Elephants in space and time

Samuel A Cushman, Michael Chase and Curtice Griffin

Autocorrelation in animal movements can be both a serious nuisance to analysis and a source of valuable information about the scale and patterns of animal behavior, depending on the question and the techniques employed. In this paper we present an approach to analyzing the patterns of autocorrelation in animal movements that provides a detailed picture of seasonal variability in the scale and patterns of movement. We used a combination of moving window Mantel correlograms, surface correlation and crosscorrelation analysis to investigate the scales and patterns of autocorrelation in the movements of three herds of elephants in northern Botswana. Patterns of autocorrelation of elephant movements were long-range, temporally complicated, seasonally variable, and closely linked with the onset of rainfall events. Specifically, for the three elephant herds monitored there was often significant autocorrelation among locations up to lags of 30 days or more. During many seasonal periods there was no indication of decreasing autocorrelation with increasing time between locations. Over the course of the year, herds showed highly variable and complex patterns of autocorrelation, ranging from random use of temporary home ranges, periodic use of focal areas, and directional migration. Even though the patterns of autocorrelation were variable in time and quite complex, there were highly significant correlations among the autocorrelation patterns of the different herds, indicating that they exhibited similar patterns of movement through the year. These major patterns of autocorrelation seem to be related to patterns of rainfall. The strength of correlation in movement patterns of the different herds decreased markedly at the cessation of major rain events. Also, there was a strong crosscorrelation between strength of autocorrelation of movement and rainfall, peaking at time lags of between three and four weeks. Overall, these approaches provide a powerful way to explore the scales and patterns of autocorrelation of animal movements, and to explicitly link those patterns to temporally variable environmental attributes, such as rainfall or vegetation phenology.

S. A Cushman, USDA Forest Service, Rocky Mountain Research Station, PO Box 8089, Missoula, MT 59801, USA (scushman@fs.fed.us). – M. Chase and C. Griffin, Dept of Natural Resources Conservation, Univ. of Massachusetts, 160 Holdsworth Way, Amherst, MA 01003 USA.

Location data obtained from radio and satellite telemetry are widely used in studies of animal space use, habitat selection and behavior (White and Garrott 1990, Aebisher et al. 1993). It has been argued that in some cases 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 the error is proportional to the time between observations and will vary by species and by habitat (Swihart and Slade 1985, Harris et al. 1990). Accordingly, many scientists recommend that researchers calculate time to independence using time-distance curves (Litvaitis et al. 1994). There is

no a priori way to determine what the time to independence will be (Harris et al. 1990) and many scientists recommend using Shoener's (1981) V statistic to produce correlograms indicating the time to independence.

However, filtering data to achieve statistical independence often incurs heavy costs in terms of information loss, and such filtering is often not necessary (Swihart and Slade 1997, Rooney et al. 1998). 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. 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 auto-correlated 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.

The patterns of temporal and spatial autocorrelation of locations are an important part of the information that telemetry data provide (Swihart and Slade 1997, Rooney et al. 1998, Otis and White 1999). Statistical methods to measure levels of autocorrelation may be particularly useful for comparing patterns of behavior and range use among individuals so long as the same sample interval is used. Legendre (1993) and Legendre and Fortin (1989) argue that spatial autocorrelation is often a highly informative ecological parameter that can elucidate scales and patterns of ecological processes which are 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. In addition, for many organisms the time to independence of locations is a fixed home range, which may be an entirely inappropriate question. First, it is only applicable to organisms that randomly utilize a fixed home range. Organisms that do not have a fixed home range and organisms that non-randomly use portions of a fixed home range will show significant spatial autocorrelation at long time lags (Cushman et al., unpubl.). Second, movement autocorrelation profiles are often non-stationary across seasons. Non-stationarity is a

violation of autocorrelation analyses and is not solved by subsampling the data to the resolution of time to independence. Indeed, time to independence itself may be variable under non-stationarity.

If random utilization of a fixed home range is a relatively rare occurrence in nature, and if non-stationarity is common, then ecologists should explicitly consider the patterns of movement autocorrelation themselves and how they change through space and time. For many questions it may be more appropriate to treat autocorrelation as a biological signal to be analyzed and interpreted (Legendre and Fortin 1989, Legendre 1993). Furthermore, instead of treating non-stationarity as a serious statistical assumption that is difficult to meet, scientists may gain understanding through investigating the details of non-stationarity of animal movement patterns, by plotting changes in autocorrelation through time. We feel that for many questions about animal movement and ecology it is important to explicitly account for non-random, spatially complex, long term patterns of spatial autocorrelation that change through time and across seasons. Doing so will help wildlife researchers to address questions about the relationships between time, season, space, resources, social interactions and animal movement patterns which otherwise are difficult or intractable.

In this paper we present an approach to analyzing autocorrelation patterns in animal movements that provides a detailed picture of seasonal variability in the scale and patterns of movements. We use a combination of moving window Mantel correlograms, surface correlation and crosscorrelation analysis to investigate the scales and patterns of autocorrelation in the movements of three herds of elephants in northern Botswana. Our primary goals were to determine if there is a meaningful time to independence for elephants in our study area, if it changes through the seasons, if there are other important attributes of the autocorrelation structure, and what they may indicate about the scale and patterns of elephant movements, as well as how they are related to seasonal changes in forage and water availability.

Methods

Study area

The study was conducted within Chobe National Park in northeast Botswana. Chobe National park is the second largest National Park in Botswana, covering 10 566 square kilometers. The park is primarily composed of four distinct ecosystem types: the extensive marshlands of the Linyani Swamps, moist grasslands of the Savuti Marsh, the riparian zone around the Chobe River, and extensive upland mopane scrub savanna. The dominant cover type is dry mopane scrub savanna which covers over 70% of the park. The research here

was conducted in the Chobe River front region near the towns of Kasana and Kazangula and surrounding mopane scrub.

A major feature of Chobe National Park is its elephant population. The elephants of Chobe National Park comprise part of what is the largest surviving elephant population in the world, which covers most of northern Botswana plus northwestern Zimbabwe. Botswana's elephant population is currently estimated at approximately 120 000 (Chase et al., unpubl.). This population has recovered from a few thousand in the early 1900s and escaped the massive poaching losses that decimated other African elephant populations in the 1970s and 1980s. Portions of the Chobe elephant herd are migratory. Large numbers of elephants make seasonal movements of up to 200 kilometers from the Chobe and Linyanti rivers, where they concentrate in the dry season, to the pans of the southeast of the park, to which they disperse in the rains (Chase et al., unpubl.).

Pre-collaring test of spatial precision of telemetry locations

Locations derived from telemetry are estimates (Springer 1979). Scientists who use telemetry should always report error parameters with their results (Litvaitis et al. 1986). Prior to capturing and collaring any elephants we tested the expected precision of Argos collar telemetry locations by placing several collars at known locations (Litvaitis et al. 1986). These locations were roof tops of several buildings distributed across the study area. These collars were monitored over a period of one week, with fixes acquired every four hours. At the end of this period we calculated the mean and variance of the difference between the predicted and actual locations. The average location accuracy was within 100 meters of the actual location. All class 2 and class 3 fixes all fell well within the accuracy range specified by Argos of 150 and 350 meter error standard deviations. We attribute our high accuracy to the fact that our study area has exceptional coverage by Argos satellites, has sparse vegetation that does not interfere with signal transmission and is extremely flat topographically.

Movement data collection

The matriarchs of three breeding herds (labeled herds 55, 56, and 57) were captured and fitted with Argos satellite telemetry collars in August 1999 along the Chobe River front near the towns of Kasane and Kazangula. These elephants were monitored for 345 days. Only fixes of precision class 1, 2 or 3 were retained for analysis. The number of fixes acquired varied among the three herds. We acquired 2195 locations for herd 55, of which 24% of the locations were of precision class 1, 38% class 2 and 37% class 3. For herd 56 we obtained 2620 fixes. Of these 22% were class 1, 39% class 2 and 39% class 3. We obtained 1964 locations for herd 57, of which 24% were class 1, 40% class 2, and 34% class 3.

Data preparation

Prior to analysis we preformed several data filtering tasks to retain the most accurate and least biased movement data. First we dropped all class 1 locations due to their low expected accuracy. We then selected the highest quality location for each herd in each 12 hour period. This reduction resulted in a final set of 709 locations for herd 55, of which 22% were class 2 and 78% class 3. 713 locations were retained for herd 56, 16% of which were class 2 and 84% class 3. For herd 57 we retained 699 locations, of which 28% were class 2 and 72% class 3.

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, with the first starting on August 12, 1999. We 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 several 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 (Legendre and Vaudor 1991). This resulted in a distance matrix containing the geographical distances between all pairs of locations for each herd in each of the 20 time windows. 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 hour periods over the 60 day sampling windows.

Mantel correlogram analysis

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 matrices across a range of lags between them. This is conceptually the same as the familiar 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 lag-distance. In this study we use the Mantel correlogram in a slightly different application. We use it to create correlograms comparing the distance between organisms in geographical space with distance between them in time. In this application, the Mantel correlogram presents the patterns of spatial autocorrelation among animal movements across a range of lag distances in time.

The Mantel correlogram has a number of advantages over alternative ways of computing autocorrelograms. First, correlograms of the V statistic (Schoener 1981) do not have an analytical 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 non-parametrically with Monte-Carlo methods (Legendre and Legendre 1998). Because of these advantages we feel that the Mantel correlogram is a sensitive and robust tool for analyzing the details of autocorrelation in animal movements.

Like all correlogram analyses, the Mantel correlogram assumes stationarity. As patterns of movement in temporally variable environments are likely to change through the year, non-stationarity in movement data is very likely in long movement series, violating the assumptions of the Mantel correlogram and all other correlogram analyses. The solution chosen in this study is to use a moving window approach, as discussed above, to extract relatively short periods of movement that are much more likely to be stationary than a broader temporal window that spans over several seasons. We used the R-Package 4.0 (Legendre and Vaudor 1991) to compute the Mantel correlograms. For each herd we computed 20 correlograms, one for each of the 20 time periods. We retained only the first 30 days of these 60 day correlograms, as autocorrelation from lag distances over half the temporal span of the data set are often spurious due to the small number of lag-pairs at those lag distances (Legendre and Legendre 1998).

We plotted the 20 correlograms from each herd as a surface. The X axis of this surface is the time window (1–20), corresponding to the number of two week periods from the start of the data set when the window begins; the Y axis is the lag distance in time (1–60), corresponding to the lag distance, in 12-hour units, between distance classes compared in the correlogram. We used Monte-Carlo permutation procedures with 1999 permutations to test the significance of autocorrelation of each correlogram at each lag distance. However, statistical testing in correlograms is a form of multiple testing and therefore the alpha level must be adjusted to avoid inflation of type I error. We corrected the error rates within each time period using a standard Bonferroni procedure. The nominal significance level used at each comparison thus was 0.0008, which corresponds to an alpha level of 0.05 within the correlogram at each of the 20 time periods.

We produced surfaces from the correlograms using linear interpolation methods. These surfaces provide a detailed visual picture of the scales, patterns, and statistical significance of autocorrelation of elephant movements across the year. The variability of these surfaces across the X dimension shows variability in autocorrelation across the year. Variability across the Y dimension shows variability in autocorrelation within each time window at various lag distances. We described the patterns and changes in the surfaces of each herd and what the different patterns indicate in terms of the scale and pattern of herd movement.

Surface correlation and profile crosscorrelation

We were also interested in comparing the herds in terms of their patterns of autocorrelation across the year. We used two approaches to conduct this comparison. The first was to compute pair-wise surface correlations between the autocorrelation surfaces of each herd. These surface correlations show the strength in association between the autocorrelation surfaces of the different herds. High association would indicate that the two herds being compared have highly similar patterns of autocorrelation through the year, across all lag distances. For this surface correlation we computed the Pearson's product moment correlation between the surfaces. We then randomized the surfaces among lag distances and calculated the correlation between each unrandomized surface and 199 randomized realizations of the surfaces for each of the other two herds. This randomization test tests the null hypothesis that there is no more similarity among the autocorrelation surfaces for the three herds than would be expected by chance.

We were also interested in comparing the correlation among surfaces across specific time-period profiles. Specifically, we wanted to determine if there were particular periods when the autocorrelation patterns of the three herds were very similar and others where they differed. To compute these correlation profiles we plotted the Pearson's product movement correlation

between the autocorrelation profiles of the three herds across the 20 time periods. This shows how the strength of similarity between autocorrelation profile changes through the seasons.

Comparison of rainfall profile with herd profile crosscorrelation

We wanted to determine if the strength of similarity between autocorrelation profiles among herds was related to patterns of rainfall. We computed a rainfall profile by averaging the total precipitation record at the three weather stations in the study area over 30-day periods coinciding with the time windows used in the movement analysis. We were interested in determining if the pattern of autocorrelation of each herd was correlated with the pattern of rainfall. To do this we computed the crosscorrelation between the Mantel correlogram profiles with the rain profile. We also were interested in seeing if there was a time lag in the relationship between elephant autocorrelation and rainfall, as many things that are related to rainfall, including the filling of water holes and vegetation green-up, can lag rain events by some time. Accordingly we calculated the crosscorrelation between rainfall profile and the Mantel correlogram profiles at lags between zero and 60 days at 15 day intervals. This analysis produced surfaces showing the crosscorrelation between rainfall and the autocorrelation of elephant movements at various lag distances. The surfaces allow us to determine the strength and the lag in the relationship between rainfall amount and the strength of autocorrelation in elephant movements for each of the three herds.

Results

Mantel correlogram analysis

The moving-window Mantel correlogram surfaces derived for the three elephant herds show strikingly complex, long-term and seasonally variable patterns of autocorrelation (Fig. 1). For example, herd 56 shows a gradient-like pattern of autocorrelation in time period two, associated with a prolonged period of direction movement (Fig. 1, 2). In contrast, in time period 10, herd 56 exhibits a rapid drop in autocorrelation over five days to random use of a temporary home range (Fig. 1, 3). In period 14 this herd exhibits a strongly periodic pattern of autocorrelation, with period of approximately 15 days (Fig. 1, 4). In period 20 the herd exhibits a more complex pattern of movement which combines directional and periodic movement (Fig. 1, 5). As the autocorrelation surfaces for the other two herds are very similar to that of herd 56 and are highly correlated they are omitted here to save space (Fig. 6).

Comparison of correlograms and movement trajectories

The moving window Mantel correlogram surfaces show that autocorrelation of elephant movements in northern Botswana is highly variable in temporal range and pattern (Fig. 1). The autocorrelation surfaces exhibit all of the major types of correlogram structure (Legendre and Fortin 1989), including gradients that do not indicate decreasing autocorrelation with increasing time (Fig. 2), periodic patterns of regularly spaced peaks of positive and negative autocorrelation (Fig. 4), and random use of temporary home ranges with a characteristic time to independence of subsequent locations (Fig. 3), as well as a number of more complex transitional autocorrelation patterns (Fig. 5).

Surface correlation and profile crosscorrelation

The surface correlation analysis showed very strong similarities among the three herds in the structure of their autocorrelation surfaces across the entire year. The average Pearson's correlation between the surfaces for the three pairs of elephant herds was 0.736, compared to an average of 0.016 for the randomized analyses (Fig. 6). This indicates that there is great overall similarity between the three herds in terms of autocorrelation pattern across the year and across time lags of up to 30 days, and significantly more than would be expected by chance. This pattern of high correlation among herds in their autocorrelation profiles generally held when we considered individual time periods. However, in four periods there appeared to be a drop in the correlation of autocorrelation profiles among herds. These drops occurred in time periods 4, 8–9, 14, 18–19 (Fig. 7).

Comparison of rainfall profile with herd profile crosscorrelation

We were interested in determining the causes of the drops in profile crosscorrelation during these four time periods. We investigated this by comparing the herd profile crosscorrelation with the rainfall profile. We found that the four periods of decreased herd profile crosscorrelation matched important changes in the rainfall pattern. For example, period 4 corresponds to the onset of rain at the beginning of the rainy season (Fig. 8). A decrease in crosscorrelation is expected here as the onset of rainfall was probably spatially heterogeneous and likely impacted the herds differently, with some being located in areas receiving the early rains and others perhaps on the edge or beyond the rain receiving area. Time period 8–9 corresponds to a temporary cessation of the rains, and is four weeks after the first

major peak in rainfall. Similarly, time period 14 corresponds to another temporary cessation of the rains and is three weeks after the second major rainfall peak. Again, time period 18 corresponds to the end of the rainy season, and is three weeks after the third and final peak in rainfall. This implies that the similarity of movement patterns among the herds decreases following pulses of rainfall.

Crosscorrelation of rainfall profile with mantel correlogram profiles

The crosscorrelation of rainfall and the Mantel correlogram surfaces indicates a strong relationship between rainfall and the strength of movement auto-

correlation (Fig. 9). The crosscorrelation surface shows the strength of association between the autocorrelation of elephant movements and rainfall across a range of time lags for herd 56. Herd 55 and 57 show a similar pattern, with a strong negative relationship between rainfall and movement autocorrelation up to a Mantel lag of 15 days. Beyond 15 days the relationship becomes positive (Fig. 9). This pattern of strong negative correlation between autocorrelation and rainfall holds for all crosscorrelation lags up to 50 days, peaking at a crosscorrelation lag of around 20 days. This indicates that there is a lag in the response of movement autocorrelation to rainfall, but that this lag effect is not abrupt, with influences beginning immediately after rainfall and extending for at least 50 days.
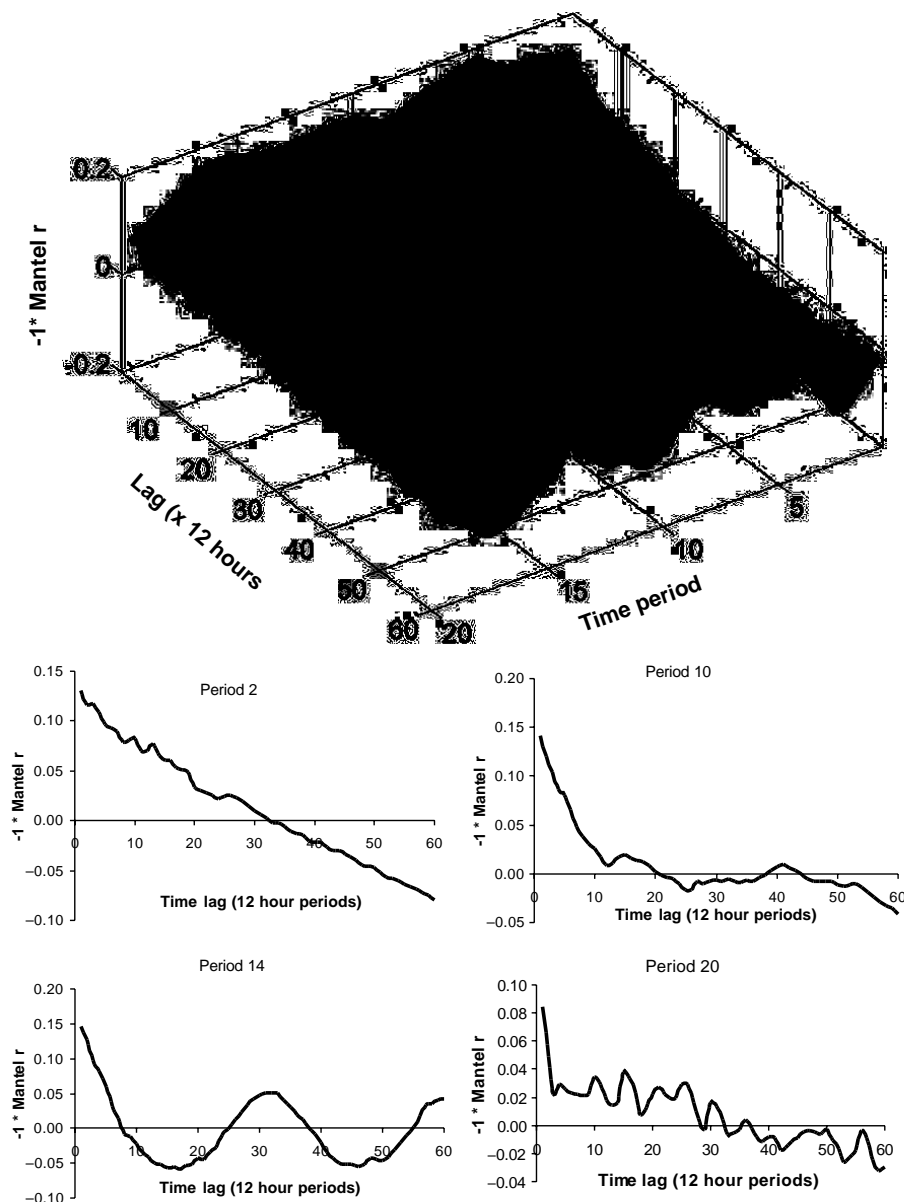

Fig. 1. Mantel correlogram surface for elephant herd 56. Time period refers to the sequential temporal window of analysis. The periods are 60 days in length, overlap with a start and 15 days apart. The first time period begins on August 12, 1999; the last period ends 345 days later on July 23, 2000. For each time period we computed the Mantel correlation between distance in time and distance in space for time lags running from 12 hours to 30 days between locations, at 12 hour intervals. The dashed contour indicates the isocline of zero autocorrelation. The two dark contours mark the upper and lower bounds of statistical significance. Surface area above the upper contour is significantly positively autocorrelated; the surface area below the lower contour is significantly negatively autocorrelated, after Bonferroni correction. The surface indicates that the movements of herd 56 showed longterm, complex and seasonally variable patterns of autocorrelation. The graphs at the bottom of the figure are correelograms from periods 2, 10, 15 and 20, exhibiting long range directional movement (period 2), cyclical use of focal areas (period 14), random use of a temporary home range (period 10) and transitional patterns (period 20).
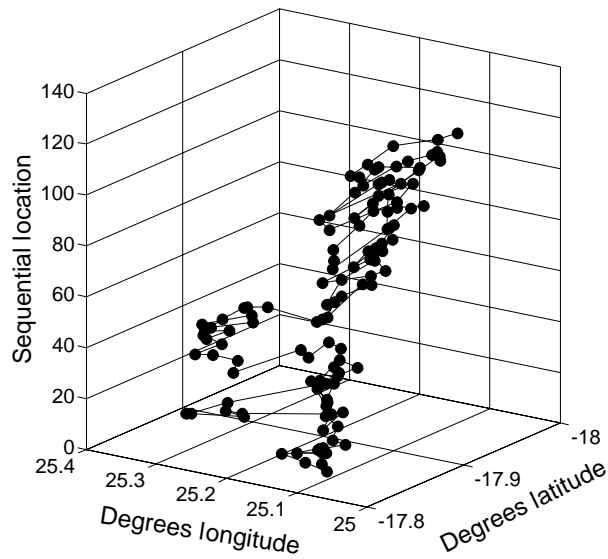
Fig. 2. Movement trajectory for herd 56 in time period 2. Colored circles are locations estimated from Argos telemetry. The color range indicates sequence of locations in time. The first location is dark blue; the last location is dark red. The blue line connects consecutive locations. The vertical axis also indicates time and is included to facilitate interpretation of the patterns of location points. The trajectory of herd 56 in time period 2 exhibits a pattern of divergence from the initial location progressively through time. The longer apart the locations are in time the farther apart they tend to be in space, leading to the gradient-shaped correlogram for time period 2 in Fig. 1.
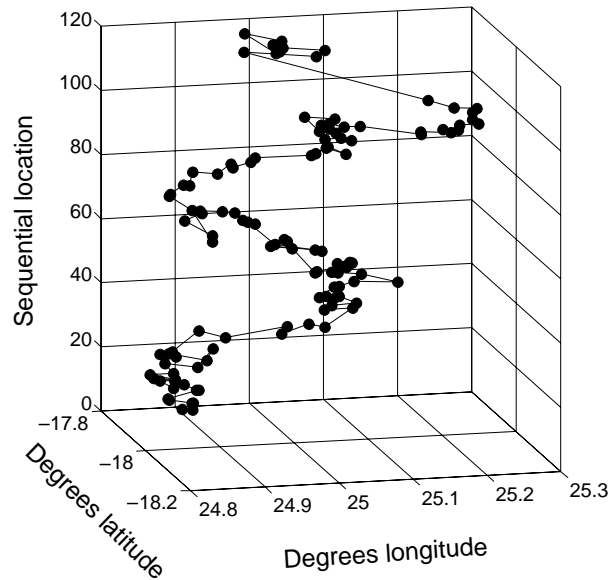

Fig. 4. Movement trajectory for herd 56 in time period 14. The trajectory of herd 56 in time period 14 exhibits a strong pattern periodic use of focal areas on a period of approximately 15 days. The distance locations are apart in space is related to their distance in time, with the herd cycling between focal areas at an approximately two week period, leading to the periodic correlogram for time period 14 in Fig. 1.
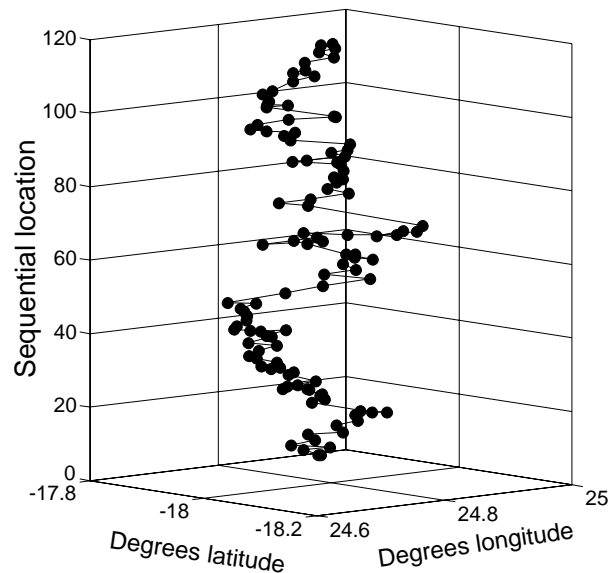

Fig. 3. Movement trajectory for herd 56 in time period 10. The trajectory of herd 56 in time period 10 exhibits a pattern of short-term autocorrelation up to a period of 5 days followed by random use of a temporary home range. After the initial drop in autocorrelation, there is no relationship between distance apart in space and distance apart in time, leading to the flat correlogram for time period 10 in Fig. 1.
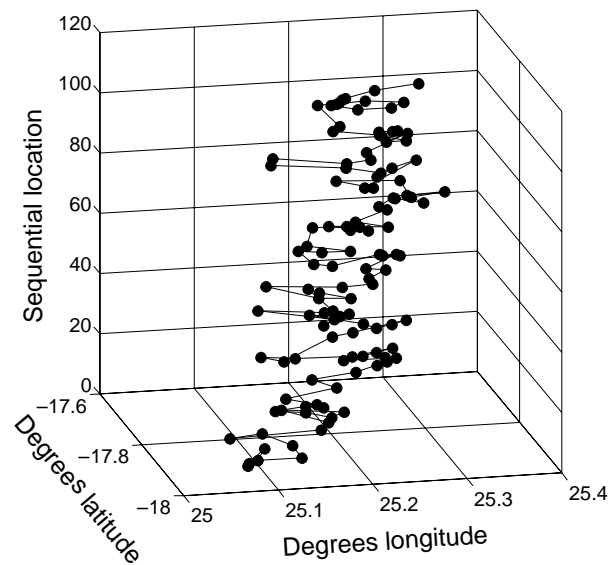

Fig. 5. Movement trajectory for herd 56 in time period 20. The trajectory of herd 56 in time period 20 exhibits a somewhat more complex pattern of movement which includes a rapid initial drop in autocorrelation, followed by a directional trend which contains an internal pattern of periodicity at periods of about 5 and 8 days. In the trajectory, the trend in movement is seen as a drift of the points toward the right as you move up the vertical temporal axis. The periodic pattern is seen in the horizontal pattern of movement back and forth at a period of approximately 5 and 8 days.
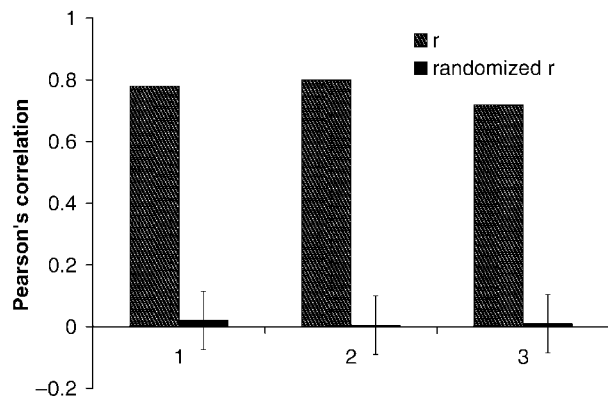
Fig. 6. Correlation of autocorrelation surfaces among herds. The correlations among pairs of hers were much higher than any derived in the randomization test, indicating that the three herds were much more similar to each other than would be expected by chance in the structure of autocorrelation across the year for time lags of up to 30 days.

Discussion

Autocorrelation in animal movements can be both a serious nuisance to analysis and a source of valuable information about the scales and patterns of animal use of space. Traditionally, wildlife researchers utilizing telemetry have sought to remove autocorrelation from their analyses (Swihart and Slade 1985, Alldredge and Ratti 1986, Thomas and Taylor 1990) in order to meet the assumptions of numerous statistical tests which assume independence of observations (Neu et al. 1974). This effort typically involves calculating the autocorrelation among successive locations in time until the spatial dependence among them drops to near zero. Then the researchers typically subsample the data, selecting observations that are at least as far apart in time as the calculated time to independence. This approach has some important limitations. First, it is only applicable to
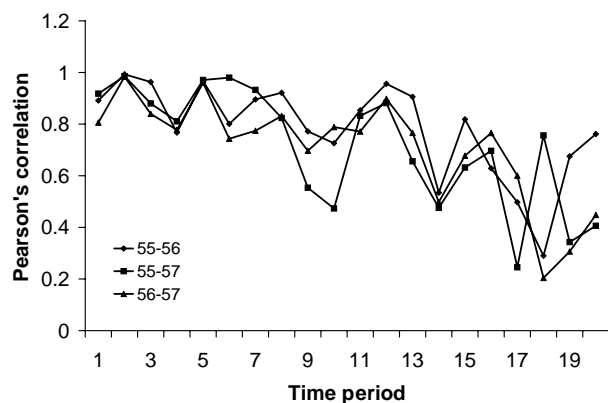

Fig. 7. Correlation of autocorrelation profiles among herds across the 20 time periods of the analysis. The figure shows generally very high correlation at all periods, with drops in the similarity of autocorrelation patterns among herds in time periods 4, 8–9, 14, and 18–19.
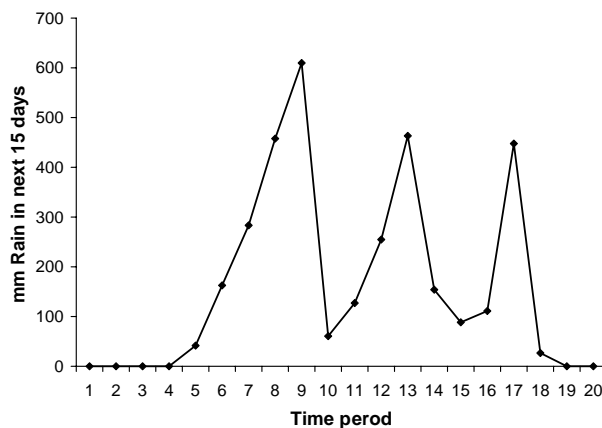

Fig. 8. Total bi-weekly rainfall as an average from the three weather stations in our study area.

organisms that randomly utilize a fixed home range. Organisms that do not have a fixed home range and exhibit a random walk or a correlated random walk will exhibit significant autocorrelation among locations for all time lags, and organisms that non-randomly use portions of a fixed home range will also show significant spatial autocorrelation at long time lags (Cushman et al., unpubl.). Second, the autocorrelation profiles of many organisms may be non-stationary across seasons. This non-stationarity is a serious violation of autocorrelation analyses and is not solved by subsampling the data to the resolution of time to independence. We believe the random utilization of a fixed home range may be a rare occurrence in nature, that non-stationarity is common, and subsampling more complex behavioral patterns to fit into a random utilization of a fixed home range model at the very least ignores interesting information about the details of animal use of space, and may often be misleading.

Alternatively, we believe valuable information about animal space and resource utilization can be gained by explicitly considering the patterns of movement auto-correlation themselves. Instead of treating autocorrelation as a nuisance to be removed, for many questions it would be more profitable to treat it as a biological signal to be analyzed and interpreted (Legendre and Fortin 1989, Legendre 1993). Furthermore, instead of treating non-stationarity as a crippling assumption, we advocate explicitly quantifying the changes in the autocorrelation profiles through time and across seasons. By computing correlograms within a sliding temporal window of appropriate length, researchers can determine the details of how the patterns of movement autocorrelation change through time, in response to changes in the seasons, the occurrence of environmental perturbations, or changes in social interactions. In combination, the ability to explicitly account for nonrandom, spatially complex, long term patterns of spatial autocorrelation that change through time and across seasons is of great importance

Fig. 9. Crosscorrelation surface between the autocorrelation of herd 56 and total bi-weekly rainfall. The black contour is the isocline of zero crosscorrelation. The crosscorrelation surface shows a strong relationship between rainfall amount and the strength of movement autocorrelation, peaking at a crosscorrelation lag of around 15 days. The crosscorrelation surface indicates that heavy rains lead to a decrease in short term autocorrelation and an increase in long term autocorrelation, indicating a trend toward more random movements following large rain events. The crosscorrelation surfaces for the other herds are very similar and are omitted to save space.
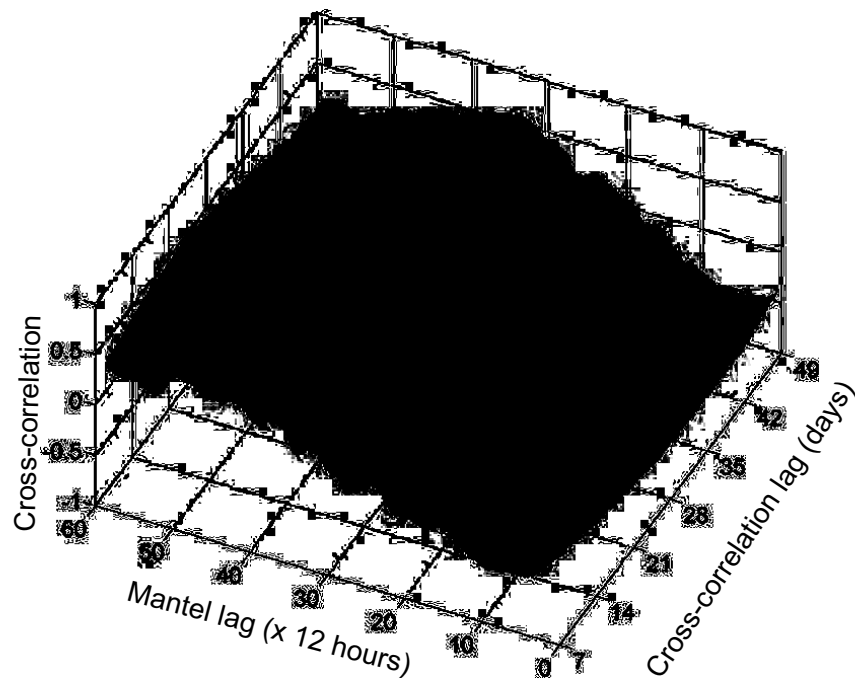
and will enable wildlife researchers to address much more realistic and sophisticated questions about the relationships between time, season, space, resources, social interactions and animal movement patterns.

In this paper we analyzed autocorrelation patterns in elephant movements. The analysis provides a detailed picture of seasonal variability in the scale and patterns of movement of three herds of elephants in northern Botswana. Patterns of autocorrelation of elephant movements were long range, temporally complicated, seasonally variable and closely linked with the onset of rainfall events. Specifically, for the three elephant herds monitored there was often significant autocorrelation among locations up to lags of 30 days or more. During many seasonal periods there was no indication of decreasing autocorrelation with increasing time between locations. Over the course of the year, herds showed highly variable and complex patterns of autocorrelation, ranging from random use of temporary home ranges, periodic use of focal areas, and directional migration. Over the course of the year all three herds exhibited all major types of autocorrelation pattern (Legendre and Fortin 1989) as well as many transitional and complex autocorrelation profiles. Thus, for elephants in northern Botswana the question of time to statistical independence of subsequent locations is inappropriate. There is often no meaningful time to independence of elephant locations in northern Botswana. Furthermore, given the striking non-stationarity of autocorrelation patterns across the year, it would be totally inappropriate to analyze the entire data set simultaneously across its full temporal span. Given the strong seasonally related patterns of

non-stationarity, we believe it is essential to analyze autocorrelation continuously across the temporal span of the data using a moving temporal window. This allowed us explicitly to quantify the changes in the autocorrelation profiles through time, and allowed us to describe the temporally complicated, long term and non-stationary patterns of movement autocorrelation and associate them with important environmental changes in the landscape, such as major rainfall events.

Even though the patterns of autocorrelation were variable in time and quite complex, there were highly significant correlations among the autocorrelation patterns of the different herds, indicating that they exhibited synchronous patterns of movement through the year. These major patterns of autocorrelation seem to be related to patterns of rainfall. The strength of correlation in movement patterns of the different herds decreased markedly at the onset of major rain events. There could be several biological explanations for this observation. First, it could reflect the spatial heterogeneity of the rainfall events. If the rain events were patchy and differently affected the areas the three herds were residing, then one could expect the herds to respond in different ways, leading to a breakdown of the similarity of their movement patterns. Alternatively, heavy rain leading to abundance of water and forage may release the elephants from restrictive behavior patterns and allow them more flexibility in their movements, which would also lead to decreases in the correlation among the herds.

We found strong crosscorrelation between strength of autocorrelation of movement and rainfall, peaking

at time lags of between 15 and 30 days. The inverse relationship between rainfall and movement autocorrelation indicates a change in elephant behavior following major rain events, such that movements become less autocorrelated. This indicates a release from restrictive behavior patterns driven by water or forage limitations to more random use of space in which water and forage are abundant and widespread. The crosscorrelation analysis, which shows that large rainfall events trigger movements that are less autocorrelated, suggests that rainfall pulses result in elephant herds moving more randomly, with less pronounced patterns of autocorrelation and lower similarity among herds in autocorrelation profiles.

Overall, these approaches provide a powerful way to explore the scales and patterns of autocorrelation of animal movements, and to explicitly link those patterns to temporally variable environmental attributes, such as rainfall or vegetation phenology. The emergence of new technology such as GPS and Argos telemetry systems have made it possible for ecologists to gather continuous streams of data on animal locations and movements at fine temporal resolutions. These kinds of data contain a wealth of information about the rates and patterns of organism movement, and its relationships with multiple scales of environmental factors, seasonality and social interactions. These kinds of data are also inherently highly autocorrelated. To realize the potential such movement trajectories offer it is essential for scientists to address autocorrelation explicitly within their analytical frameworks. Doing so not only will allow researchers to utilize movement trajectories to analyze and interpret the relationships between organism behavior and the spatial structure of the environment, but patterns of autocorrelation themselves can offer insight to a variety of questions. For example, the shape of the correlograms offers direct insight into the type of periodic, directional or random movements which are occurring in that time period. These different kinds of movements in turn indicate differences in organism behavior which can be further examined to explore linkages with causal mechanisms, such as resource availability or social interactions. In addition, how these patterns of autocorrelation change over time, or across seasons, offers insight into how organisms interact with their changing environments.

The analysis presented here illustrates that the traditional focus on time to independence is an inappropriate question for elephants in northern Botswana, and may be inappropriate for many other organisms as well. This analysis, rather, shows that elephant movements exhibit strong, complex and long term patterns of autocorrelation that are non-stationary and seasonally variable. Our approach, which combines explicit attention to the structure of the autocorrelograms and moving temporal windows to account for non-stationarity, provides a comprehensive picture of the scales and patterns of autocorrelation. The picture is a complex one. It reflects the complexity elephant behavior and its relationships to changing seasonal conditions and particularly major rainfall events.

Our analysis could be extended by considering the spatial details of movements, such as where the animals were at particular time periods in relation to water sources or vegetation resources, or the spatial characteristics of their movement paths. By combining analyses of autocorrelation with habitat resource associations and analysis of the spatial characteristics of movement paths it would be possible to achieve a more complete picture of the factors that drive elephant movements in northern Botswana. Nonetheless, our analysis provides some useful information about the movement ecology of elephants. In particular, autocorrelation of elephant movements are long-range, temporally complicated, seasonally variable, and closely linked with rainfall events. There is no time to independence of elephant locations and given the non-stationarity of autocorrelation patterns, it is essential to use multi-temporal moving window based analyses. We feel that paying explicit attention to the details of autocorrelation patterns and how they change through time will pay large dividends in terms of increased understanding of animal movements and the ecological patterns and processes that drive them.

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