is available, I have shown that walk analysis of routes can make great headway in the investigation of orientation, search, and home range even in the absence of the usual contextual requisites.

For instance, I knew nothing about what orientational targets the turtles were employing, which precluded an analysis of the distribution of azimuths. Nonetheless, I was able to demonstrate the importance of orientation quite easily, and in fact showed it to be a highly complicated process, involving klinokinetic modulation of deflectivity, klinotactic search for directional information, and seve-

ral different nested levels of control. Most of these findings, moreover, would be overlooked in more conventional methods of orientational analysis, which focus on the sensory apparatus instead of on organization of control, and which make use of a deterministic model rather than a stochastic one.

Since I knew nothing of the turtles' orientational targets, I was likewise ignorant of any goals they might have had for their movements, even whether or not they knew in advance where their resources were to be found, a prime requisite of the search paradigm. Furthermore, I had no information on the environmental circumstances, such as encounters with food, mates, or enemies, that modulate the turtles' search paths. Nevertheless, I was able to discover marked differences in deflectivity between turtles and between different portions of the routes of single individuals, all of which at least suggest changes in motivational state, if not in search strategy itself. In addition, I demonstrated that any search that does occur takes place in the context of oriented movements; there was no indication whatsoever of a correlated or random walk, the two models upon which the search paradigm has been primarily built. The deflectivities I discovered were not represented by simple turn angles but instead by more complicated variables requiring some form of orientational analysis.

Finally, I saw no sign of any sort of fixed routines among my subjects; there was far more flexibility and dynamism in their routes than rigidity. The conventional spatial analyses of home range were consequently of no avail. Even so, by using just the route data, I was able to demonstrate the clear presence of long-term spatial constraints among the Residents and their absence, at least over compar-

able lengths of time, among the two non-resident groups. While the presence of these constraints might or might not indicate the possession of a home range, as it has traditionally been conceived, and their absence might indicate excursions as much as true vagrancy, the model of range usage that emerges is at least more parsimonious than any based on spatial constancy. It is thus capable of embracing the movements of box turtles as well as the more conventional subjects of home range studies.

In making these arguments I do not wish to imply that the more traditional approaches to the study of animal movements have no further value; they still are quite useful in obtaining information on the contexts of movement. Just because walk analysis can extract some information from even the bare routes of travel does not mean that context is not wanted; Chapter V was explicit in emphasizing the need for obtaining yet greater amounts of information concerning the circumstances of the routes. Here is where the experimental manipulation of perceptual mechanisms and environmental stimuli can play a major role, as can the simple recording of the environmental and social contexts in which the movements occur.

There are several questions I would like to address along these lines that should illustrate the value of integrating walk analysis with the more traditional approaches.

(1) What would be the effects on the hierarchical structure of the routes of manipulating various sensory modalities?

(a) Would the effects of magnetic or olfactory disorientation show up only at the highest scale of measurement, leaving the turtles their ability to tra-

vel straight paths but abolishing their capacity for overall vector-navigation? A prediction drawn from the hypotheses discussed previously would be that both Residents and Transients would come to resemble the Experimentals in their behavior. Mathis and Moore's (1985) results are consistent with this hypothesis.

(b) At the other extreme, would the effects of frosted contact lenses (obscuring local visual cues) show up only as an inability to travel straight paths or to control lateral drift, and leave intact the ability to maintain spatial constraints or long-distance orientation? The prediction would be for all turtles to show large increases in deflectivity (and probably a great reduction in overall movements), but not to change in residency status or in the ability to return home (eventually) from an excursion.

(2) What would be the short-term effects on path structure of various positive or negative stimuli?

(a) Would the presentation of food items or conspecifics of the opposite sex affect only the deflectivity of the subject's route or would it also change the type of orientation displayed or other aspects of the walk structure? The prediction here would depend on what rate the presentations were made. Single presentations might not effect even deflectivity, given the normally non-patchy distribution of resources. Repeated presentations, on the other hand, could in-

crease deflectivity, decrease walk length, and invoke short-term spatial constraints, depending on whether the turtles can opportunistically switch to a search strategy more appropriate for the exploitation of resource patches.

(b) Would the effects of aversive stimuli be just the opposite of those expected for rewarding stimuli? One prediction would be that even a single presentation of a sufficiently noxious stimulus would be enough to greatly reduce deflectivity and increase walk lengths. Repeated harassments, on the other hand, might or might not have any additional influence except possibly to induce the turtle to burrow into the leaf litter; box turtles normally cannot outrun their enemies and they probably also treat them as occurring unpredictably in both space and time.

(3) What would be the long-term effects of the same sorts of positive and negative stimuli?

(a) Can the turtles develop site-specific associations for consistently positive experiences? Given the evidence for returns to nest sites and hibernacula, such associations seem likely. Places that are constantly stocked with food or where members of the opposite sex are repeatedly presented should develop into major targets for the orientational system. These targets would be evident by becoming points where changes in heading occur in the upper-level walks.

They might also develop into important hubs within the overall network of trails, with connections established to other parts of the home range. Through continued provisioning of certain sites, the movements within the home range overall could thus become much more predictable, as the turtles seize the opportunity to exploit dependable resources. The routes between the provisioning points, concomitantly, could show a decrease in deflectivity, reflecting a decline in the importance of pure search as well as an increase in the efficiency of travel towards the well-stocked points. The overall pattern should become more and more network-like.

(b) Opposite effects might be expected to develop from consistently negative experiences with a site. Repeated harassments at a formerly well-visited site should lead to its abandonment as a walk endpoint or even to its avoidance altogether. Connections to other parts of the range would be re-routed around such sites. To a lesser degree, a similar loss in importance might be expected at formerly rewarding sites once the provisioning has ceased. It would be interesting to observe the decay that should occur in a well organized network of routes if the balance were tipped from predictability in resource exploitation back to a situation favoring pure search.

(c) Can more scattered, spatio-temporally diffuse influences effect the spatial constraints, even if not



contributing to site-specific behavior? The search-model of home range suggests they can. A favorable assessment of range quality, induced by a high rate of rewarding contacts, would show up as a reduction of the distance between spatial constraints or in the degree of turning behavior seen at major points of discontinuity, like the form sites. An unfavorable assessment, conversely, should induce further exploration, accompanied by an increase in the distance between spatial constraints or in a decrease the strength of their influence. A balance, moreover, would be expected to occur between positive and negative influences; if such effects are regionally separated, even if diffuse, then shifts in the range towards the rewarding areas should gradually occur, just as the less favorable areas are gradually abandoned. If site-specific behavior is additionally involved in these shifts, then the process should be that much quicker.

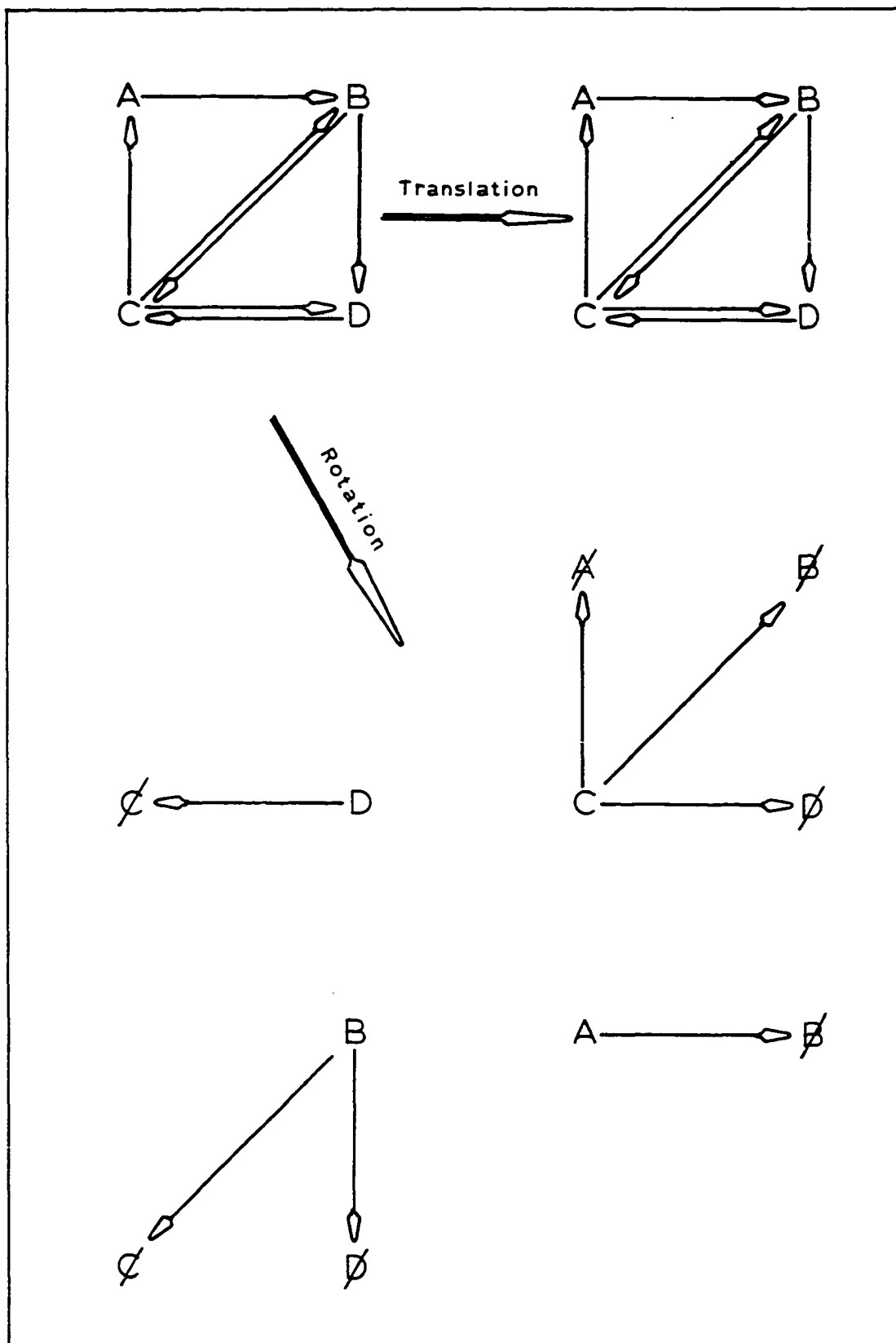
(4) What would be the effect on the spatial constraints of manipulating more neutral stimuli?

a. Can the turtles incorporate conspicuous, artificial beacons into their vector navigation system, even without associating them with any form of reward. I suspect they can, given that naturally occurring points of constraint, the form sites, do not appear to be strongly associated with resource patches. One prediction would be that major changes in orientation

should become clustered within a certain distance of newly created, prominent features. It would be additionally interesting to see how site-specific rewards or punishments would interact with this process, by modifying the rate or distance at which the discontinuities occur relative to the beacon.

(b) Given that landmarks or beacons have some importance, then what would be the effect on route structure of moving them? The hypothesis I outlined earlier that landmarks are of importance only at the initiation and termination of navigational vectors, and that otherwise the courses are maintained only by indirect means, suggests that any effects might depend on the nature of the displacement. I would predict that translation of a constellation of beacons through space would produce a much smaller disruption of movement patterns, if any, than would a rotation of the pattern: the former would not change the headings the turtles should use to get from one known point to another, while the latter would change them drastically (Figure 7.7). Although the exact nature of the disruption might be hard to specify, given the unpredictability of the box turtles' choices of paths relative to any particular point in space, I would expect the turtles whose range markers have been rotated to show greater deflectivities at all scales of measurement. They might initiate some convoluted form of search when they

**FIGURE 7.7** The effects of translation and rotation of range markers on vector-navigation within the home range. Simple translation without rotation produces no changes in the normal pattern of movements whether the orientation represents vector-navigation or direct telotaxis. Rotation of the range markers, on the other hand, produces complete disruption of the pattern, but only if the movements are governed by vector-navigation. If direct telotaxis is the governing mechanism then only a rotation of the normal pattern will be produced. mechanism.



do not find their beacons where they expect them to be (as in Wehner and Srinivasan's ants or Hoffman's isopods). They could also become disoriented upon encountering familiar landmarks in the wrong places, which would tend to shorten walk lengths and might again induce exploration.

Although the experiments described above are all appropriate as field studies, it should be apparent that walk analysis can be applied equally well in laboratory investigations. The sequential information on which it is based is simply superior to the old data consisting of isolated azimuths, disjointed turns, or unconnected points. For that reason alone, walk analysis would be worth incorporating into the standard methodology for movement studies.

Of far greater value, however, is its service in tying together the separate threads of movement investigation. Consider how I was able to compare such different patterns as those of the Residents, Transients, and Experimentals, and how I was able to draw on the entire range of movement theory to arrive at an integrated set of conclusions. Perhaps the most striking result of this study is my finding that the classes of turtles did not differ in any qualitative way, that only quantitative differences accounted for all their different patterns of movement. None of the separate branches of movement study could have achieved this insight by themselves. Nor would they, I believe, even have thought such a comparison to be worthwhile; this null hypothesis has relevance only within a unified conceptualization of movement processes.

The hypothesis of no qualitative differences, however, does not imply that the underlying rules of movement are essentially simple. Consider the hypotheses listed in Section I.H. The first null hypothesis ( $H_{01}$ ), that a single sequential model could account for all behavior, was easily disproved. The patterns of the Residents clearly involve spatial constraints. Any fundamental model of movements, must incorporate positional rules as well as sequential rules, which already makes it more complex than most current models for orientation, search, and even home range.

It is the failure to disprove the second null hypothesis ( $H_{02}$ ), however, that really drives this point home. Contrary to the assumptions of the home range paradigm, "transients" and "residents" were not that easy to distinguish. At least one Transient,  $T8_{tr}$ , possessed a demonstrable "home range", and her "excursions", moreover, were also delimited by spatial constraints. The similarity of her "off-range" movements to those of the other Transients further supports prediction  $P_{021}$ , that Residents and Transients might differ only in the scale over which their positional rules of movement operate, but that both groups, in fact, make use of the same sorts of route processes. Even the Experimentals, who might indeed have been operating without positional guidance, did not do so in any seemingly functional manner. Instead their aberrancy could have been due to their attempting to re-establish a set of positional rules, not to their rejecting them.

While these findings do not refute the possibility that true vagrants exist among box turtles, as was in fact indicated by the findings of Kiester et al. (1981), there was, in my study at least, no positive support for it either. For the time being, it seems more

parsimonious to accept the null hypothesis that all turtles use, or attempt to use, the same fundamental set of processes governing movements, including positional rules of movement as well as sequential rules

At the same time, it is not clear that all turtles operate within some sort of home range. Even the strong positional rules seen within the movements of the Residents appear to be far too flexible to allow for the definition of home range as a fixed entity. The ranging patterns of animals such as T10 suggest that prediction  $P_{022}$  is instead true, that the spatial constraints of the Residents as well as the Transients change over time, although perhaps at different rates. There is also no necessary implication that spatial constraints correspond to specific, learned sites; they might in some cases be generated by some yet higher-order sequential process that my methods were too unrefined to detect.

The finding of basic similarities in the routes of the different classes, while not actually proving that the underlying processes are identical, at least serves to redirect thinking away from the traditionally compartmentalized viewpoints. It might suggest, for instance, that a complex system of interacting positional and sequential rules of movement is needed just as much by true vagrants (if any exist) as by true residents (if any exist). The multi-leveled hierarchy of controls I found in all my turtles could be a reflection of a multiple functions of movements; the complexity of the system could serve simply to allow for a wide assortment of patterns. Given a basic set of processes to generate routes, an animal could then draw upon all of them for any particular job. The complexity of the sys-

tem, alternatively, could permit the use of just one basic but powerful design for handling all jobs more or less the same way.

In either case, an explication of the rules of movement demands a unified approach; all three of the traditional branches of movement study must be called on to explain even a single route of a transient animal. More than that, however, it requires an entire refocussing of the goals to movement study. Instead of pursuing the various sensory apparati, target qualities, and areas needed for sustenance — the objects of conventional studies — a unified investigation of movement patterning would find its natural subject matter to be the rules that generate the route structures.

The theory of route processes sketched in Chapter III and the findings that movement decisions can occur within a nested hierarchy both suggest that movement studies have a lot to say about animal cognition. This idea is not new; Tolman's (1948) hypothesis of the cognitive map has already played a large role in the study of cognition generally (Neisser, 1976; O'Keefe and Nadel, 1978). A unified theory of route patterns, however, could suggest a role for planning, and hence cognition, even in animals that lack a formal cognitive map. The Experimentals in this study, for example, still displayed a complex hierarchy of decision making even in the absence of known surroundings. Perhaps true vagrants would do the same.

At the time of this writing, the study of the behavior of individual organisms in their natural circumstances has fallen out of favor, and with some reason. The study of social behavior, communication, and population-level phenomena generally is now making great headway towards the solution of a number of important problems. At



the same time the more traditional paradigms for understanding the behavior of individual animals have grown stale. This disenchantment applies especially well to movement studies: the fascination with utilization distributions and areal formulas for home range is approaching a bitter end; the grail of homing and navigation studies remains unclaimed, despite the discoveries of sixth, seventh, and even eighth senses; the study of search keeps happily puttering around in random circles. These days, it is difficult even to hold a productive conversation about the nature of animal movements.

Given this state of affairs, it is fitting that the box turtle offers such a worthy challenge to accepted beliefs. Can the behavior of a lowly, unsociable, and taciturn reptile really be that complicated? Does it actually rival the homing pigeon in the number of sensory systems it can employ; rival the rat in its ability to learn the features of its world; rival even primates in its complexity of decision making? Planning by a non-mammal? Cognition in a turtle? Perhaps not; my final point is only that the behavior needed to run even the normal routines of simple animals is much more complicated than we have supposed. One key to appreciating that fact can come from a revitalized study of movements, the physical, observable outcome of many internal considerations. By understanding how route processes generate the array of movement patterns shown by free-ranging animals, we can begin to see how organisms give order to their lives.

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## APPENDIX I. SYMBOLS\*

### I. Theoretical Quantities

#### A. Variables

$\tau_i$	the target heading for a step beginning at point i
A	an azimuthal target that is constant over all steps
$\vec{d}_i$	a deflection vector occurring at point i
$d_i =  \vec{d}_i $	the length component of a deflection vector
$\delta_i$	the directional component of a deflection vector

#### B. Population parameters

$\vec{\mu}_\delta$	the mean vector of the directional components of deflections
$\mu_\delta$	the directional component of the mean vector of deflection directions
$\rho_\delta$	the length component (concentration parameter) of the mean vector of deflection directions

### II. Measurable Quantities

#### A. Variables

$\vec{s}_i$	a step vector beginning at point i
$s_i =  \vec{s}_i $	the length of a step vector
$\alpha_i$	the azimuth of a step vector
$\theta_{ij}$	the angular difference (turn angle) between the azimuths of steps i and j
$\theta_k$	a turn angle of order k, where k is the number of steps that separate points i and j (i.e., $k = j - i$ )

\* This choice of symbols represents a compromise between the literature of stochastic walks and orientational statistics

$\vec{D}_n = \sum \vec{s}_i$       the net vector of travel over n step vectors  
 $D_n = |\vec{D}_n|$       the net distance of travel over n steps  
 $R_n = |\sum \alpha_i|$       the length of the azimuthal resultant over n steps  
                                  (a quantity similar to  $D_n$  but where the step lengths  
                                  are treated as having unit values)

#### B. Sample statistics

$m_\alpha$       the mean angle for a sample of step azimuths  
 $r_\alpha = R_n / n$       the concentration parameter for a sample of step  
                                  azimuths  
 $m_{\theta_k}$       the mean angle for a sample of  $k^{\text{th}}$  order turns  
 $r_{\theta_k}$       the concentration parameter for a sample of  $k^{\text{th}}$  order  
                                  turns  
 $c_{\theta_k} = m(\cos \theta_k)$       the mean cosine for a sample of  $k^{\text{th}}$  order turns  
 $m(D_n^2)$       the mean squared distance of travel over n steps (also  
                                  denoted by "MSD")  
 $m(R_n^2)$       the mean squared resultant over n steps  
 $m(s^2)$       the mean squared step length