INFLUENCE OF SAMPLING INTERVAL ON ESTIMATES OF HOME-RANGE SIZE

ROBERT K. SWIHART, Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045
NORMAN A. SLADE, Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045

Abstract: Accurate estimation of home-range size often requires large numbers of observations. Radiotelemetry and direct observation are capable of yielding large sample sizes in a short period of time, but observations collected using a short sampling interval often are autocorrelated (i.e., not independent). We examined the effect of autocorrelation on six measures of home range and found that positive autocorrelation resulted in underestimation of home-range size. In long-term studies of movement, sampling intervals should be chosen so that autocorrelation between successive observations is negligible. If home-range estimates must be obtained in a relatively short period of time, collection of autocorrelated data may be unavoidable; under these circumstances nonstatistical measures of home-range size are more appropriate than statistical measures.

J. WILDL. MANAGE. 49(4):1019–1025

Accurate estimation of size of home range is an important prerequisite to a better understanding of a species' behavioral ecology and management (Sanderson 1966, Bekoff and Mech 1984). Not surprisingly, accuracy of many home-range estimates is closely linked to sample size (Stickel 1954, Jennrich and Turner 1969, Schoener 1981, Bekoff and Mech 1984). The method used to collect movement data also influences home-range estimates (Hackett and Trevor-Deutsch 1982, Jones and Sherman 1983), with direct observation and radiotelemetry generally acknowledged as being superior to conventional livetrapping (Adams and Davis 1967, Hackett and Trevor-Deutsch 1982).

With the advent of a statistical concept of home range that depicted an organism's use of space as a bivariate probability distribution (e.g., Calhoun and Casby 1958, Van Winkle 1975, Anderson 1982, Don and Rennolls 1983), sampling interval emerged as a potentially important element affecting home-range estimation. As pointed out by Dunn and Gipson (1977), all probabilistic models of home range assume that locational observations are independent of one another, i.e., an animal's current position is not influenced by its position during past observations. But short time intervals between successive observations undoubtedly lead to a lack of independence (autocorrelation), at least between successive points (Tester and Siniff 1965, Dunn and Gipson 1977). Although short sampling intervals are common when movements are recorded via direct observation or radiotelemetry (e.g., Tester and Siniff 1965, Reeve 1982, Harrison 1983), we are not aware of studies that have examined the effect these autocorrelated data might have on statistical estimates of home range.

Despite the recent profusion of probabilistic models of home range (see above), nonstatistical techniques of estimating home range (e.g., minimum convex polygon) are frequently used (Bekoff and Mech 1984). In addition, home-range indices are often calculated (Metzgar 1979, Gaines and Johnson 1982, Slade and Swihart 1983). Because nonstatistical models and home-range indices do not explicitly involve the assumption of independence, they might be expected to display less sensitivity when used in conjunction with autocorrelated data. Nevertheless, some of these measures (e.g., polygon measures, observed range length) are sensitive to the number of nonredundant (i.e., independent) observations used. Because dependent data by definition contain redundant information, N autocorrelated observations will yield less information on home-range use than N independent points. Thus, autocorrelated observations may indeed produce biased estimates for certain indices and nonstatistical measures of home range.

In this paper we examine the effect of autocorrelated observations (and by implication sampling interval) on home-range size as estimated by three home-range models (bivariate normal, Koeppl et al. 1975; minimum convex polygon and minimum polygon, Jennrich and

Turner 1969) and three home-range indices (observed range length, Stickel 1954; distance between successive observations, Davis et al. 1948; and mean squared distance from the center of activity, Calhoun and Casby 1958, Slade and Swihart 1983).

We thank S. C. Hillmer and J. R. Sauer for statistical help and D. H. Johnson for providing us with the impetus to explore the effects of autocorrelation on nonstatistical measures of home range. R. A. Dolbeer, R. S. Hoffmann, and M. L. Johnson provided constructive criticism of the manuscript. Funding for this project was provided by Univ. of Kansas Gen. Res. Grant 3509-0038 to N. A. Slade and a Univ. Honors Fellowship to R. K. Swihart. Computer resources were provided by the Univ. of Kansas Acad. Comput. Cent.

METHODS

Bivariate Autocorrelation

Although univariate measures of autocorrelation are readily available (Box and Jenkins 1976:26–29), selecting an appropriate scalar representation of bivariate autocorrelation is more difficult because first-order cross correlations ($\rho_{x_t y_{t-1}}$, $\rho_{x_{t-1} y_t}$) must be considered in addition to first-order autocorrelations ($\rho_{x_t x_{t-1}}$, $\rho_{y_t y_{t-1}}$) (Box and Jenkins 1976:370–375). To our knowledge, Schoener (1981) has developed the only scalar bivariate measure of autocorrelation to be applied to ecological data, but his measure dealt only with $\rho_{x_t x_{t-1}}$ and $\rho_{y_t y_{t-1}}$ and not with cross correlations. Our simulations indicated that cross correlations were important in determining the shape of the observed home range as well as the distribution of activity within the home range; hence, Schoener's (1981) measure was incomplete for our purposes. We defined our bivariate measure of autocorrelation, which includes terms for both autocorrelations and cross correlations, as

$$\psi = \rho_{x_t x_{t-1}} + \rho_{y_t y_{t-1}} + |\rho_{x_t y_{t-1}}| + |\rho_{x_{t-1} y_t}|.$$

Reasons for choosing this measure are discussed in the Appendix.

Simulation Procedures

Monte Carlo techniques were used to generate N locational observations within bounded home ranges. A circular home range with a radius of three units was used for the bivariate normal model, whereas all other measures were calculated within a square home range with sides four units in length. For each sample of N points, home-range estimates and the sample autocorrelation, $\hat{\psi}$, were calculated. Autocorrelated observations were generated using the expressions $X_i = X_{i-1} + \epsilon_x$ and $Y_i = Y_{i-1} + \epsilon_y$, where X_i and Y_i represent Cartesian location coordinates at time i, X_{i-1} and Y_{i-1} denote the location during the previous observation, and ϵ_x and ϵ_y are random error terms (Appendix). Different values of $\hat{\psi}$ were obtained by varying the variances of ϵ_x and ϵ_y (Appendix); small variances produced large values of $\hat{\psi}$, whereas variances 5–10 times greater in magnitude than the maximum length of the home range yielded N essentially independent points (i.e., $\hat{\psi} \cong 0$). We focused on $\hat{\psi}$ values ranging from approximately 0–4 because we doubted the frequency with which large negative $\hat{\psi}$ values occurred in nature (Appendix). Relationships between $\hat{\psi}$ and the six home-range measures were examined for $N = 10$, 30, 50, and 100. Bekoff and Mech (1984) concluded that between 100–200 (independent) observations were necessary to estimate home-range area reliably via the minimum convex polygon method. Thus, we also simulated home ranges of $N = 200$ for the two nonstatistical models of home range. For the three home-range models, $\hat{\psi}$ was calculated for 300 home ranges at each N, whereas 500 home ranges each consisting of N points were generated for use with the three home-range indices.

Random error terms for the Cartesian location coordinates were normally distributed with means of zero for the bivariate normal model. Error terms for all other measures of home range were uniformly distributed with means of zero (Appendix). Pearson product-moment correlations were used to quantify relationships between $\hat{\psi}$ and the home-range measures. All tests of significance were one-tailed.

RESULTS

Autocorrelated observations markedly affected both the observed movement path and the proportion of the home range covered by N points (Fig. 1). Large positive autocorrelations produced especially dramatic reductions in movements (Fig. 1A); such large values of $\hat{\psi}$ could only be attained by using an extremely short sampling interval over a time frame much less than the time necessary for an animal to move throughout its home range. Various techniques exist for estimating the length of tracking (or observation) time necessary to estimate an animal's home range (Cooper 1978, Birks and Linn 1982). Because at least rough approximations of such times are known for many wildlife species, we doubted that data characterized by large autocorrelations would commonly be used in home-range studies. Consequently, all data sets were trimmed so they included only samples with low or intermediate levels of autocorrelation (i.e., $\hat{\psi} < 1.5$).

The area contained in a 95% confidence ellipse computed from the bivariate normal model was inversely correlated with $\hat{\psi}$ for all sample sizes, although the correlation was fairly small for $N = 10$ (Table 1). Because of the fixed boundaries of the home range and the method necessary to generate autocorrelated observations (Appendix), activity distributions for the model of bivariate normality were decidedly nonnormal. However, by restricting the analysis to a small range of $\hat{\psi}$ values, we succeeded in generating distributions that were comparable to each other, albeit nonnormal. Hence, we believe that the inverse relationships between $\hat{\psi}$ and the confidence ellipses are real.

For both the minimum polygon and minimum convex polygon models, estimates of home-range size from autocorrelated data were smaller than corresponding estimates calculated with independent observations (Table 1). This inverse relationship held for all sample sizes and increased with increasing N (Table 1). $\hat{\psi}$ was consistently more negatively correlated with estimates from the minimum polygon than with those from the minimum convex polygon (Table 1).

The three home-range indices were also inversely correlated with $\hat{\psi}$ (Table 1). As suggested in Fig. 1, this relationship was most pronounced for distance between successive observations (Table 1). Further, the negative correlation with $\hat{\psi}$ was strengthened as N increased for distance between successive observations and mean squared distance from the center of activity but not for observed range length (Table 1).

Two related problems may be associated with estimates of home-range size derived from autocorrelated data. As summarized in Table 1, autocorrelation results in underestimation of home-range size. In addition, if home-range measures are sensitive to sample size, the use of autocorrelated observations may encourage a spurious impression of accuracy by producing misleadingly large sample sizes. To determine which of the six home-range measures were sensitive to sample size, we compared estimates

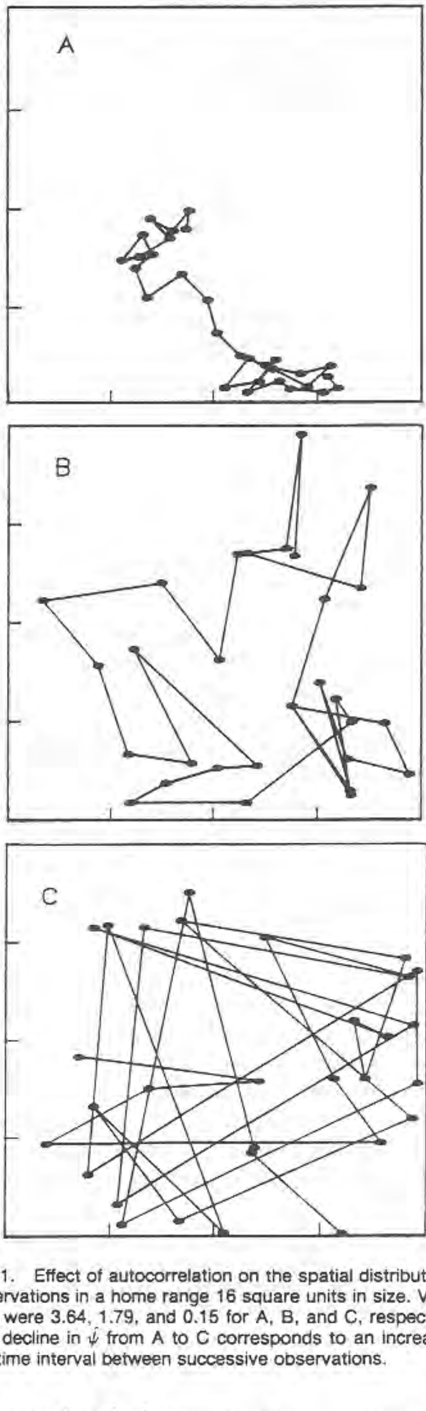

Fig. 1. Effect of autocorrelation on the spatial distribution of observations in a home range 16 square units in size. Values of $\hat{\psi}$ were 3.64, 1.79, and 0.15 for A, B, and C, respectively. The decline in $\hat{\psi}$ from A to C corresponds to an increase in the time interval between successive observations.

Table 1. Correlations (*r*) between bivariate autocorrelation and six measures of home-range size: (1) area contained in the 95% confidence ellipse for the bivariate normal; (2) area contained in the minimum polygon; (3) area contained in the convex polygon; (4) distance between successive observations (DS); (5) mean squared distance from the center of activity (MSD); and (6) observed range length (ORL). *N* represents the number of locational observations used in calculating the home-range measures, whereas *M* represents the number of samples of size *N* used in a correlation analysis.

Home-range measure	N = 10		30		50		100		200	
	r	*M*	*r*	*M*	*r*	*M*	*r*	*M*	*r*	*M*
Bivariate normal	−0.19*	204	−0.42**	169	−0.36**	187	−0.57**	180		
Minimum polygon	−0.16*	174	−0.34**	164	−0.33**	145	−0.55**	115	−0.71**	142
Convex polygon	−0.15*	174	−0.31**	164	−0.31**	145	−0.45**	115	−0.45**	142
DS	−0.44**	302	−0.80**	335	−0.88**	292	−0.96**	125		
MSD	−0.18**	302	−0.41**	335	−0.52**	292	−0.76**	125		
ORL	−0.21**	302	−0.31**	335	−0.38**	292	−0.33**	125		

* $P < 0.05$; ** $P < 0.001$.

calculated from independent observations for different values of N. For all measures, the degree of bias was estimated as 1 minus the ratio of the mean observed value to the true (or expected) value. A ratio of zero characterized an unbiased estimate, whereas values greater than zero indicated the proportion by which the observed value underestimated the true value. The true value for the polygon measures was 16, the area of the home range, and the true observed range length was 5.66, the length of the diagonal of the home range. The area contained in a 95% confidence ellipse for the bivariate normal was calculated as $(2\pi \times F_{2,N-2})(N - 1)/(N - 2)$ (Koeppl et al. 1975). Madden and Marcus (1978) noted that if the parametric center of activity were known, the bivariate normal estimate would not depend on N. The expected value for mean squared distance was derived analytically, and numerical integration was used to obtain the expected value for distance between successive observations.

Sample size influenced all of the measures except distance between successive observations and mean squared distance from the center of activity (Table 2). Independence of the latter index from N was not surprising, because it can be shown that the expectation of the mean squared distance from the center of activity depends only on the means and variances of the Cartesian coordinates (cf. Schoener 1981). For small sample sizes, the home-range indices and the bivariate normal came closer to estimating their true values than did the polygon models, and the minimum polygon performed poorly at all sample sizes (Table 2).

DISCUSSION

As sampling intervals become shorter (or, equivalently, autocorrelation increases), successive observations for an individual grow closer together until at the shortest interval possible (i.e., continuous sampling) successive locations are, on average, barely discernible from one another. Distance between successive observations declined as autocorrelation increased (Fig. 1, Table 1). If movement data are autocorrelated, distance between successive observations is not a valid index of home-range size (but see Reeve 1982). Rather, this measure becomes an

Table 2. Sensitivities of six home-range measures to sample size. Abbreviations for the home-range measures follow those used in Table 1. *N* represents the number of independent observations used in the calculations. One hundred samples of size *N* were used in calculating the mean area via the bivariate normal, whereas 50 samples of size *N* were used in calculating mean values for each of the remaining home-range measures.

N	Bivariate normal		Minimum polygon		Convex polygon		DS		MSD		ORL	
	Area	Bias	Area	Bias	Area	Bias	Distance	Bias	(Distance)^2	Bias	Distance	Bias
10	35.6	0.17	5.1	0.68	6.6	0.59	2.07	0.02	2.70	0.00	4.10	0.28
30	25.6	0.07	6.5	0.59	11.0	0.31	2.09	0.00	2.70	0.00	4.72	0.17
50	23.8	0.07	6.8	0.58	12.7	0.21	2.08	0.01	2.67	0.00	4.95	0.12
100	22.9	0.06	7.0	0.56	13.9	0.13	2.10	0.00	2.67	0.00	5.12	0.10
200	22.4	0.06	7.1	0.56	14.7	0.08	2.09	0.00	2.66	0.00	5.30	0.06

index of rate of use of the home range when autocorrelation is present. Unfortunately, equivalent levels of autocorrelation are required before values of the rate index can be compared among members of a population. Swihart and Slade (1985) developed an alternative measure of the rate of home-range use. We used Schoener's (1981) bivariate measure of autocorrelation in developing a test to determine the sampling interval at which autocorrelation (as defined in Schoener 1981) became nonsignificant. This "time to independence" is inversely proportional to the rate of home-range use.

For all three home-range models as well as observed range length, increasingly accurate estimates were obtained by increasing N (Table 2). However, if observations are collected using a sampling interval shorter than the interval necessary to obtain independent observations, the effective sample size will be smaller than the number of observations collected. Biologists need to understand the implications of using autocorrelated data when estimating measures of home range, because merely increasing N by shortening the sampling interval may not lead to more accurate estimates (Table 2). Even if accuracy is increased by collecting N autocorrelated observations, the increase will invariably be less than that achieved by using N independent points.

Short sampling intervals are essential in studies of activity budgets, foraging ecology, and temporal patterning of home-range use (see Getty 1981*a*,*b*, Krapu et al. 1984). If home-range measures are desired in these types of studies, the following guidelines may be helpful. Our results indicate that over a specified time frame nonstatistical estimates and indices (polygon measures, observed range length) become increasingly accurate as N increases, even when autocorrelation increases. The opposite is true if distance between successive observations or mean squared distance from the center of activity is used (Tables 1, 2). If the bivariate normal model of Koeppl et al. (1975) is used with N autocorrelated points, home-range size will be underestimated because the sample standard deviations of X and Y will be smaller than the standard deviations calculated for independent points collected over the same time frame. However, autocorrelated data may be used with home-range measures that are sensitive to autocorrelation, because it is possible to objectively select a subset of the data that are not significantly autocorrelated (Swihart and Slade 1985). Models such as the bivariate normal or distance between successive observations may then be used with this subset of data.

IMPLICATIONS

When estimating home-range size, the time frame over which the study is conducted plays a pivotal role in selection of an appropriate sampling interval. In studies characterized by long time frames and unlimited manpower, estimation of home-range size does not pose a serious problem, even when the sampling interval is short. If statistical models are used, an independent subset of points can be selected for analysis (Swihart and Slade 1985). And if nonstatistical techniques are preferred, the long time frame of the study ensures that sample size will be sufficiently large to yield accurate estimates despite the autocorrelated nature of the observations. In reality, though, home-range studies usually are conducted under constraints on time, manpower, or both. For example, a wildlife biologist may be able to monitor animal movements over a period of several months, but only 1 or 2 man-hours/day can be spent on the project. In this situation we advocate collection of one or two locational observations every 24 hours for each animal, resulting in statistically valid samples for many individuals. Any of the six home-range measures could be used with this type of data. However, if the time frame of the study is restricted rather than the number of man-hours per day, we recommend shortening the sampling interval so that fewer individuals can be followed more intensively. With this type of data, only nonstatistical measures of home range are appropriate.

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Received 26 December 1984.
Accepted 14 March 1985.

APPENDIX

In the univariate case, a first-order autoregressive process may be expressed as $X_i = \rho_{x_i x_{i-1}} \times X_{i-1} + \epsilon_x$, where X_i and X_{i-1} are values of X at times i and $i - 1$, respectively, $\rho_{x_i x_{i-1}}$ is the first-order autocorrelation coefficient, and ϵ_x is a random error term. Extension of this process to the bivariate case yields

$$\begin{bmatrix} X_i \\ Y_i \end{bmatrix} = \begin{bmatrix} \rho_{x_i x_{i-1}} & \rho_{x_i y_{i-1}} \\ \rho_{x_{i-1} y_i} & \rho_{y_i y_{i-1}} \end{bmatrix} \begin{bmatrix} X_{i-1} \\ Y_{i-1} \end{bmatrix} + \begin{bmatrix} \epsilon_x \\ \epsilon_y \end{bmatrix}.$$

Notice that X_i is now a function of the first-order coefficient of cross correlation as well as $\rho_{x_i x_{i-1}}$ and ϵ_x. An analogous situation describes the second variable, Y_i. As described in the text, we used

$$\psi = \rho_{x_i x_{i-1}} + \rho_{y_i y_{i-1}} + |\rho_{x_i y_{i-1}}| + |\rho_{x_{i-1} y_i}|$$

as our bivariate measure of autocorrelation. Two observations drawn from our simulations influenced our choice of ψ. First, positive autocorrelations yield dramatically different home-range shapes and activity distributions as compared to negative autocorrelations; i.e., large positive autocorrelations produce a compact cluster of points (Fig. 1A), whereas large negative correlations cause successive observations to alternate from one edge of the home range to the other. Secondly, switching the signs of the cross correlations does not alter the shape of the observed home range or the distribution of activity; switching of signs only changes the orientation of the home range about the standard reference axes.

Perhaps the most obvious approach for generating autocorrelated observations consists of specifying distributions for ϵ_x and ϵ_y and selecting values between -1 and 1 for each element of the ACC matrix. Using this approach, ψ is known with $-\infty < X < \infty$ and $-\infty < Y < \infty$. However, if X and Y are bounded, the parametric value of ψ may not be obtainable from the ACC matrix. In addition, intermediate and high levels of autocorrelation may result in unrealistic movement paths when this approach is used with boundaries on X and Y; observations quickly "walk" to one edge of the home range and subsequent points remain close to the home-range boundaries.

Because of these problems, we opted for a more intuitive approach to generating autocorrelated observations. We assumed that as the sampling interval declined, the potential distance moved from the previous point also declined. Hence, changing $\mathrm{Var}(\epsilon_x)$ and $\mathrm{Var}(\epsilon_y)$ may be interpreted as changing the sampling interval. When $\mathrm{Var}(\epsilon_x)$ and $\mathrm{Var}(\epsilon_y)$ were small relative to the length and width of the home range, autocorrelation was high. Likewise, for large error variances, independence was closely approximated. When conducting our simulations, we set the ACC matrix equal to the identity matrix and used $\hat{\psi}$, calculated from sample auto and cross correlations, as our measure of bivariate autocorrelation. Cross correlations may be emphasized within this scheme by using an ACC matrix with nonzero off-diagonal elements instead of the identity matrix.

In generating observations with large values of $\hat{\psi}$, any choice of error variance sufficed if it were too small to generate points beyond the boundaries of the home range. We arbitrarily chose the largest of these error variances as the starting point for our simulations; specifically we used an iterative approach to select error variances that were capable of exceeding the home-range boundaries in 10–20% of the trials conducted. Subsequent reductions in $\hat{\psi}$ were achieved by increasing $\mathrm{Var}(\epsilon_x)$ and $\mathrm{Var}(\epsilon_y)$. Although error terms were generated using uniform or normal distributions, the combination of boundary conditions and autocorrelation ensured that distributions of activity differed from the joint distributions of ϵ_x and ϵ_y.