Chapter 7
Animal Movement Data: GPS Telemetry, Autocorrelation and the Need for Path-Level Analysis

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In the previous chapter we presented the idea of a multi-layer, multi-scale, spatially referenced data-cube as the foundation for monitoring and for implementing flexible modeling of ecological pattern–process relationships in particulate, in context and to integrate these across large spatial extents at the grain of the strongest linkage between response and driving variables. This approach is powerful for developing information about the conditions of multiple ecological attributes continuously across the analysis area. However, there are a number of ecological questions that involve processes that are not functions of ecological conditions at point locations alone. Many of these involve spatial processes and mobile agents, such as the spread of disturbances, dispersal of propagules, and the movement of mobile animals. The focus of this chapter is on animal movement data.

In mobile animals, movement behavior is used to maximize fitness by maximizing access to critical resources and minimizing risk of predation. As organisms move through spatially complex landscapes, they integrate the distributions and conditions of multiple ecological attributes, adopting movement paths that optimize fitness benefits while minimizing fitness costs. There is exceptionally rich information in intersecting the space–time movement paths organisms follow with the kind of multi-variate, spatially explicit ecological data base described in the previous chapter. Until recently, however, it was not possible to obtain sufficiently precise records of movement paths of sufficient length to meaningfully associate movement behavior with ecological conditions across large and complex landscapes. However, that has changed dramatically in the past decade with the advent of GPS telemetry technology. It is a classic example of the phenomenon described in Chapter 1, of advances in methodology leading to entirely new kinds of data, which in turn drive the emergence of new analytical approaches and theoretical paradigm shifts. Also, as described in Chapter 1, the often acrimonious and frequently confused arguments relating to the statistical properties and proper analyses of such movement

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data streams reflect to some degree a struggle between an old tradition and its procedures, assumptions and a new paradigm.

Location data obtained from radio and satellite telemetry have become very widely used in studies of animal space use, habitat selection and behavior (White and Garrott 1990; Aebisher et al. 1993; Cushman et al. 2005). These new data have both presented an unprecedented view into animal movement behavior and an unprecedented challenge to traditional thinking about statistical analysis of habitat use. Traditionally, analysis of habitat use has been based on comparing the habitat characteristics of a large number of statistically independent utilized locations with a large number of available or not utilized locations with compositional analysis or linear models, such as logistic regression. These approaches developed during the time when location data were obtained infrequently using VHF telemetry or networks of detection plots, such as remote cameras, hair snares or track plates. In the latter method, the investigator can establish a network of sampling stations which yield presence and pseudo-absence data. These can be effectively independent spatially if the design is carefully developed. In the former case, infrequent re-location of individuals through telemetry results in a sequence of utilized points which can then be compared to available points within some spatial extent, often the animals minimum convex polygon home range. These infrequent VHF points may appear to be statistically independent and not show significant autocorrelation. However, as Fortin and Dale (2005) note, sparse sampling of an autocorrelated data stream does not remove the effect of autocorrelation from the data, it only reduces power to detect it.

With the advent of GPS telemetry it is now possible to obtain relocation data as frequently as one desires. Sampling frequency of down to 5 min intervals is common. Animal movements are inherently highly autocorrelated because an animal’s next step has to be to a location available from its current step, leading to a pathway in which locations are autocorrelated with previous locations for long time durations. This poses a major challenge to traditional point-based approaches which assume spatial independence of observations. In point based approaches, temporal autocorrelation of locations leads to underestimation of home range size and bias in predictions of habitat selection, core area, and intensity of resource use (Swihart and Slade 1985; Alldredge and Ratti 1986; Thomas and Tylor 1990; White and Garrott 1990; Cresswell and Smith 1992; Palomares and Delibes 1992; Litvaitis et al. 1994). The magnitude of these errors is proportional to strength of autocorrelation between observations across time-lags and will vary by species and by habitat (Swihart and Slade 1985; Harris et al. 1990). Accordingly, many scientists previously recommended that researchers calculate time to independence using time–distance curves (Litvaitis et al. 1994).

A priori, there is no way to determine what the time to apparent independence will be (Harris et al. 1990). Shoener’s (1981) V statistic and Mantel correlograms (Cushman et al. 2005) have been recommended to produce correlograms to illustrate the structure and duration of autocorrelation. However, filtering data to achieve statistical independence often incurs heavy costs in terms of information loss. In addition, the apparent independence achieved may often merely indicate a loss of power to detect autocorrelation due to reduced sample size from a globally autocorrelated movement path (Fortin and Dale 2005; Cushman et al. 2005). In addition, many researchers have argued that such filtering may not be necessary (Swihart and Slade 1997; Rooney et al. 1998). For example, Rooney et al. (1998) argue that strict attempts to achieve statistical independence by subsampling result in substantial underestimation of range size and rates of movement. It also obliterates fine-scale patterns in habitat use that may be present in the data (Rooney et al. 1998). Also, even long sampling intervals do not guarantee independence (Cushman et al. 2005). The correct strategy for the best estimation of home range size, intensity of spatial use and quantification of fine-scale behavioral decisions may be to use the shortest possible sampling interval over the longest possible period (Rooney et al. 1998).

Swihart and Slade (1997) argue that regular sampling intervals resulting in autocorrelated data will not invalidate many estimates of home range size so long as the study time frame is adequate. Otis and White (1999) extend this argument and propose that the key requirement is to define a specific monitoring time frame appropriate for the study question and restrict inferences to the temporal and spatial scope justified by that time frame. However, if one uses a point-based analytical approach that assumes statistically independent spatial observations this is a conundrum in that the optimal estimate of utilization will come from the most frequent possible remeasurement, but the severity of violation of statistical assumptions will also increase with increasing frequency of observations. This suggests a necessary shift from point-based to path-based analyses, as discussed in Chapter 19.

Recently, there has been the realization that autocorrelation in many cases isn't a problem to be solved through carefully controlling sampling design, but a critical signal about the underlying structure of pattern–process relationships in spatially structured environments (Legendre 1993). Indeed, autocorrelation reflects the fact that ecological processes occur in a spatial context and their effects are expressed partly as functions of spatial location and distance. As we argued in Chapters 1 and 2, there is great advantage and enormous potential in addressing spatial complexity and temporal variability directly as critical attributes of ecological systems. Autocorrelation of animal movement data is a prime example of this opportunity.

The patterns of temporal and spatial autocorrelation of locations are an important part of the information that telemetry data provide (Cushman et al. 2005). Legendre (1993) and Legendre and Fortin (1989) argue that spatial autocorrelation is an informative ecological parameter that reveals scales and patterns of ecological processes which are often not resolvable through other methods. In terms of animal movements, addressing the details of the strength, scale and patterns of autocorrelation may illustrate details about animal use of space and its relationships to changes in the environment in response to perturbations, social interactions or seasonality (Cushman et al. 2005). In this chapter we review some of the issues relating to GPS telemetry data, investigate the structure and range of spatial autocorrelation of sequential relocation points under 18 different movement rules using simulation modeling, and then compare these to the structure and range of spatial autocorrelation in a mobile mammal, the African elephant. We use these analyses to argue against traditional point-based analyses of movement data, in favor of path-level analysis. This motivates the case study example on elephant movement presented in Chapter 19.

7.1 Methods

7.1.1 Movement Path Simulation

We simulated 18 different movement path varieties, consisting of a two-way factorial of path type and mean turning angle (Table 7.1). We replicated each of the 18 path varieties ten times. In all cases each path began by heading north, with subsequent steps all one unit in length. All paths were simulated to 1,000 steps. There were three path types, consisting of correlated random walk, bounded correlated random walk, and central place random walk. There were six turning angle distributions, each consisting of a normal random distribution with a specified mean. The mean turning angles for the six distributions were 1°, 6°, 12°, 24°, 45°, and 90°. In the correlated random walk the turning angle for each step from the previous step direction was taken from a normal random variable with the mean of the turning angle for that normal random distribution. This walk represents an unconstrained walk, with the only spatial parameter consisting of the normal random turning angle between steps. In the bounded correlated random walk the walk was calculated exactly the same, except with the additional constraint that it not exceed ten distance units from the origin. This reflects a correlated random walk within a fixed circular home range with radius of ten distance units. When a walk reached ten units distance from origin the next step was taken directly toward the origin, with subsequent steps correlated random walks from that new direction. The central place random walk consisted of correlated random walks of 100 steps, followed by an azmithal return to the origin in the next 100 steps, with this combination repeated five times over the 1,000 steps of the simulation. This simulates correlated random foraging paths out from a central place, such as a nest or natal den, followed by direct return, such as after capturing prey. Examples of each of these 18 path varieties are shown in Figs. 7.1–7.3, with Fig 7.1 showing correlated random walks, Fig. 7.2 showing bounded random walks, and Fig. 7.3 showing central place random walks.

Table 7.1 Factorial of the 18 path varieties simulated. They are a combination of three path types across six distributions of turning angle. The path types are unconstrained correlated random walk (UCW), random walks constrained to remain within ten step lengths of the origin by reflecting off the edge (BCW) and correlated random walks beginning at the origin and returning along the back azmuth at 100 steps (CCW). The six distributions of turning angle are obtained from normal random variables with mean of 1°, 6°, 12°, 23°, 45°, and 90°

	1°	6°	12°	23°	45°	90°
Unconstrained correlated random walk	UCW1	UCW6	UCW12	UCW23	UCW45	UCW90
Bounded correlated random walk	BCW1	BCW6	BCW12	BCW23	BCW45	BCW90
Central place correlated random walk	CCW1	CCW6	CCW12	CCW23	CCW45	CCW90

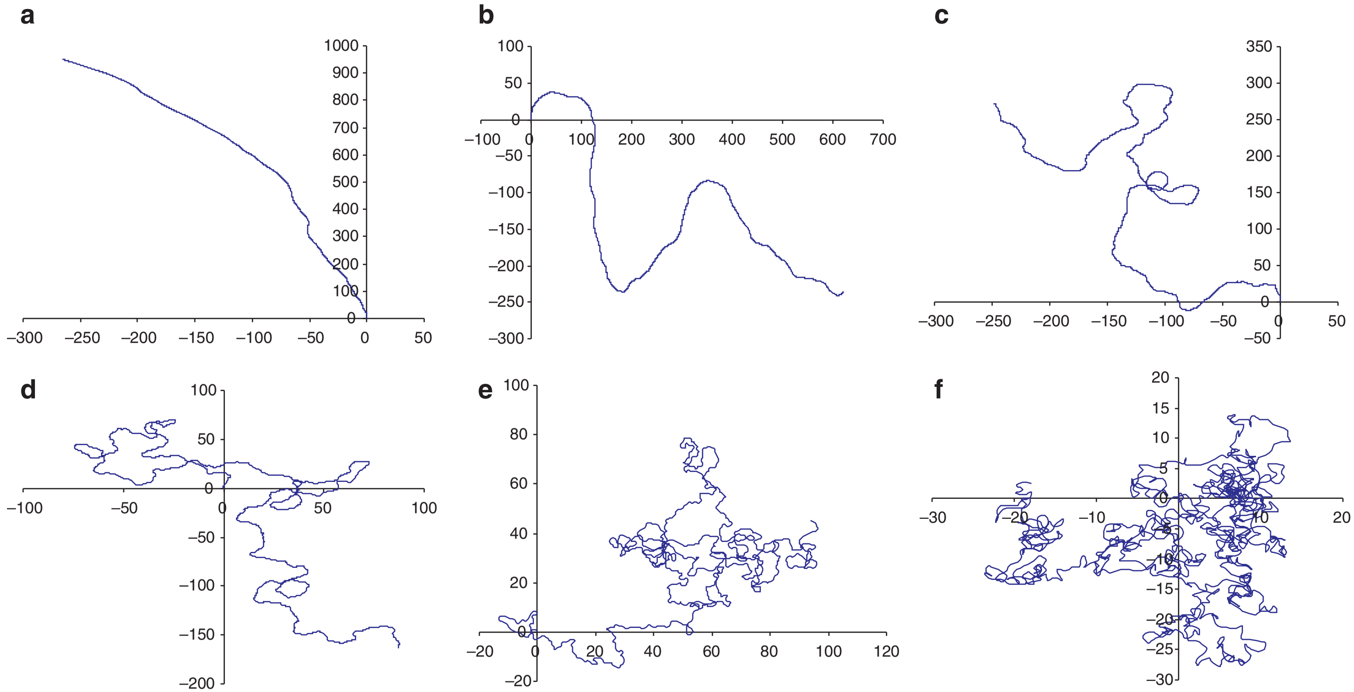

Fig. 7.1 Example paths for unconstrained correlated random walks for each of the six turning angle distributions

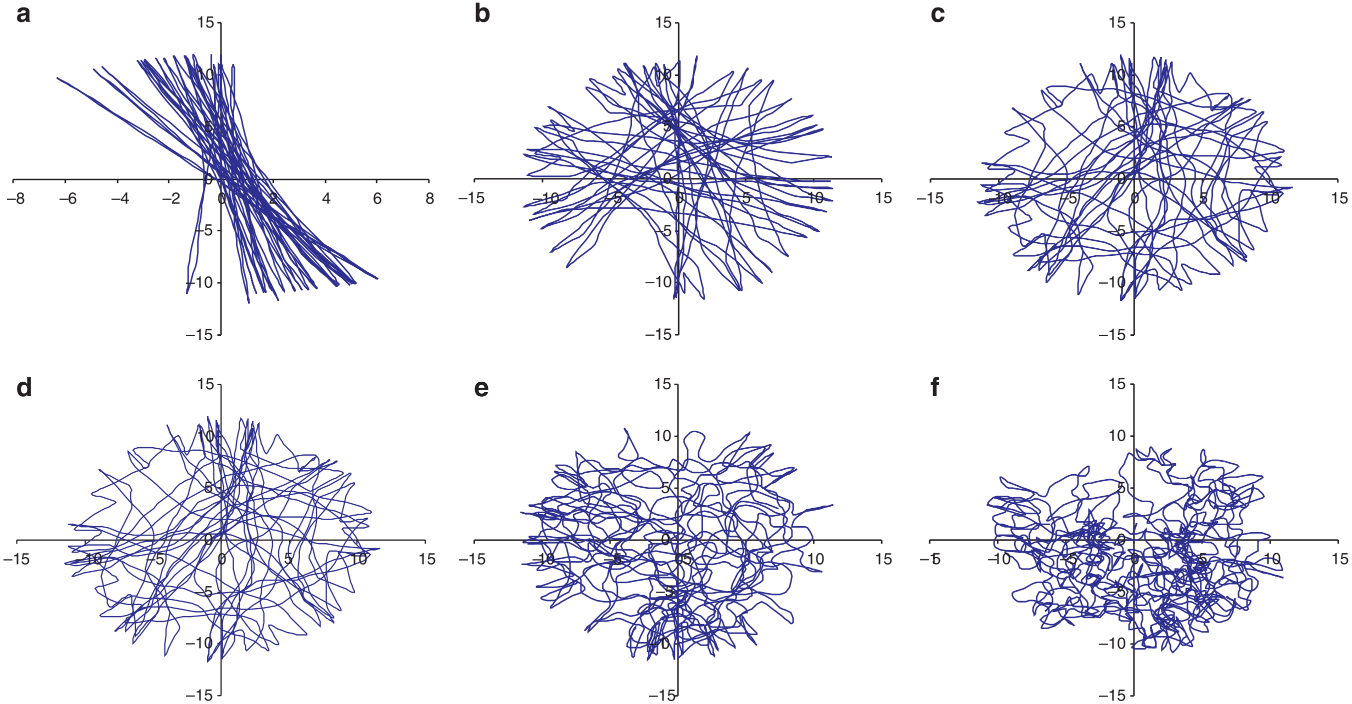

Fig. 7.2 Example paths for bounded correlated random walks for each of the six turning angle distributions

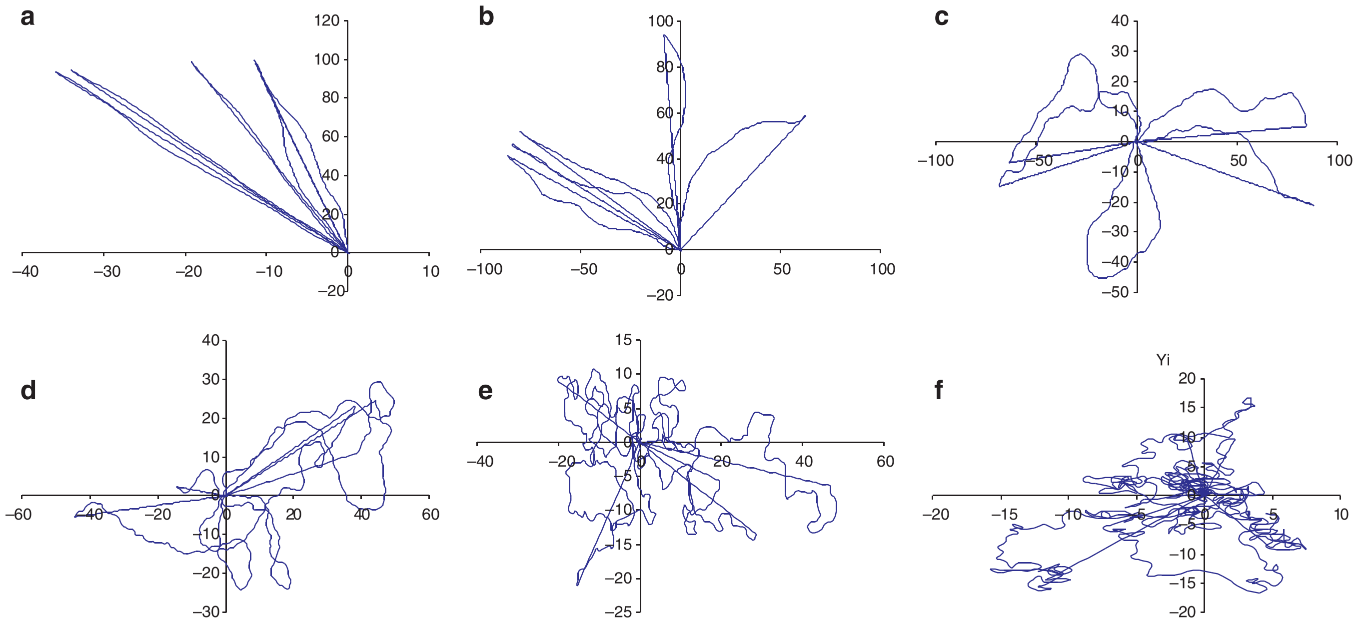

Fig. 7.3 Example paths for central place correlated random walks for each of the six turning angle distributions

7.1.2 Autocorrelation Analysis

We produced Mantel correlograms for each of the 180 movement paths using the Ecodist library in R (R-development team 2008). The Mantel test tests the degree of association between two distance matrices (Mantel 1967). In ecological research these distance matrices describe the pairwise dissimilarity or ecological distance between each pair of samples. Because any number of variables describing each sample can be included in the calculation of these distance matrices, the Mantel test is a multivariate test of the association between two data sets. When one of the distance matrices is coded as distance classes it is possible to construct a multivariate correlogram (Oden and Sokal 1986; Sokal 1986). The resulting correlogram shows the strength of correlation between the two multivariate distance mat rices across a range of lags between them. As discussed in Cushman et al. (2005), this is conceptually similar to univariate correlograms produced using Moran's I or Geary's C (Legendre and Legendre 1998), except that Mantel correlograms produce description of how multivariate correlations vary across several classes of lag-distance whereas univariate correlograms describe the relationships between one response variable and one lag variable across several classes of lagdistance.

In this study we create correlograms comparing the distance between organisms in geographical space with distance between them in time. Cushman et al. (2005) noted that the Mantel correlogram has a number of advantages over alternative ways of computing autocorrelograms for animal movement analysis. First, correlograms of the V statistic (Schoener 1981) do not have a significance test, and assume a bounded and elliptical home range. In contrast, the Mantel correlogram does not assume a fixed and elliptical home range and has both an asymptotically correct analytical significance test, and is readily tested nonparametrically with Monte-Carlo methods (Legendre and Legendre 1998).

These correlograms record the mantel correlation between distances between points across lag distances (e.g. Cushman et al 2005). The lag distances used in this analysis were 5, 15, 25,… 995, for a total of 99 lag distance classes. We calculated significance of mantel correlation at each lag distance using Monte Carlo permutation with 1,000 randomizations, for a point-wise significance level of 0.001. Our analysis included plotting the ten replicate correlograms for each of the 18 path varieties and overlaying the confidence intervals for statistically significant autocorrelation to determine the time to spatial independence, if any, for each path. This analysis provides a relatively comprehensive assessment of the structure, range and variability of autocorrelation in three common path types across a reasonably broad range of turning angle behavior. Such evaluation of simulated paths generated with known and controlled spatial processes is essential for evaluating autocorrelation in empirical movement paths.

7.1.3 Empirical Analysis of Autocorrelation of Elephant Movement

We also calculated Mantel correlograms for three elephants (*Loxodonta africana*) collared in Botswana (Cushman et al. 2005). Prior to analysis we preformed several data filtering tasks to retain the most accurate and least biased movement data. This reduction resulted in a final set of 709 locations for herd 55, 713 locations were retained for herd 56, 699 locations for herd 57 (Cushman et al. 2005). Next, we broke the three data sets into overlapping windows in time, to allow us to evaluate changes in autocorrelation patterns through seasons, and to reduce the effects of non-stationarity. We selected time windows of 60 days, and slid these across the 345 day sampling period, with 15 day time steps between the start of successive periods. This resulted in 20 overlapping time periods retained for the analysis; each 60 days long and beginning 15 days apart. For each of these windows we created two distance matrices for use in the Mantel correlogram analyses. First, we computed the geographical distances along the curvature of the earth between all pairs of points in each movement database. Next, we computed distance matrices for the same movement data, but for distance between points in time rather than in space. These time distance matrices were then recoded into distance class matrices, containing 120 distance classes each, corresponding to the number of 12 h periods over the 60 day sampling windows.

7.2 Results

7.2.1 Structure, Range and Variability of Autocorrelation Within Simulated Movement Paths

Each path variety had a characteristic autocorrelation structure (Figs. 7.4–7.6). Correlated random walks showed clines of increasing negative spatial autocorrelation between locations as time distance between them increased, with this pattern consistent across all six turn angle distributions. The six turn angle distributions were primarily related to variability among replicate correlograms, with variability increasing with larger mean turning angles. This is exactly as one would expect with correlated random walks. Importantly, for all turning angle distributions these correlograms indicate a global cline in autocorrelation such that there is never a lag distance at which points become spatially independent.

Bounded random walks all showed the same basic pattern of initial high positive autocorrelation of location, followed by a drop to negative autocorrelation and subsequent fluctuation between positive and negative autocorrelation. This fluctuation between positive and negative autocorrelation was highly sensitive to mean

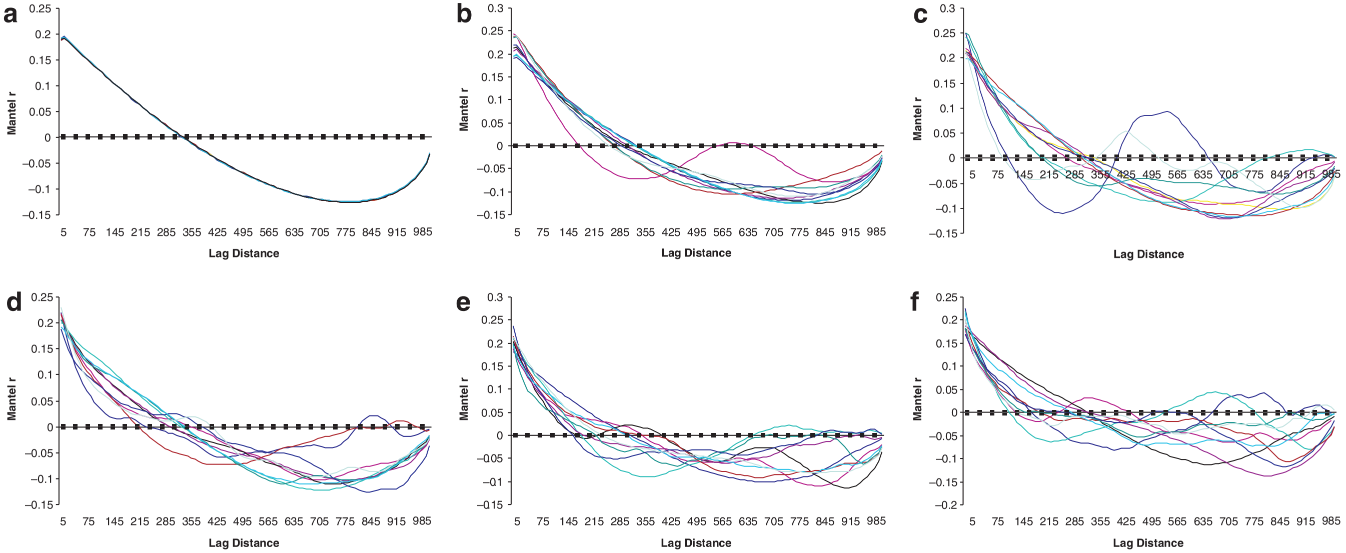

Fig. 7.4 Mantel correlograms for unconstrained paths across the six distributions of turning angle. Each plot shows ten overlain correlograms derived from the ten replicate realizations of each path type

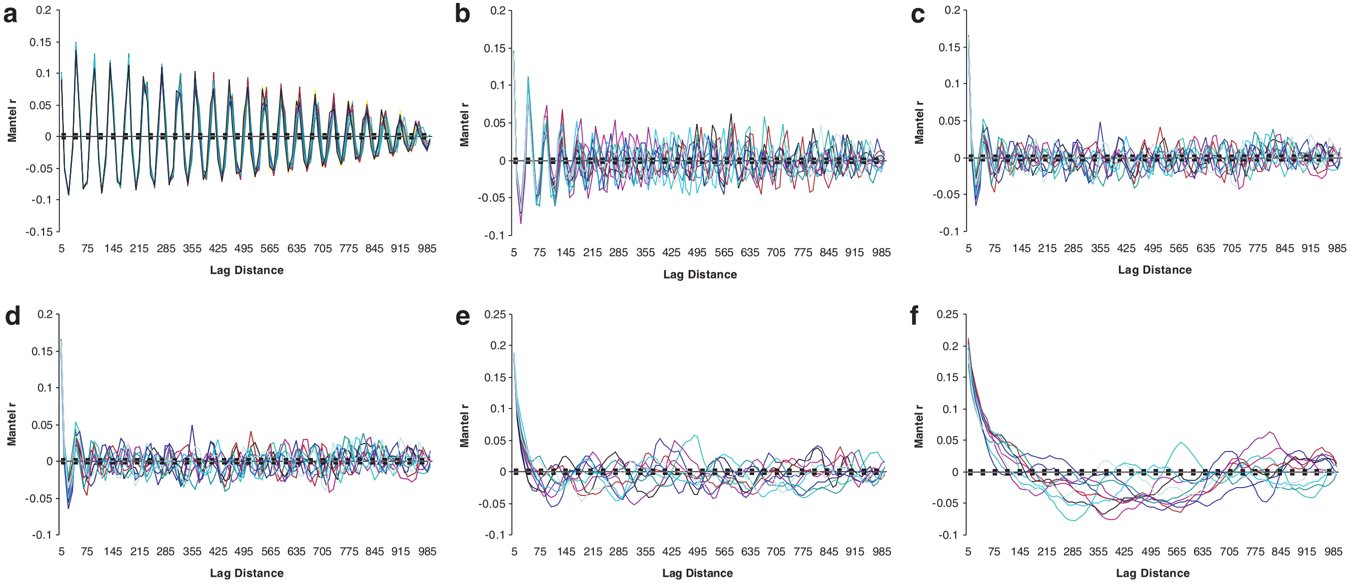

Fig. 7.5 Mantel correlograms for bounded paths across the six distributions of turning angle. Each plot shows ten overlain correlograms derived from the ten replicate realizations of each path type

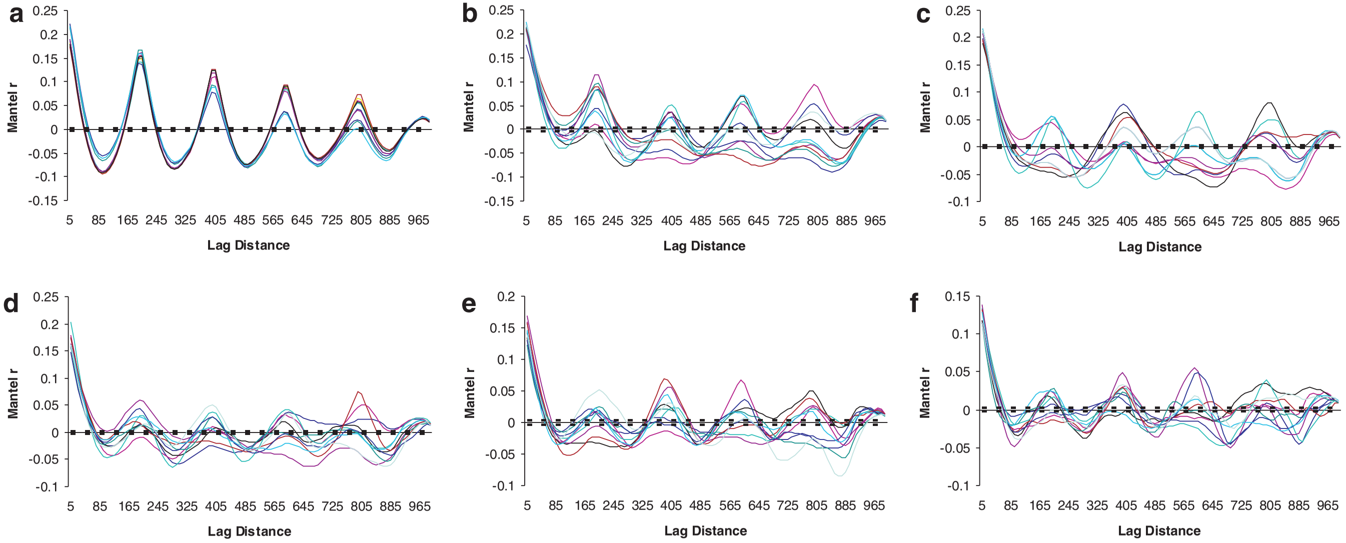

Fig. 7.6 Mantel correlograms for central place paths across the six distributions of turning angle. Each plot shows ten overlain correlograms derived from the ten replicate realizations of each path type

turning angle. For example, when mean turning angle was very small, such as 1°, this resulted in very strong periodic autocorrelation as the path zigzagged back and forth across the home range, bouncing off the frontier, with relatively little change in direction between. This periodic autocorrelation became more damped as the mean turning angle increased, but persisted in a detectable form up to at least a mean turning angle of 45°, and arguably all the way to a mean turning angle of 90°. As in the case of the unconstrained correlated random walks discussed above, variability among path correlograms increased with increasing mean turning angle. Also, as in the case of unconstrained correlated random walks, but perhaps surprisingly, there was no time to independence for bounded walks in any combination with turning angle distribution. This is surprising because random utilization of a fixed home range is held as the ideal and perhaps only case when there is an expectation of a time to spatial independence among sequential locations (Cushman et al. 2005). In this case, across all lag distances, there remained highly significant autocorrelation among locations. This is because a correlated random walk within a bounded home range does not equate to random utilization of a fixed home range. The utilization modeled here is a correlated random walk. This imparts randomness in turning angle, but not randomness in sequential location, as each location is contrained to be one step length from the previous and in a direction correlated to the previous step length. All real movement paths of actual organisms have this kind of constraint. This constraint results in very persistent and complex patterns of autocorrelation across very long time lags.

Central place random walks all shared a common basic form, characterized by repeated cycles between strong positive and strong negative autocorrelation with a period equal to 200 steps, or the time to complete a full cycle of foraging correlated random walk and azmithal return to the central place. As in the cases of unconstrained and bounded correlated random walks, increasing mean turn angle increased variability among replicate correlograms and damped the strength of the general pattern. Like the previous cases, there is no time lag sufficient to ensure spatial independence of locations. The periodic pattern of return to the central place burns in a cyclic pattern of positive to negative to positive autocorrelation that extends indefinitely.

7.2.2 Autocorrelation of Elephant Movement

Cushman et al. (2005) report long-term, spatially complex and seasonally variable patterns of autocorrelation among these elephants. Figures 7.7–7.9 show the correlogram surfaces for each collared elephant. The simulation analyses reported above provide a highly useful framework for understanding the structure of these empirical correlogram surfaces. This comparison indicates that across the year the pattern of autocorrelation of movement for each elephant show a full range of forms from smooth clines, strongly periodic use of central place, and occasional bounded correlated random use of temporarily fixed home ranges (Cushman

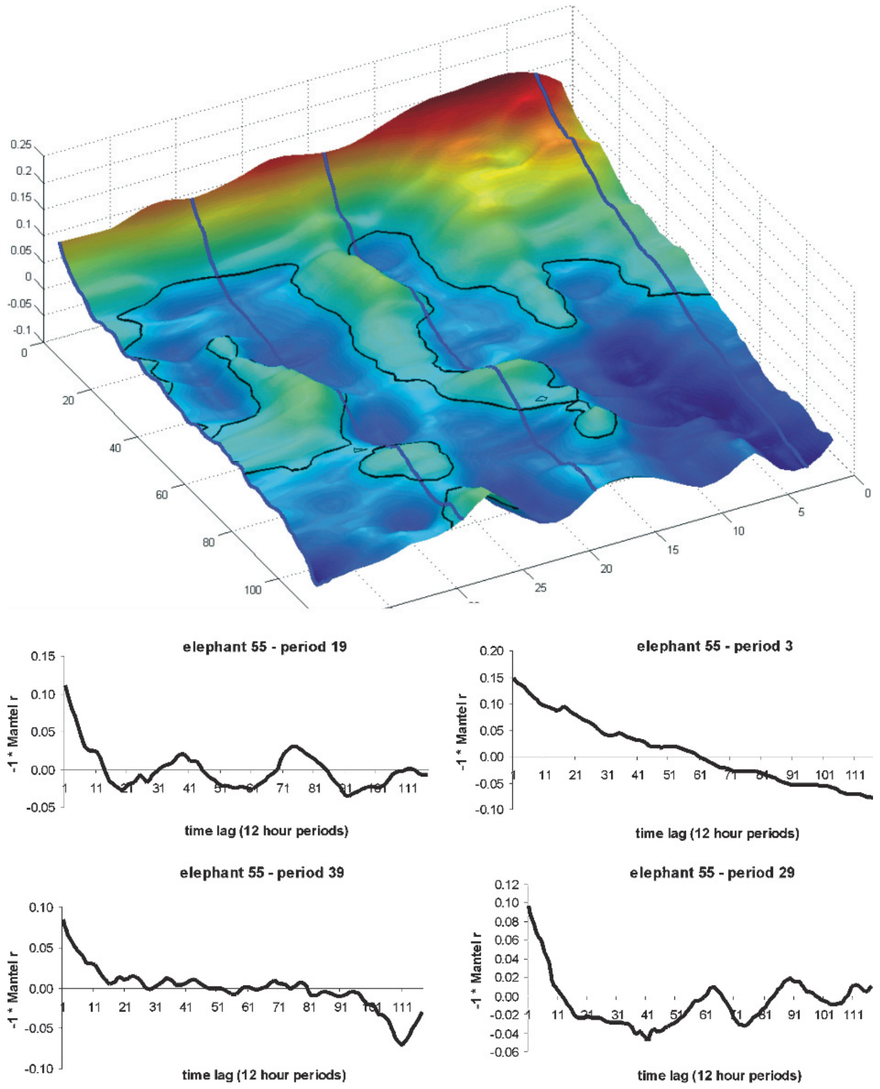

Fig. 7.7 Autocorrelation surface for elephant herd 55

et al. 2005). Interestingly, while the autocorrelogram surfaces for each elephant are highly complex, there is a strong degree of agreement between them, which in turn is related to the pattern of rainfall through the year (Cushman et al. 2005). This indicates that the structure of movement correlograms for these elephants provides highly interpretable information about movement behavior in relation to temporal changes in environmental conditions. During dry periods with little rain the elephants exhibit strongly periodic movement behavior corresponding

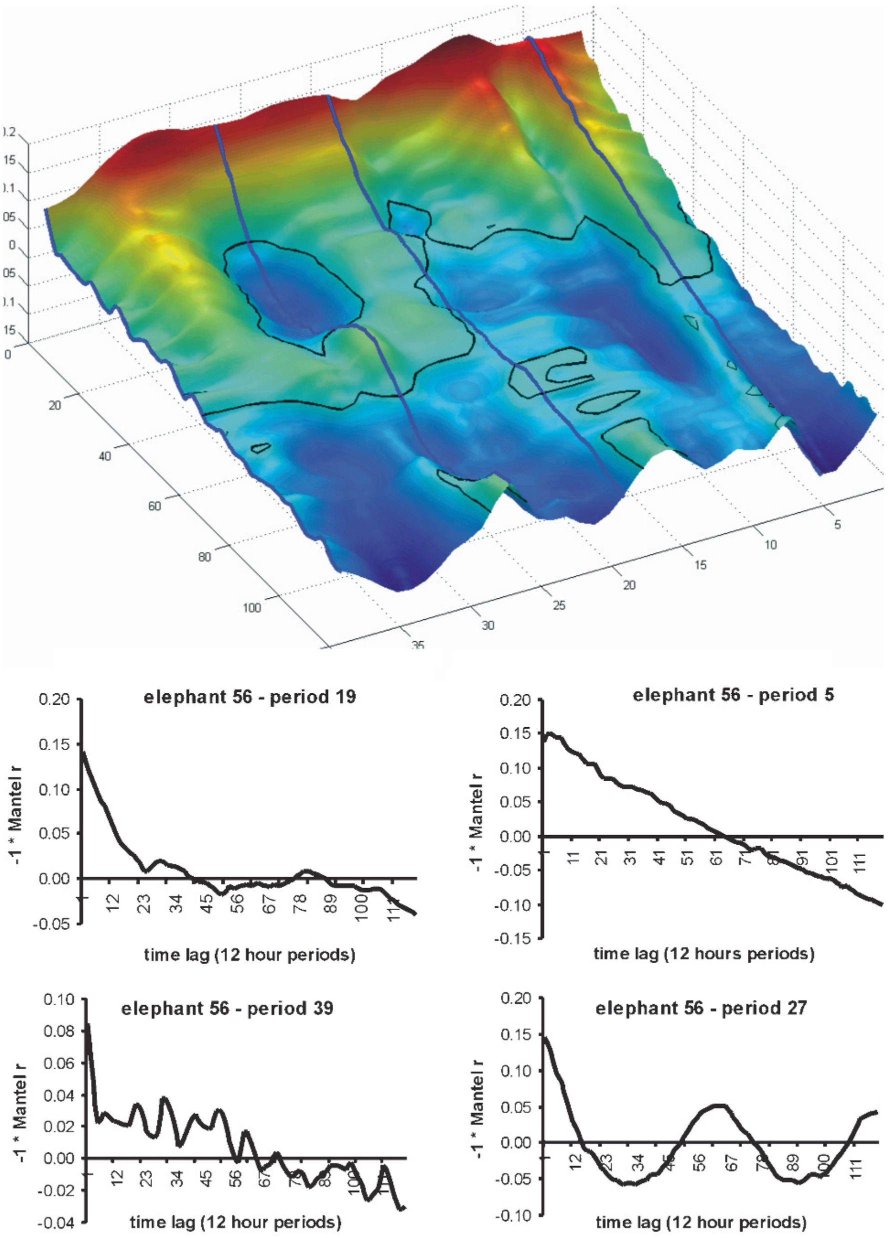

Fig. 7.8 Autocorrelation surface for elephant herd 56

to repeated visits to one or several permanent water holes interspersed with long foraging excursions away from the heavily over-grazed proximity of these water sources. During the rainy season when water is relatively continuously distributed,

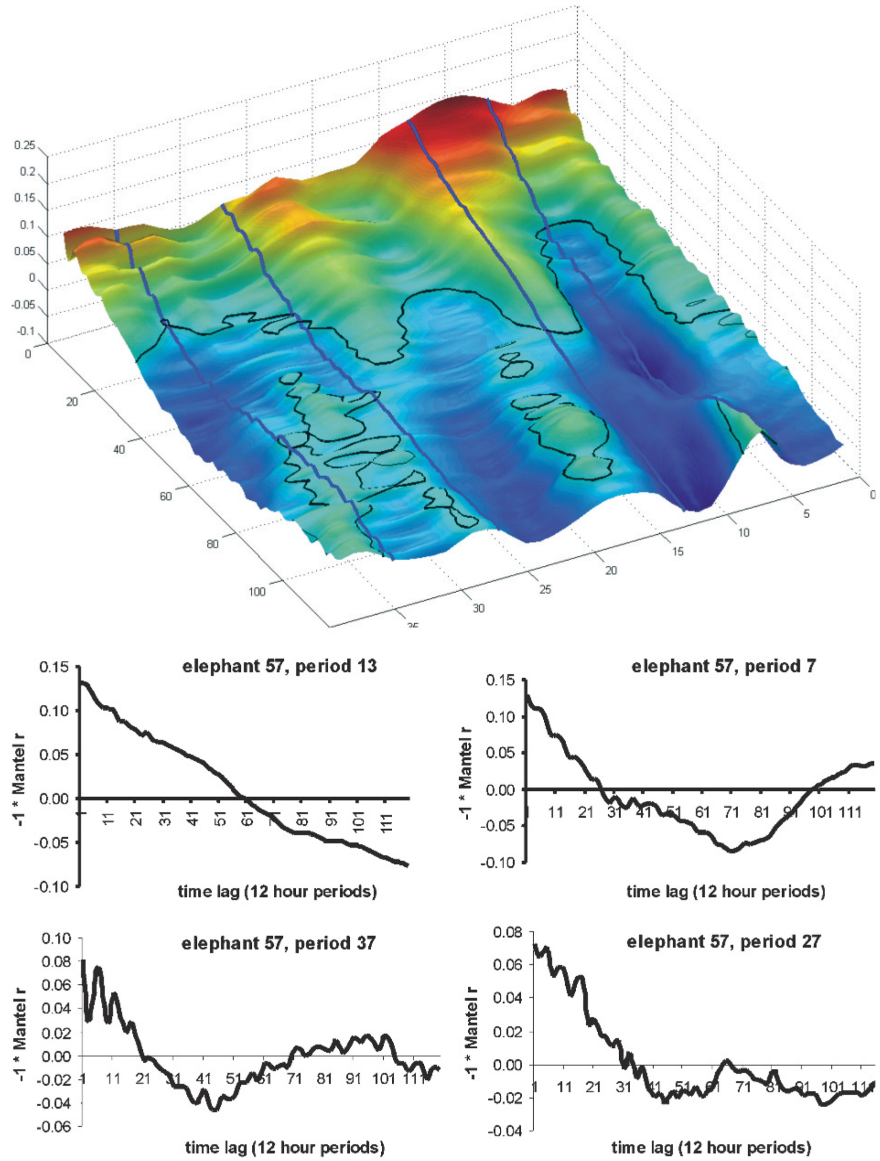

Fig. 7.9 Autocorrelation surface for elephant herd 57

the elephants fluctuation between unbounded correlated random walks, indicated by smooth clines in the correlogram surfaces, and random walks in temporarily bounded home ranges, as indicated by rapid drop to near zero followed by minor fluctuations around zero in the correlogram surfaces.

7.3 Discussion

7.3.1 Deep Autocorrelation in Animal Movement

Both simulation of movement paths with known process characteristics and analysis of empirical movement paths of a large and mobile mammal have clearly shown that autocorrelation is a fundamental attribute of movement data. In no simulated case did analyses show a meaningful time to independence. Even in the case of correlated random walks bounded within a fixed home range we found persistent periodic fluctuations between negative and positive autocorrelation as a result of the constraint that each step be within one step length of the previous one and in a direction to some degree correlated with the previous direction. No amount of subsampling of the data would remove the autocorrelation effects. In unconstrained correlated random walks and central place correlated random walks there are very strong patterns of autocorrelation that do not diminish appreciably over the full span of the walk. Subsampling data to a point where autocorrelation is no longer detected in such a case produces only an illusion of independence. It is conceptually similar to sampling a single point on the line. That point carries no information about the linear process that produced it, but it is entirely dependent on that process. Similarly, correlograms produced on subsampled or sparsely collected data on highly correlated pathway likely will show no significant long-range pattern of autocorrelation, even though there is underlying strong autocorrelation at every point and time lag.

7.3.2 Movement Paths Are Rich Source of Information

The consistent identification of persistent and often spatially complex patterns of autocorrelation in both controlled simulations and empirical analysis suggests that it will rarely be possible to satisfy assumptions of spatial independence among points for methods of analysis that require it. As mentioned in the introduction, this suggests the need for a change in focus from utilization points which are assumed to be a random sample of the full utilization distribution independent of sequential autocorrelation effects, to an explicit focus on the sequential, continuous nature of the movement paths themselves. The sequential spatial process of movement through complex landscapes contains rich information about the behavioral processes of foraging, resting, hiding, mating, defending territory, migrating and many other important behaviors in relation to underlying ecological gradients across a range of spatial scales. This linkage has largely been neglected, although some Markov chain approaches have begun to investigate it. In Chapter 20 we present an alternative approach, focusing on path-randomization and comparison of the ecological conditions encountered along utilized paths with those which would be encountered along potentially available paths of identical length and topology.

In addition, the strong and consistent structure of correlograms resulting from paths generated using different known spatial processes show that correlograms themselves can be highly useful tools to explore movement behavior and identify dominant movement processes, which then can be used to generate ecological and behavioral hypotheses. For example, the simulation results presented here clearly show three distinct correlogram shapes. The identification of one of these shapes in correlograms produced from empirical data will invalidate hypotheses about the existence of the process that would generate one of the other two correlogram forms. For example, if we hypothesize that an organism will exhibit random use of a fixed home range, and discover that its movement path produces a cline or periodic shaped correlogram we would be able to safely reject that hypothesis. Correlograms have some use, but less certainty, in confirming dominant underlying processes. For example, if we propose that an organism has an unconstrained correlated random walk, and discover its path produces a cline shaped correlogram, this is consistent with that explanation, but does not fully demonstrate its truth. This is a variety of the issue of affirming the consequent discussed in the first and second chapters. In this case, while a cline shaped correlogram is consistent with an unconstrained correlated random walk it may also be possible to obtain a similar cline shaped correlogram from other spatial processes, such as any walk in which locations tend to get farther away from each other in space as they become farther apart in time. Similarly, if one proposes a central place movement behavior and observes a strongly periodic correlogram, this observation is consistent with the hypothesis but does not prove it to be true. There are several ways one can obtain a similar periodic correlogram, including cyclic repeat of a similar route through a home range, or cyclic return to several foraging or resting locations. However, the form of correlograms are diagnostic for rejecting inconsistent movement hypotheses and are useful in determining the degree of support for alternative explanations of movement process.

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