On Testing for Independence of Animal Movements

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On Testing for Independence of Animal Movements

Robert K. Swihart and Norman A. Slade

In a previous study, we showed that $n$ independent locational observations contain more spatial information than $n$ autocorrelated observations. We also developed a statistical test of the null hypothesis that successive observations are independent. Here, we expand our discussion of testing for independence by clarifying assumptions associated with the tests. Specifically, the tests are robust when used with data collected from utilization distributions that are not normal, but they are sensitive to nonstationary distributions induced by shifts in centers of activity or variance-covariance structure. We also used simulations to examine how negative bias in kernel and polygon estimators of home-range size is influenced by level of autocorrelation, sampling rate, sampling design, and study duration. Relative bias increased with increasing levels of autocorrelation and reduced sample sizes. Kernel (95%) estimates were less biased than minimum convex polygon estimates. The effect of autocorrelation is greatest when low levels of bias ($\geq -5\%$) are desired. For percent relative bias in the range of $-20\%$ to $-5\%$, though, collection of moderately autocorrelated data bears little cost in terms of additional loss of spatial information relative to an equal number of independent observations. Tests of independence, when used with stationary data, provide a useful measure of the rate of home-range use and a means of checking assumptions associated with analyses of habitat use. However, our results indicate that exclusive use of independent observations is unnecessary when estimating home-range size with kernel or polygon methods.

Key Words: Autocorrelation; Bias; Home range; Migration; Randomization; Stationary distribution; Statistical independence.

1. INTRODUCTION

Most methods of estimating home-range size are sensitive to the number of locational observations, $n$, collected for an animal (Bekoff and Mech 1984; Swihart and Slade 1985a; Ackerman, Leban, Samuel, and Garton 1990). The sensitivities of some estimators to $n$ are explicit in their formulation. For instance, $n$ occurs in the denominator of the variance estimator of the bivariate normal (Koop, Slade, and Hoffmann 1975). For other estimators, the sensitivity to $n$ is embedded within the properties of the estimator. For example, the minimum convex polygon may be thought of as a bivariate rank-
order statistic, with gradual addition of extreme values to the convex set occurring with increasing \( n \).

Previously, we pointed out that not all locational observations are equally valuable for purposes of home-range analysis (Swihart and Slade 1985a,b). Researchers collecting data via direct observation or radio telemetry can amass large numbers of locational records, with successive records separated by short time intervals. With short sampling intervals, the probability that the \( i \)th observation of an animal will occur at a point \((X_i, Y_i)\) depends in part on its previous location \((X_{i-1}, Y_{i-1})\). That is, these autocorrelated points contain redundant information. Put another way, \( n \) autocorrelated observations contain less information regarding the size of an animal’s home range than \( n \) independent observations. Simulations have confirmed the intuitive notion that home-range estimates derived from \( n \) autocorrelated observations exhibit negative bias as compared to estimates from \( n \) independent points (Swihart and Slade 1985a). Schoener (1981) devised a bivariate measure of autocorrelation, \( t^2/r^2 \), and we developed tests for independence and for the sampling interval needed to attain quasi-independence (Swihart and Slade 1985b, 1986), hereafter referred to as TTI.

Briefly, for a temporally ordered set of \( n \) bivariate locational records \((X_i, Y_i)\), \( t^2/r^2 \) is the ratio of the mean squared distance between successive observations \((t^2)\) and the mean squared distance from the center of activity \((r^2)\); that is,

\[
t^2 = \sum (X_{i+1} - X_i)^2/m + \sum (Y_{i+1} - Y_i)^2/m,
\]

and

\[
r^2 = \sum (X_i - \bar{X})^2/(n - 1) + \sum (Y_i - \bar{Y})^2/(n - 1),
\]

where \( m \) represents the number of pairs of successive observations (Schoener 1981). We used simulations to show that \( t^2/r^2 \) is approximately normally distributed with a mean of 2 and a sample standard deviation that can be accurately predicted from knowledge of \( m \) and the eccentricity of the home range [defined as \((\lambda_1/\lambda_2)^{1/2}\), where \( \lambda_1 \) and \( \lambda_2 \) are eigenvalues of the variance-covariance matrix of \( X \) and \( Y \); Swihart and Slade 1985b]. TTI is determined by calculating \( t^2/r^2 \) for records separated by a specified time lag and multiples thereof, yielding an autocorrelation function. We arbitrarily defined TTI as the smallest time lag exhibiting a nonsignificant \( t^2/r^2 \) ratio and followed consecutively by \( \geq 2 \) additional nonsignificant ratios (Swihart and Slade 1985b).

Although earlier work had addressed (Dunn and Gipson 1977) or mentioned (Anderson 1982) independence of locational data, the development of statistical tests of independence apparently spawned a heightened awareness of its potential importance when examining home-range size (Worton 1987, 1989), spatial interactions (Doncaster 1990; Minta 1992), and habitat use (Thomas and Taylor 1990), as well as recent improvements in testing procedures (Solow 1989). Tests of independence have been conducted on locational data of several species (e.g., Swihart, Slade, and Bergstrom 1988; Andersen and Rongstad 1989; Gese, Andersen, and Rongstad 1990; Reynolds and Laudre 1990; Swihart 1992) and incorporated into commercial software for home-range analysis (e.g., Ackerman et al. 1990). Unfortunately, several misconceptions remain regarding the assumptions and interpretations related to tests of independence and the associated concept.
of TTI. Our objectives in the present paper are to clarify the assumptions associated with the tests, and to examine in more detail the sensitivity of home-range estimators to varying degrees of autocorrelation and to different sampling strategies.

2. CORRECTING SOME MISCONCEPTIONS REGARDING TESTS OF INDEPENDENCE

Recently, McNay, Morgan, and Bunnell (1994) analyzed locational data for 44 resident and 28 Columbian black-tailed deer (Odocoileus hemionus columbianus). They found that even when 6-week intervals were used between successive observations, 59% of resident deer and 82% of migratory deer exhibited significant levels of autocorrelation. Six weeks would seem to be more than enough time to ensure independence between successive observations (Swihart et al. 1988); thus, McNay et al. were correct to examine the validity of assumptions underlying the use of the test for independence as described by Swihart and Slade (1985b). An examination of movement patterns of individuals revealed that significant levels of autocorrelation were associated with migratory movements, or movements to previously unvisited sites near the periphery of a home range by resident deer (or migratory deer within a season) (McNay et al.). McNay et al. mistakenly attributed their rejection of the hypothesis of independence to utilization distributions of deer that deviated from normality, which they claimed was a requisite for hypothesis testing. It is not necessary to assume that locational data are normally distributed when testing for independence, as we discuss in Section 2.1.

2.1 DATA NEED NOT BE NORMALLY DISTRIBUTED

Temporally ordered sets of locational observations can be modeled as a bivariate autoregressive process. A first-order autoregressive process was considered by Schoener (1981, pp. 313–314) when formulating $t^2/r^2$. Schoener’s statistic can be calculated for any set of bivariate data consisting of ≥ 2 unique locations; Schoener (1981) did not provide a derivation of higher moments of $t^2/r^2$, nor did he speculate regarding its distributional properties. Because locational data often are not normally distributed, we explicitly examined the distribution of $t^2/r^2$ when locations were taken from a variety of bivariate sampling distributions, including normal, uniform, funnel-shaped Beta, and multimodal (Swihart and Slade 1985b).

Approximately normal distributions of $t^2/r^2$ resulted from all of these utilization distributions, with only slight differences in variances. Based on these results, we concluded that “... for reasonable sample sizes, the $t^2/r^2$ distribution is not affected by the underlying distribution of $X$ and $Y$.” (Swihart and Slade 1985b, p. 1181) Our test is robust to departures from normality, contrary to the interpretation offered by McNay et al. (1994).

Although not mentioned by McNay et al. (1994), a limitation of the test we (Swihart and Slade 1985b) proposed was its reliance on a shape parameter, eccentricity. Poor estimates of eccentricity are particularly likely when sample sizes are small, and can lead to actual significance levels that differ from nominal levels (Solow 1989). Solow proposed
a randomization test for independence of successive observations which eliminated the need to estimate eccentricity. Moreover, Solow’s test is truly nonparametric because the null distribution of $t^2/r^2$ is conditioned on the set of observed locations. Solow felt that his test was most useful with small samples ($<10$). However, locational data consisting of $<10$ observations seldom are subjected to home-range analysis. Moreover, randomization tests consisting of large numbers of permutations are computationally feasible for larger datasets than those examined by Solow (see also Manly 1991). Preliminary analyses indicated that Solow’s randomization test is comparable in power to our test, and its use completely eliminates concern over the shape of the utilization distribution. Hence, we feel that it should be used to test for independence of locational observations for larger sample sizes than those originally considered by Solow.

### 2.2 Home Ranges Are Assumed To Be Stationary

A key assumption associated with our test of $t^2/r^2$ is that locational observations must be collected from a stationary distribution during the time frame over which home-range size and independence are to be examined (Swihart et al. 1988). A stationary distribution is one whose characteristics do not change over time. Tests of stationary distributions vary greatly in detail, ranging from tests of constancy in centers of activity or variances and covariances of $X$ and $Y$ to tests of constancy of a utilization distribution in its entirety (reviewed by White and Garrott 1990, pp. 133–137). Nonstationary home ranges arising from shifts in centers of activity create drops in $t^2/r^2$ resulting from the increased mean value of $r^2$. To illustrate this point, we simulated movements of an animal occupying a square home range. All points were generated from a bivariate uniform distribution (Appendix). After 250 locations were generated, the animal’s home range was shifted from the original site with center of activity $(X, Y)$ to a new locality with center of activity $(X + k, Y + k)$, and 250 additional locations were obtained. The procedure was then repeated for a variety of values of $k$. We also conducted the simulations for datasets in which successive observations were independent (stationary $t^2/r^2 = 2$) and dependent (stationary $t^2/r^2 < 2$). Because results were comparable for a wide range of dependent values of $t^2/r^2$, we present only data using a stationary $t^2/r^2 = 1$. Our results (Fig. 1) indicate that (1) shifts in home-range centers reduce overall $t^2/r^2$, as expected; (2) reductions in overall $t^2/r^2$ are more pronounced for larger shifts; and (3) the percent relative change in overall $t^2/r^2$ resulting from a shift does not depend on the level of autocorrelation (and hence the rate of movement) between successive observations measured under stationary conditions.

Nonstationary home ranges also can occur if an animal markedly expands or contracts its home range during the time frame over which the home range is defined. If no other change in the utilization distribution occurs, this is equivalent to a nonstationary home range induced by shifts in the variance-covariance matrix of $X$ and $Y$. We explored the effects of an expanding home range on $t^2/r^2$ by generating 250 locations from a bivariate uniform distribution within a square home range (Appendix). The home range was then increased in size by a specified amount (Fig. 2), and an additional 250 points were generated using the same movement rules governing the initial 250 observations.
Expansion of home ranges without a concomitant increase in rate of movement results in a reduction of $t^2/r^2$, and this effect becomes more pronounced as the magnitude of the expansion increases (Fig. 2). The overall value of $t^2/r^2$ did not equal the level of autocorrelation either before or after the home-range expansion occurred, but it always fell between these values (Fig. 2). The percent relative change of overall $t^2/r^2$ was independent of the rate of movement, which determines the degree of autocorrelation in stationary home ranges of a given size (Fig. 2).

To reiterate, nonstationary home ranges induced by shifts in centers of activity yielded overall values of $t^2/r^2$ that neither matched nor averaged the $t^2/r^2$ values calculated using only data from before or after the shift (Fig. 1). Thus, shifts in centers of activity represent the most serious problem associated with nonstationary home ranges. Nonstationary utilization distributions induced by shifts in variance-covariance structure yielded overall values of $t^2/r^2$ between the values before and after the shift (Fig. 2). In the event of either of these forms of nonstationary home range (due to shifts in center-of-activity or variance-covariance structure), $t^2/r^2$ calculated over an interval of time that excludes the shift would yield values that more closely meet the assumptions set forth for drawing statistical inferences regarding independence. At present we recommend that tests of stationary home ranges, at least for shifts in activity centers, be conducted before proceeding with tests of independence.

Violations of the assumption of stationary home ranges contributed to the failure of McNay et al. (1994, p. 425) to detect independence of observations for migratory deer. McNay et al. also noted that dependence was apparent for resident deer or migratory deer within a season if “the deer moved to a unique place at the periphery of its range.”

Figure 1. Effect of Shifts in Center of Activity on Calculated Level of Autocorrelation, as Measured Using Schoener’s $t^2/r^2$ Ratio. Magnitude of shift in center of activity is expressed as % of home-range width. Horizontal lines depict expected values of $t^2/r^2$ for simulated data within stationary home range; $\bullet = t^2/r^2$ calculated after inclusion of home-range shift halfway through study; —— = independent and $\cdots =$ autocorrelated observations.
Because these types of movements are indicative of either a shift or expansion of a home range, it is likely that the assumption of stationary home ranges was violated in these instances as well.

If home ranges are stationary, it is possible to determine the time interval at which observations consistently exhibit independence (TTI, Swihart and Slade 1985b).

McNay et al. (1994, p. 425) claimed that under these conditions, $t^2/r^2$ fluctuated erratically between dependence and independence for their data. In fact, less than 90% of the tests for deer #NIM12901 (McNay et al. 1994, fig. 2) failed to reject the null hypothesis of independence. The 10% rejection rate is considerably less than might be expected solely due to chance when using a significance level of .25. Moreover, the value of $t^2/r^2$ was within 5% of the critical value for all tests in which the null hypothesis of independence was rejected. We contend that determination of TTI is reasonable when the necessary assumptions are satisfied, although refinement of our ad hoc definition of TTI may be desirable. One reviewer noted the similarity between TTI and the geostatistical concept of “zone of influence,” and a more suitable definition might well be obtained from this subject area.

### 2.3 Time Frame and Sampling Design May Influence Home-Range Estimates

Previously, we demonstrated the negative bias introduced into estimates of home-range size by using autocorrelated observations instead of the same number of indepen-
dent points (Swihart and Slade 1985a). Such a comparison is overly simplistic, because observations can be collected using a variety of sampling strategies and over varying periods of time. If shorter sampling intervals result in greater levels of autocorrelation, then collection of \( n \) autocorrelated points will take less time than collection of \( n \) independent points. Typically, locational observations are collected over a specified period of time. Thus, it might be more appropriate to compare the relative bias in estimates of home-range size associated with the collection of \( n \) independent points and \( b \cdot n \) autocorrelated points \((b > 1)\) over some equal interval of time.

Sampling design (i.e., whether observations are evenly spaced or clumped in time) may also influence the degree to which autocorrelation and sample size interact to affect estimates of home-range size. Our earlier conclusions were based only on sequentially spaced observations (Swihart and Slade 1985a). Locational data commonly are collected in bursts characterized by short time intervals separating successive observations within a burst and comparatively long time intervals between bursts (Dunn and Gipson 1977). Observations within bursts often are highly autocorrelated, whereas observations between bursts may be less autocorrelated or independent. Thus, the level of autocorrelation for all observations is a function of autocorrelation within and between bursts, weighted by the proportion of all successive distances occurring within bursts. The manner in which sampling design affects relative bias of home-range estimates is complex and deserves more careful consideration. Studies of red-tailed hawks (\( Buteo jamaicensis \), Andersen and Rongstad 1989) and coyotes (\( Canis latrans \), Gese et al. 1990) have demonstrated that home-range estimates derived from burst data do not differ significantly from estimates based on sequential locations. If this phenomenon is true in general, then the logistically simpler design (bursts) is clearly preferable.

### 3. SOURCES OF BIAS IN HOME-RANGE ESTIMATION

To examine in more detail the role of time frame and sampling design, we conducted a simulation study in which sampling design, time frame, sample size, and rate of movement were varied. Our objective was to determine the influence of each of these factors on the percent relative bias of various estimators of home-range size.

Movements were simulated within a square home range. Autocorrelated data were generated following the procedures outlined in Swihart and Slade (1985a) for a bivariate uniform distribution (Appendix). Fifty evenly spaced observations were produced within each day of a simulated tracking study, resulting in a sample of 50 × DAYS locational records, where DAYS is the number of simulated days over which observations were collected. Our analysis relied upon subsamples drawn from these larger samples. Fifty points per “day” were generated because this was the maximum sampling rate used in our analysis (see following paragraph).

A factorial design was used to vary study duration (DAYS), sampling rate (SR, points/“day”), and degree of autocorrelation \((t^2/r^2)\), and a new sample of points was generated for each combination of these factors. DAYS was set at 10, 20, 30, 40, and 50. Sequential sampling was conducted at a sampling rate of 10, 5, 2.5, 1, and .5. Thus, the range of sample sizes was 5–500. Burst sampling was simulated using the following
approach. First, 50 evenly spaced records were generated for each simulated day. These records can be thought of as those locations at which the animal would have been observed if a sequential sampling scheme had been used with SR = 50. A burst was defined as five consecutive points taken from such a set of records. Thus, the sampling rate within a burst was equivalent to 50 points per “day.” Unlike sequential samples, burst samples are characterized by two sampling intervals, the intraburst interval just described as well as an interval between bursts. We used two different interburst intervals in our simulations, either one or two bursts per day. When 2 bursts were taken each day, they were separated by 12 hours and staggered so that each of the 5 possible burst periods during a 12-hour interval was sampled every fifth day. In a real-world context, this would be comparable to initiating burst sampling on Monday at 0 h and 1200 h, on Tuesday at 0224 h and 1424 h, on Wednesday at 0448 h and 1648 h, on Thursday at 0712 h and 1912 h, and on Friday at 0936 h and 2136 h, with the entire sequence beginning again on Saturday. When 1 burst was taken per day, each of the 10 possible burst periods during a 24-hour interval was sampled every tenth day in a manner analogous to the scheme described for sampling 2 bursts per day. For the burst design, then, sample sizes ranged from 50–500. We varied the movement rate so that the level of $t^2/r^2$ calculated for the most intense sequential sampling scheme (10 points/day) averaged 1.0, 1.5, 1.7, 1.8, 1.9, and 2.0. Thus, for the sequential sampling design, we produced a factorial design with 5 levels of study duration, 5 levels of sampling intensity, and 6 levels of movement rate, yielding 150 combinations. For burst sampling, we generated 5 levels of study duration, 2 levels of sampling intensity, and 6 levels of movement rate, yielding 60 combinations. We simulated five sets of locational observations for each combination.

For each set of observations, we calculated the minimum convex polygon (MCP, Mohr 1947) and kernel estimators (Worton 1989) of home-range size using RANGES IV (Kenward 1990). We calculated kernel estimates of the smallest area within which 95% (Kernel95) of the volume of the kernel surface occurred. The smoothing parameter, $h$, of a bivariate normal kernel was estimated as $h = [((s_x^2/2) + (s_y^2/2))^{1/2}] / n^{1/6}$ (Worton 1989). Percent relative bias (PRB) was computed for each home-range estimate, where $PRB = 100(A_c - A_t)/A_t$, and $A_c$ and $A_t$ represent the estimated and true home-range area, respectively. Overall values of $t^2/r^2$ were computed for each dataset. For burst data, we also computed the mean squared distance between successive points within bursts and between bursts.

Regression models were developed to predict PRB for each estimator as a function of $t^2/r^2$, DAYS, and SR (points/day for sequential sampling, bursts/day for burst sampling). We examined initial plots of PRB versus each of these variables as well as $n$, which can be thought of as an interaction term. These plots suggested that logarithmic transformations of DAYS and SR might provide better fits than the linear terms. We explored combinations of these variables using best subsets regression in MINITAB (1991) and found that the logarithmic transformations produced better fits, all four predictor variables contributed significantly to the regression model, and the residuals showed some curvilinearity when plotted against number of locational points. Adding the square of $n$ gave a significantly better fit to all models, but the residuals were heteroscedastic when plotted against $n$ or DAYS. We calculated the variance of residuals for each combination of $n$ and DAYS, and repeated the regression, using the inverse of the vari-
Table 1. Results of Weighted Least Squares Regressions Relating Percent Relative Bias (PRB) in Home-Range Estimators Derived From Simulations in a Square Home Range to Autocorrelation \( (t^2/r^2) \), Study Duration (DAYS), Sampling Rate (SR) for Observations Collected Sequentially (SEQ) or in Bursts (BURST), and Total Number of Locational Observations \( (n) \)

<table>
<thead>
<tr>
<th>PRB in home-range estimator</th>
<th>Kernel(_{95})</th>
<th>Convex polygon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable</td>
<td>SEQ</td>
<td>BURST</td>
</tr>
<tr>
<td>Intercept</td>
<td>-83.13***</td>
<td>-60.69***</td>
</tr>
<tr>
<td>(t^2/r^2)</td>
<td>2.16**</td>
<td>3.68***</td>
</tr>
<tr>
<td>ln(DAYS)</td>
<td>18.48***</td>
<td>19.04***</td>
</tr>
<tr>
<td>ln(SR)</td>
<td>18.77***</td>
<td>22.11***</td>
</tr>
<tr>
<td>(n)</td>
<td>-0.128***</td>
<td>-0.106**</td>
</tr>
<tr>
<td>(n^2)</td>
<td>1.08 \times 10^{-4***}</td>
<td>0.76 \times 10^{-4***}</td>
</tr>
<tr>
<td>(R^2)</td>
<td>0.58***</td>
<td>0.30***</td>
</tr>
</tbody>
</table>

**NOTES:** Results given are coefficients for explanatory variables: * = \( p \leq 0.10 \), ** = \( p \leq 0.05 \), *** = \( p \leq 0.001 \). \( R^2 \) is calculated using weighted sums of squares. SR is measured in units of bursts per day, with 1 and 5 points/burst for SEQ and BURST designs, respectively.

ances as weights. Residuals from the models constructed using weighted least squares regression did not exhibit heteroscedasticity.

### 3.1 Effect of Study Duration and Sampling Rate on Bias

Increasing the study duration resulted in reduced levels of bias for all estimators and sampling designs (Table 1), although the amount of bias reduction per unit increase in duration diminishes as PRB approaches zero (Fig. 3). For a given level of sampling intensity and degree of autocorrelation, Kernel\(_{95}\) estimates exhibited less bias at all study durations than MCP estimates. This pattern held for both sequential and burst sampling designs (Fig. 3).

Sampling rate was significantly related to bias for both estimators and sampling designs (Table 1). Of course, for a given animal, increasing the sampling rate will result in a smaller calculated value of \( t^2/r^2 \) (Swihart and Slade 1985a). Hence, for a given sample size, any gain associated with increasing sampling rate may be more than offset by the increased autocorrelation. For example, in our simulations, sequential sampling of 100 points at the rate of 2.5 points per day produced a mean \( t^2/r^2 \) of 1.96 and a bias for MCP of -14.8%, whereas sequential sampling of 100 points at 10 points/day produced a mean \( t^2/r^2 \) of 1.42 and a bias for MCP of -17.0%.

### 3.2 Effect of Autocorrelation on Bias

Increases in \( t^2/r^2 \) resulted in reduced bias in both estimators and sampling strategies (Table 1). For a given sampling rate and study duration, Kernel\(_{95}\) estimates were most sensitive to changes in \( t^2/r^2 \) (Table 1, Fig. 4). The cost associated with autocorrelation was low, however, as use of moderately autocorrelated (\( t^2/r^2 = 1.5 \)) rather than independent (\( t^2/r^2 = 2 \)) data increased PRB by < 2% (Table 1).
3.3 Effect of Sampling Strategy on Bias

To compare differences in bias induced by sampling strategy, we first must assess the degree to which \( t^2/r^2 \) is affected by sampling sequentially versus in bursts. For data collected in bursts, overall \( t^2/r^2 \) was predicted quite well \((R^2 = .94, p < .001)\) by mean squared distance between successive observations within \( (t_{in}^2) \) and between \( (t_{out}^2) \) bursts: 
\[
    t^2/r^2 = 0.17 + 0.008(t_{out}^2) + 0.058(t_{in}^2).
\]
In general, then, overall \( t^2/r^2 \) can be partitioned into intra- and interburst components, with the relative importance of each determined by the relative frequency of intraburst distances, as discussed earlier. As an example, for \( n = 150 \) observations, sampling of 5 points per day for 30 days yielded simulated mean \( t^2/r^2 \) values of 1.86 and 1.00 for simulated data generated sequentially and in bursts, respectively. Predicted levels of relative bias corresponding to samples collected sequentially versus in bursts, after correcting for differences in overall \( t^2/r^2 \) induced by the different sampling strategies, were -2.8% and -6.4% for Kernel95, and -11.9% and -12.5% for MCP (Fig. 4).

4. Discussion

4.1 Factors Influencing Bias in Home-Range Estimates

To illustrate the tradeoff between sample size and autocorrelation in determining bias of home-range estimators, we constructed bias isoclines from the regressions in Table 1 (Fig. 5). Sampling was conducted at a rate of five points per “day” for both sequential and burst designs (i.e., 1 burst per day). Because the regressions (Table 1) failed to explain a substantial proportion of the variation in PRB, these isoclines and the
predictive equations from which they are derived should be viewed only as indicators of general patterns rather than as precise predictions.

Perhaps the most notable result is that for data with moderately low levels of autocorrelation ($t^2/r^2 > 1.5$), changes in autocorrelation have little effect on bias (Fig. 5). Put another way, if violation of the assumption of independence is relatively minor, slight increases in sample size attained by increasing study duration may be sufficient to maintain the same bias as with independent points. The lone exception to this rule appears to be Kernel95 estimates derived from burst sampling, when low levels of bias are desired (Fig. 5).

Sampling design, choice of home-range estimator, and the level of bias a researcher deems acceptable all must be considered when assessing the importance of autocorrelation. As indicated earlier, choice of a burst sampling design can simultaneously increase autocorrelation and $n$, thereby complicating comparisons with sequential sampling. In general, our results suggest that any advantages associated with sequential sampling are limited to situations involving relatively unbiased estimates, particularly Kernel95 estimates (Fig. 5).

Because MCP estimates rely exclusively upon observations obtained at the periphery of the utilization distribution, negative bias associated with MCP should increase for utilization distributions exhibiting marked central tendencies. No such problem exists for kernel estimators, because all observations contribute to the estimate of home-range size. Our simulations used a uniform distribution, yet PRB values for Kernel95 estimates were consistently smaller than for MCP. With irregular, multimodal utilization distributions
typical of many animals, we expect the performance of kernel estimators to improve relative to performance of MCP.

In summary, our results indicate that (1) negative bias (PRB) in home-range estimators increases with increasing levels of autocorrelation (smaller $t^2/r^2$, Fig. 4); (2) the increase in negative bias is minor (< 5%) for moderate levels of autocorrelation ($1.5 < t^2/r^2 < 2$, Fig. 5); (3) Kernel95 estimates exhibit lower levels of negative bias than MCP (e.g., Figs. 3, 4); and (4) for the sampling regimes we examined, differences in PRB due to sequential versus burst sampling were small (Figs. 4, 5). Taken together, these findings suggest that Kernel95 estimates of home-range size computed using moderately autocorrelated observations will yield real values only slightly more biased than if independent observations had been used.
4.2 IMPLICATIONS FOR WILDLIFE STUDIES

Our simulation results agree with empirical data on red-tailed hawks (Andersen and Rongstad 1989) and coyotes (Gese et al. 1990). In these studies, equal numbers of observations ($n = 30$ for hawks, $60$ for coyotes) were collected by sampling sequentially and in bursts. Average values of $t^2/r^2$ indicated that data collected in bursts (hawks = 1.42, coyotes at night = .71) were more highly autocorrelated than data from sequential sampling (hawks = 1.86, coyotes = 1.90), but differences in mean MCP estimates were not significant for either species.

Our regression results predict the following PRB values for MCP estimates derived from these data: $-37.2\%$ for hawks (sequential); $-40.6\%$ for hawks (burst); $-24.4\%$ for coyotes (sequential); and $-28.2\%$ for coyotes (burst). We do not mean to suggest that these values reflect the actual levels of bias associated with the home-range estimates reported by Andersen and Rongstad (1989) and Gese et al. (1990). The sequential and burst strategies they employed differed from those adopted in our simulations, and the utilization distributions of the animals they studied presumably were not uniform. Rather, the predicted PRB values for a given species are instructive when compared to each other because they illustrate in an entirely independent fashion how little of an effect sampling strategy had on MCP estimates of home range for coyotes and red-tailed hawks. Similar calculations for Kernel$_{95}$ suggest that choice of sampling strategy would have been more important if this estimator had been used, principally because the Kernel$_{95}$ would yield a less biased estimate [predicted PRB: $-20.0\%$ for hawk (sequential); $-24.5\%$ for hawk (burst); $-10.7\%$ for coyote (sequential); and $-16.9\%$ for coyote (burst)]. Under these conditions, sampling in a sequential fashion would provide an estimated 18% (hawk) and 37% (coyote) reduction in PRB. If the power of the statistical tests for Kernel$_{95}$ estimates is comparable to those reported for polygon estimates (minimum detectable difference = 220% for red-tailed hawks, Andersen and Rongstad 1989; 13-30% for coyotes, Gese et al. 1990), then it is possible that sequential sampling could provide detectable improvements in Kernel$_{95}$ estimators for the coyote data, but not for the red-tailed hawk data.

Considering statistical independence of successive observations requires addressing the issue of whether sufficient time has elapsed to permit an animal to move to any other point within its home range before the next observation (Minta 1992; McNay et al. 1994). Because TTI estimates this time interval for a stationary home range, we have advocated its use as a measure of the rate of movement within a home range (Swihart and Slade 1985b) and have computed estimates of TTI for several species of mammals (Swihart et al. 1988). Hansteen, Andreassen, and Ims (in press) recently used a variation on this approach to identify ultradian rhythmicity in movements of small mammals. TTI is a useful spatial statistic and can provide insight into temporal rhythmicity of movements (Swihart and Slade 1985b; Swihart 1992; McNay et al. 1994). However, use of TTI (or other attributes of the autocorrelation function of $t^2/r^2$) as a means of selecting data for use when estimating home-range size is largely unnecessary for Kernel$_{95}$ and MCP. Simulation results (Swihart and Slade 1985a; Fig. 5 of this study), as well as field studies (Andersen and Rongstad 1989; Gese et al. 1990) indicate that selection of a sampling interval < TTI (i.e., an interval yielding autocorrelated observations) generally will not invalidate several common estimators and indexes of home-range size, provided that the
time frame of the study is adequate. Exceptions include the bivariate normal estimator of Koeppl et al. (1975) and an index, the distance between successive observations (Swihart and Slade 1985a).

We agree with McNay et al. (1994) that the choice of appropriate sampling intervals for collecting locational observations should be driven principally by study objectives, not by the desire to attain statistical independence between successive records. As stated in our initial examination of \( t^2/r^2 \) (Swihart and Slade 1985b, p. 1184), “By presenting a means of testing for independence..., we do not intend to discourage frequent monitoring of individuals...” Rather, \( t^2/r^2 \) and TTI should be viewed as statistics reflecting attributes of an individual’s use of space (Swihart et al. 1988). Tests of independence of observations remain important when statistically examining aspects of habitat use (Thomas and Taylor 1990; White and Garrott 1990). Prior to testing for independence, locational data should be examined for evidence of stationary home ranges.

APPENDIX

In two dimensions, a first-order autoregressive process can be expressed as

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

where \((X_i, Y_i)\) and \((X_{i-1}, Y_{i-1})\) are values of \(X\) at times \(i\) and \(i - 1\), respectively, \(\rho_{x_i,x_{i-1}}\) and \(\rho_{y_{i-1},y_{i-1}}\) are the first-order autocorrelation coefficients, \(\rho_{x_{i-1},y_i}\) and \(\rho_{x_i, y_{i-1}}\) are first-order coefficients of cross correlation, and \(\epsilon_x\) and \(\epsilon_y\) are random error terms. A general approach to generating autocorrelated records involves specifying distributions for \(\epsilon_x\) and \(\epsilon_y\) and selecting values for each element of the autocorrelation matrix, subject to the constraint that \(-1 \leq \rho \leq 1\). For simplicity, we used an identity matrix for the autocorrelation matrix (see Swihart and Slade 1985a). Levels of \(t^2/r^2\) were manipulated within a bounded home range by drawing from independent uniform distributions for \(\epsilon_x\) and \(\epsilon_y\). We assumed that as the time interval between successive observations declined, so too did the potential distance moved from the previous point. Thus, changes in \(\text{var}(\epsilon_x)\) and \(\text{var}(\epsilon_y)\) were used as surrogates for altering the time interval between observations. Small values of error variance relative to the length and width of a home range resulted in low levels of \(t^2/r^2\), whereas large error variances resulted in \(t^2/r^2\) values of 2. Although error terms were generated using a uniform distribution, the boundedness of home ranges ensured that utilization distributions differed from the joint distributions of \(\epsilon_x\) and \(\epsilon_y\). Site fidelity is a key feature characterizing a home range (e.g., Munger 1984; Spencer, Cameron, and Swihart 1990). The boundary conditions used in our simulations, although artificial, were necessary to incorporate site fidelity.

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