Eliminating autocorrelation reduces biological relevance of home range estimates

SHANE R. DE SOLLA, RUSSELL BONDURIANSKY and RONALD J. BROOKS

Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

Summary

1. Destructive subsampling or restrictive sampling are often standard procedures to obtain independence of spatial observations in home range analyses. We examined whether home range estimators based upon kernel densities require serial independence of observations, by using a Monte Carlo simulation, antler flies and snapping turtles as models.

2. Home range size, time partitioning and total straight line distances travelled were tested to determine if subsampling improved kernel performance and estimation of home range parameters.

3. The accuracy and precision of home range estimates from the simulated data set improved at shorter time intervals despite the increase in autocorrelation among the observations.

4. Subsampling did not reduce autocorrelation among locational observations of snapping turtles or antler flies, and home range size, time partitioning and total distance travelled were better represented by autocorrelated observations.

5. We found that kernel densities do not require serial independence of observations when estimating home range, and we recommend that researchers maximize the number of observations using constant time intervals to increase the accuracy and precision of their estimates.

Key-words: Chelydra serpentina, kernel density estimation, Monte Carlo, *Protopiophila litigata*, statistical independence.

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Introduction

It is commonly asserted that most analyses of home range require independence of observations for an unbiased estimate (Swihart & Slade 1985a,b; Worton 1987; Harris *et al.* 1990; White & Garrott 1990; Cresswell & Smith 1992; Kenward 1992). Ecological relationships often depend, either directly or indirectly, on their underlying spatial or temporal structure, and thus autocorrelation can be a tool to understand underlying causes of such relationships. Unfortunately, autocorrelation can also be a barrier in ecological studies, as it interferes with standard statistical hypothesis testing. Lack of independence among observations increases the probability of a type I error, by inflating the degrees of freedom (Legendre

1993). Animals typically move in a non-random fashion, and thus ecologists are frequently faced with strongly autocorrelated data sets, particularly when frequent observations are collected using radiotelemetry. Although Swihart & Slade (1985b) state that frequent monitoring of individuals should not be discouraged, a common procedure is to eliminate autocorrelation before estimating home range size, either by subsampling (Worton 1987; Ackerman *et al.* 1990; Kenward 1992) or by restricting the sampling regime after a pilot study (Swihart & Slade 1985b). It is from these truncated data sets that hypotheses are tested and conclusions are drawn.

Eliminating autocorrelated fixes from the data set not only reduces the sample size, but may also limit the biological significance of the analysis. Some statistical methods of home range analyses produce home range sizes that are inversely proportional to the degree of temporal dependence between observations (Swihart & Slade 1985a,b). For example, restricting sampling

Correspondence: R. J. Brooks, Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1. Tel: 519-824-4120 ext. 8360. E-mail: rjbrooks@uoguelph.ca

effort to statistically independent time intervals underestimated the home range size of pronghorns (*Antilocapra americana*) and coyotes (*Canis latrans*) (Reynolds & Laundre 1990). It is questionable whether a statistically independent data set can sufficiently describe what is essentially a non-independent phenomenon, as autocorrelated observations may reveal better behavioural information than would independent observations (Lair 1987). While there have been many studies comparing home range estimates of independent and autocorrelated data sets (Swihart & Slade 1985a,b; White & Garrott 1990; Cresswell & Smith 1992), these studies have not been definitive.

The objective of this study was to compare home range estimates using statistically independent and autocorrelated observations with a known home range. First, we used a Monte Carlo simulation to generate locational observations within a bounded area and changed the degree of autocorrelation between consecutive observations to determine the effect of autocorrelation on home range size. Secondly, we compared space use within the home range. It is often assumed that the probability of detecting an animal within a given area of a home range, as estimated from an utilization distribution, represents the time spent in that area (Samuel & Garton 1987; Seaman & Powell 1996) and is often used as such. We compared the probability of locating an animal within an area, using a kernel density estimate, with the actual time spent in that area. To determine how autocorrelation affects the correlation between the probability estimate with the actual time, we used both independent and autocorrelated data sets. Thirdly, we examined the total distance travelled within the home range. Increasing the time interval between observations has been shown to under-estimate the distance travelled by an animal (Reynolds & Laundre 1990). We repeated their test to determine whether reducing autocorrelation affected the total distance travelled between consecutive observations. Finally, we determined if reducing autocorrelation affected the accuracy of the home range size estimate. We compared the total area traversed by the animal with the home range estimate after increasing the time interval between observations. We used data from the computer simulation, and two species as models: antler flies (*Protopiophila litigata*) and snapping turtles (*Chelydra serpentina*).

Male antler flies, which mate on abandoned cervid antlers, are aggressive insects that defend well-defined lek territories (Bonduriansky 1995). Males defend their territories with frequent agonistic contests, and have a high site fidelity (Bonduriansky 1996). Consequently, their small territories are well defined and their time budgets easily measured. Snapping turtles are omnivores that inhabit shallow wetlands and marshes, and have overlapping home ranges, although male snapping turtles may temporally, if not spatially,

avoid each other (Galbraith, Chandler & Brooks 1986). Since they rarely bask, and are highly cryptic, their home ranges are difficult to define and their activity patterns are hard to establish. Antler flies represent ideal study organisms for home range analyses, whereas snapping turtles represent a more typical study animal because of their enigmatic movement patterns.

Methods

DENSITY ESTIMATION AND MEASURE OF INDEPENDENCE

We used kernel estimators to measure home range because they are among the more reliable home range analyses (Worton 1987, 1995; Seaman & Powell 1996). A fixed kernel density estimate is calculated by

$$\bar{f}_h(x) = \frac{1}{n} \sum_{i=1}^{n} \frac{1}{h^2} K\left(\frac{x - X_i}{h}\right) \tag{1}$$

where K is a uni-modal symmetrical bivariate probability density for a given grid point x, h is the smoothing parameter, and X is a random sample of n independent points from the unknown utilization distribution (Worton 1989). A utilization distribution is generated by making a surface plot of the kernel densities for all of the grid points.

Seaman & Powell (1996) found that home range size estimates are more accurate using fixed kernels. The fixed kernel estimates may form spurious noise at the edges of long-tailed distributions (Silverman 1986), and so may be biased as there are often areas within a home range that receive little use by the animal. Adaptive kernels vary the smoothing parameter with the estimated density, such that noise at long-tail distributions is smoothed without 'over smoothing' areas of high density (Silverman 1986). The equation to measure the adaptive kernel is identical to equation 1, except h is replaced by h_i, where h_i varies with the density estimated by a 'pilot' estimate, such as the fixed kernel estimate (Worton 1989). We used fixed kernels to estimate home range size, which does not involve the three-dimensional shape of the distribution, but merely produces an outline of the home range, and we used adaptive kernels to estimate the shape of the probability distribution.

We used Schoener's ratio (t^2/r^2) to estimate temporal autocorrelation (Schoener 1981), where t^2 is the mean squared distance between successive observations, and is defined by

$$t^2 = \frac{1}{m} \sum_{t=1}^{m} (X_{t-1} - X_t)^2 + \frac{1}{m} \sum_{t=1}^{m} (Y_{t-1} - Y_t)^2 \tag{2}$$

where m is the number of pairs of successive observations. The mean squared distance between each observation and the centre of activity is defined as:

$$r^2 = \frac{1}{n-1} \sum_{i=1}^{n} (X_i - \bar{X})^2 + \frac{1}{n-1} \sum_{i=1}^{n} (Y_i - \bar{Y})^2 \quad (3)$$

where n is the number of observations and $(\bar{X}, \bar{Y})$ is the arithmetic mean of the observations (Schoener 1981). Swihart & Slade (1985b) used simulations to show that the expected value of t^2/r^2 if consecutive observations are independent is 2. If successive observations are positively serially correlated, then t^2/r^2 would be less than 2, and if successive observations are negatively serially correlated, then t^2/r^2 would be greater than 2. Negative autocorrelation, however, is rare, especially if frequent observations are taken, so is not relevant to home range studies.

The 'time to independence' (TTI) was estimated by subsampling sets of observations and thus increasing the time intervals between observations, and calculating t^2/r^2. We then compared the observed t^2/r^2 values with critical values calculated for bivariate uniform distributions ($\alpha = 0.25$) (Swihart & Slade 1985b), and rejected the null hypothesis of independence if the observed t^2/r^2 lay outside the critical values around the expected value of 2. Since the arithmetic mean of X and Y, which represents the centre of activity, would change with subsampling, autocorrelation may be under-estimated if the animal exhibits cyclical movement.

MONTE CARLO SIMULATION

Swihart & Slade (1985a) used a Monte Carlo simulation to model the effect of autocorrelation on home range size, in which they kept the sample size constant, but the total sampling time period was proportional to the time interval between observations. They found that using a number n of autocorrelated observations within a short period of time resulted in a smaller home range size than using n independent observations over a much longer period of time. However, we decided to take a different approach. It is more natural for researchers to have a fixed total sampling period and the main question is how many observations to have within this set period of time. We modified Swihart & Slade's (1985a) model to incorporate this approach.

To examine the effect of autocorrelation on home range size, paths were constructed using highly autocorrelated observations, and then autocorrelation was reduced by subsampling. We generated paths by randomly selecting a location using a uniform random number generator. Each subsequent location was estimated using $X_i = X_{i-1} + \varepsilon_x$ and $Y_i = Y_{i-1} + \varepsilon_y$, where X_i and Y_i are Cartesian co-ordinates at time i, and ε_x and ε_y are normally distributed random error terms (Swihart & Slade 1985a). The error terms have a mean of zero with a constant variance. All the observations were limited to a 100×100 unit square home range. Our simulation describes a trajectory of an animal as a discrete time random walk within a bounded region.

We generated 100 paths of 500 observations each by using a small variance term relative to the size of the home range, where $\varepsilon_x = \varepsilon_y = 12$, and thus the step length is 4·9 units. We chose this value so that the paths were highly autocorrelated at shorter time intervals, yet were independent, or nearly so, at longer time intervals, and so that the path filled most of the area within the home range boundaries. Very small step lengths resulted in paths that did not fill the bounded region. If the random number draw indicated movement outside the bounded area, the random number was recalculated until the observation was within the bounded area. These paths were subsampled using time intervals of 2 through 15 units, producing 1500 paths in total. Estimates of home range sizes were calculated for all paths for each time interval using a kernel density analysis. We used least squares cross validation (LSCV) to estimate the optimal value of h (Seaman & Powell 1996). We used a multiple regression to determine the effect of time interval and autocorrelation on home range size estimates. Autocorrelation was estimated using t^2/r^2.

FIELD STUDIES

In 1995, antler flies were observed at the Wildlife Research Station, Algonquin Park, Ontario (45°35′N, 78°40′W). A 2×2-cm grid was drawn on the upper surface of a discarded moose antler that was occupied by flies. Male flies were caught, placed in a restraining device, and an individual code was painted on the notum of each fly (Bonduriansky & Brooks 1997). The locations of several territorial males were recorded at 10-s intervals for the duration of their territory defence, which may last for over 30 min (Bonduriansky 1996). The movement of four antler flies were included in our analyses.

Snapping turtles were trapped at Cootes Paradise, Hamilton, Ontario (43°17′N, 79°53′W). Cootes Paradise is a highly eutrophic 90-ha marsh, which is surrounded by emergent vegetation, but has little submergent vegetation. Snapping turtles were caught using unbaited hoop traps in the summers of 1994 and 1995. Radiotransmitters (Holohil Systems Inc., 112 John Cavanagh Rd., Carp, Ont.) were attached to adult male snapping turtles by drilling two small holes in the posterior marginal scutes and tied on using 0·012 gauge steel trolling wire. Turtles were tracked from a canoe using a hand-held receiver (Wildlife Materials Inc, Carbondale, Il.) and yagi antenna. They were usually tracked up to five times a week, either on consecutive or alternate days, from May to late August 1995. The radiolocations were recorded on a 10×10-m grid. The movements of five snapping turtles were included in our analyses. The total distance travelled by both antler flies and snapping turtles were also estimated at time intervals of varying length.

For each time interval, a utilization distribution was estimated using an adaptive kernel and a grid was

superimposed over the observations. The relative time spent throughout the home range was estimated by summing the number of observations within each grid sector, where each observation represented the time span between successive observations at the shortest time interval. Thus, each antler fly observation represented 10 s, while each snapping turtle observation represented 2 days. The kernel density estimate was also summed within each grid sector, and a regression of density versus time spent was calculated for each time interval.

Initially, we used a LSCV approach to determine the optimal value of h for the kernel density estimate (Seaman & Powell 1996), but we found that this approach under-estimated the home range size. There were often multiple observations with identical observations, which causes LSCV to produce an overly small value of h, and thus under-estimate the home range (Seaman & Powell 1991). We chose to estimate h by comparing the estimate with a minimum home range size calculated by grid cells. We used the complete data set, and for each animal we counted the number of grid cells that contained observations. This defined the minimum home range size. Still using the complete data set, we calculated the value of h that produced a home range estimate equal to the minimum home range size. We used the same value of h for all subsequent time intervals to keep all home range estimates comparable. Home ranges were not calculated when there were fewer than 10 observations. We used regression to examine the effect that time interval and autocorrelation have upon home range size. First we compared the mean home range size with time interval and with the mean t^2/r^2 for each time interval. In case averaging obscured individual trends, we performed the same regressions with each individual.

Although our simulation does not include cyclical movement, there may be cyclical or repeated behaviour of both antler flies and snapping turtles. If, through subsampling, a disproportionate number of observations fall within a small portion of the total home range, the mean squared distance between each observation and the true centre of activity would be under-estimated, and thus inflate t^2/r^2. To compensate for this, we choose a static centre of activity to estimate r^2, thus reducing sampling error from subsampling. A minimum convex polygon (Mohr 1947) was constructed of all the observations, and the arithmetic mean of the corners defining the polygon was calculated. We used the corners of a minimum convex polygon to derive a static centre of activity, because this type of home range analysis is not directly affected by autocorrelation (Swihart & Slade 1985a; Harris *et al.* 1990). The arithmetic mean of the corners of the polygon was used as the centre of activity for all subsequent estimations of r^2 (henceforth called r^2_{mcp}). Both t^2/r^2 and t^2/r^2_{mcp} were calculated for each time interval, until there were fewer than 10 observations.

We calculated t^2/r^2 and t^2/r^2_{mcp} for different time intervals for both snapping turtles and antler flies, and a polynomial regression was calculated to determine the relationship between autocorrelation and time interval. Independence between observations was assumed to have occurred when there were three consecutive non-significant t^2/r^2 values, where the first of the three represents the TTI (Swihart & Slade 1985b).

Statistical analyses were performed using the program STATISTICA v.5·0 (StatSoft 1995), except for the kernel probability densities, which were generated by Kernel Home Range Program v. 4·21 (Seaman & Powell 1991). The kernel density estimates were plotted using MATHCAD PLUS v. 6·01 (Math Soft 1995).

Results

MONTE CARLO SIMULATION

There was a significant effect of both autocorrelation ($b = 0·1121$, $P = 0·005$) and time interval ($b = 0·4585$, $P < 0·0001$) on home range size (adj. $r^2 = 0·3097$, $F = 335·81$, d.f. = 2, 1497, $P < 0·0001$). Home range size shrank with both increasing autocorrelation and decreasing time interval. We present an example of the effect of subsampling on the distribution of observations (Fig. 1). Autocorrelation among locational observations declined as the time interval between observations increased, until independence was nearly reached at the longest time interval (Fig. 2). The estimates of autocorrelation were more precise at shorter time intervals (Fig. 2), probably due to the larger sample size and thus less sampling error at smaller time intervals. Home range estimates were least biased and most precise at the shortest time intervals, and thus at the highest levels of autocorrelation. (Figs 2 and 3). Both the squared standard deviation of the home ranges size estimates (adj. $r^2 = 0·8928$, $F = 117·55$, d.f. = 1, 13, $P < 0·0001$), and the squared bias of the home ranges estimates (adj. $r^2 = 0·9290$, $F = 184·32$, d.f. = 1,13, $P < 0·0001$) were positively related to the time interval. We used the squared transformation to linearize the regressions. Sample size was not included in the regression because it was redundant with the time interval. Since we have kept the total sampling period constant, the sample size is a function of the time interval.

FIELD STUDIES

Consecutive observations of antler fly movement were recorded every 10 s for a maximum of 25·5 min, yielding a total of 423 observations for four antler flies. Agonistic contests with rival male flies occurred for 18 of the observations for one of the flies, when the fly would attack and briefly leave its defended territory to chase the intruder. Because these agonistic contests occurred over a much larger area than the area normally patrolled, observations during agonistic behav-
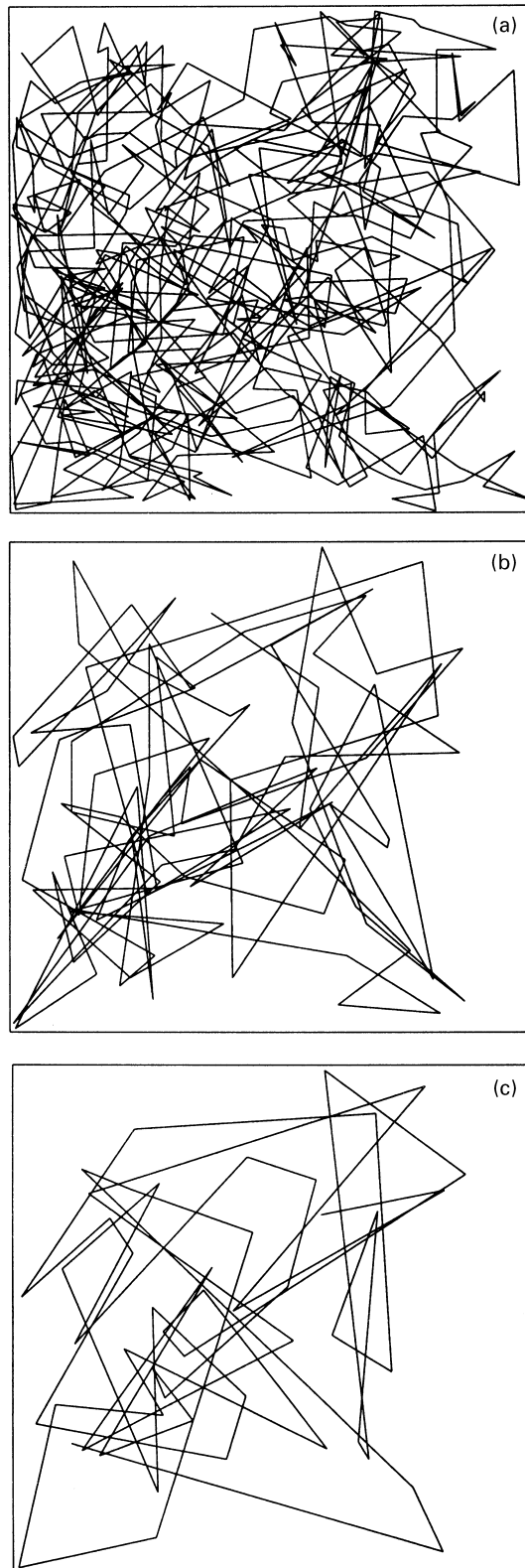
Fig. 1. Effect of subsampling on the spatial distribution of observations. The time intervals were 1, 5 and 10, respectively, and the sample sizes were 500, 100 and 50, respectively, for a, b and c.
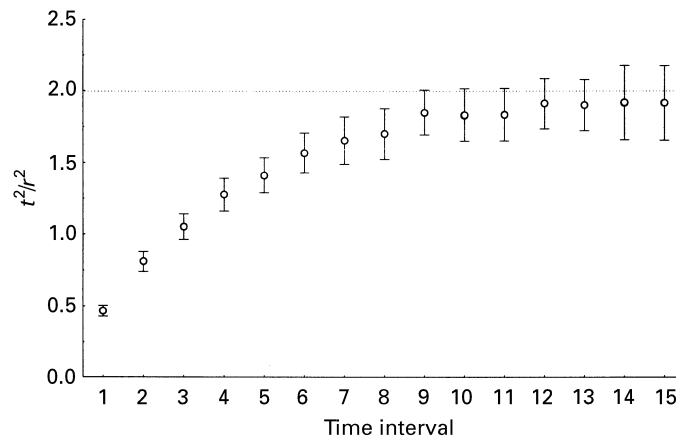
iour were excluded from the home range analyses. There were 134, 42, 116 and 113 observations for the four antler flies. The largest gap between observations after excluding agonistic contests was 40 s, although most of the gaps were 10–20 s. The mean time interval between observations was 10·43 s (SD = 2·65,

Fig. 2. Mean and standard deviation of t^2/r^2 of simulated home ranges at different time intervals. The horizontal line depicts the expected value of t^2/r^2 if the observations are independent. The degree of autocorrelation is reduced as t^2/r^2 approaches 2.
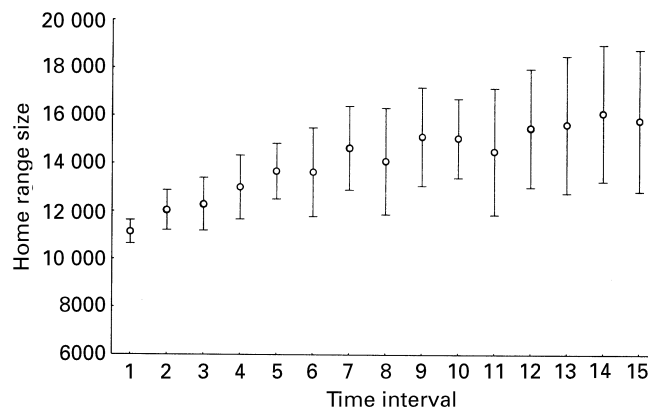

Fig. 3. Mean and standard deviation of estimates of simulated home ranges at different time intervals. The unbiased home ranges size is 10 000 units^2.

$n = 418$). As the time interval between observations increased, the estimated total distance travelled declined (Fig. 4a).

The time intervals between observations of snapping turtle were varied, and so observations were excluded to give a minimum of 1 observation every 2 or 3 days. The sample size of the five sets of observations of snapping turtles was 35, 43, 38, 41 and 28, which were recorded over 4 months. The mean time between observations was 3·12 days (SD = 1·87, $n = 178$), excepting the first observations, which were collected a month earlier than the rest when the turtles were hibernating. Deleted or missing observations increase the mean time interval between observations, and so autocorrelation would be slightly under-estimated. As the time interval between observations increased, the estimated total distance travelled declined (Fig. 4b).

We averaged the t^2/r^2 and t^2/r^2_{mcp} values of the antler flies for each time interval. There was a non-significant positive trend between the average t^2/r^2 values of antler flies and the time interval (adj. $r^2 = 0.2149$, $F = 4.559$, d.f. = 1, 12, $P = 0.0540$), but

there was a positive relationship between the average t^2/r^2_{mcp} and the time interval (adj. $r^2 = 0.2623$, $F = 5.623$, d.f. = 1, 12, $P = 0.0353$). Generally, independence was not reached despite increasing the time interval of individual antler flies (Fig. 5a,b). Only 14·29% of the t^2/r^2 values and none of the t^2/r^2_{mcp} values reached independence ($\alpha = 0.25$). Similarly, we averaged the t^2/r^2 and t^2/r^2_{mcp} values of the snapping turtles for each time interval. There was a significant relationship between the averaged t^2/r^2 and the time interval (adj. $r^2 = 0.2464$, $F = 5.250$, d.f. = 1, 12, $P = 0.0408$), and between the averaged t^2/r^2_{mcp} and the time interval (adj. $r^2 = 0.4427$, $F = 11.326$, d.f. = 1, 12, $P = 0.0056$). Although the values of t^2/r^2 and t^2/r^2_{mcp} of individual snapping turtles initially increased, they then appeared to reach an asymptote and for one turtle the values declined as the time interval between observations increased (Fig. 6a,b). Only 26·23% of the t^2/r^2 values (most from one turtle) and 0·03% of t^2/r^2_{mcp} reached independence ($\alpha = 0.25$).

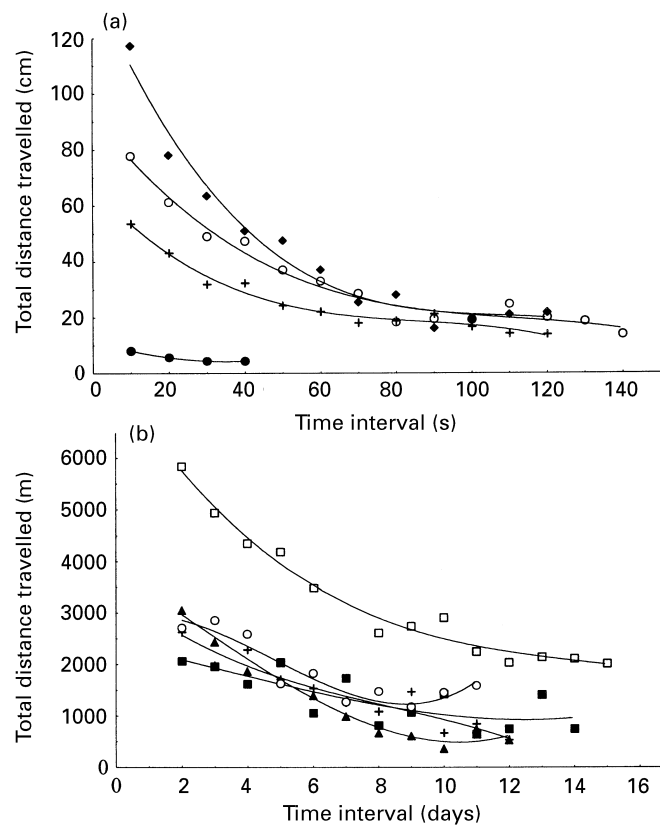Subsampling affected the distribution of observations within the home range. While the snapping

Fig. 4. Estimated total distance travelled as a function of increasing time intervals between observations. (a) Polynomial regression of total straight line distance and time interval of four antler flies. (b) Polynomial regression of total straight line distance and time interval of five snapping turtles.

turtle home range size as measured by a minimum convex polygon did not change much with sub-sampling (Fig. 7a), there were sometimes drastic reductions in antler fly home range size with sub-sampling (e.g. Figure 7b). In both cases, the sub-sampled home ranges were constructed from statistically independent observations.

A single example of an antler fly, at 10- and 70-s intervals, and a snapping turtle at 2- and 6-day intervals, illustrate the effects of subsampling on the probability distribution estimated by kernels. Although the locations of the peak densities remained the same, the relative heights were different, and the distribution at low densities (i.e. around the perimeter) were different (Figs 8a,b,c,d). Every regression was significant, but as the time interval between observations increased, the relationship between the number of observations and probability decreased (Tables 1 and 2).

The mean home range size for all antler flies showed no significant relationship with time interval (adj. $r^2 = -0.0490$, $F = 0.3932$, d.f. = 1, 12, $P = 0.5424$), but individual home ranges showed two significant negative relationships, and two non-significant trends (Table 3). The mean home range size for all antler flies showed no significant relationship with the mean t^2/r^2_{mcp} (adj. $r^2 = 0.0418$, $F = 1.567$, d.f. = 1, 12, $P = 0.2345$), nor were there any significant relation-

ships between home range size and t^2/r^2_{mcp} of individual antler flies (Table 4). We chose not to estimate snapping turtle home range sizes, because counting the number of grid cells under-estimated the minimum home range size. Many of the grid cells were isolated, thus excluding areas which the turtles must have used, and so we could not accurately describe the relationship between home range size, and the time interval or autocorrelation.

Discussion

MONTE CARLO SIMULATION

Decreasing the time interval between successive observations improved our estimates of the simulated home ranges. Although autocorrelation did have a small (but significant) effect on home range size even after the effect of the time interval was removed, this effect nevertheless reduced the bias of the home range estimate. Similarly, after the effect of autocorrelation was removed, shorter time intervals reduced the bias of the estimates. The precision of our estimates also improved at shorter time intervals, although we do not know if this is due mainly to reduced sampling error associated with larger samples sizes or due to an improved performance of the kernel estimator.
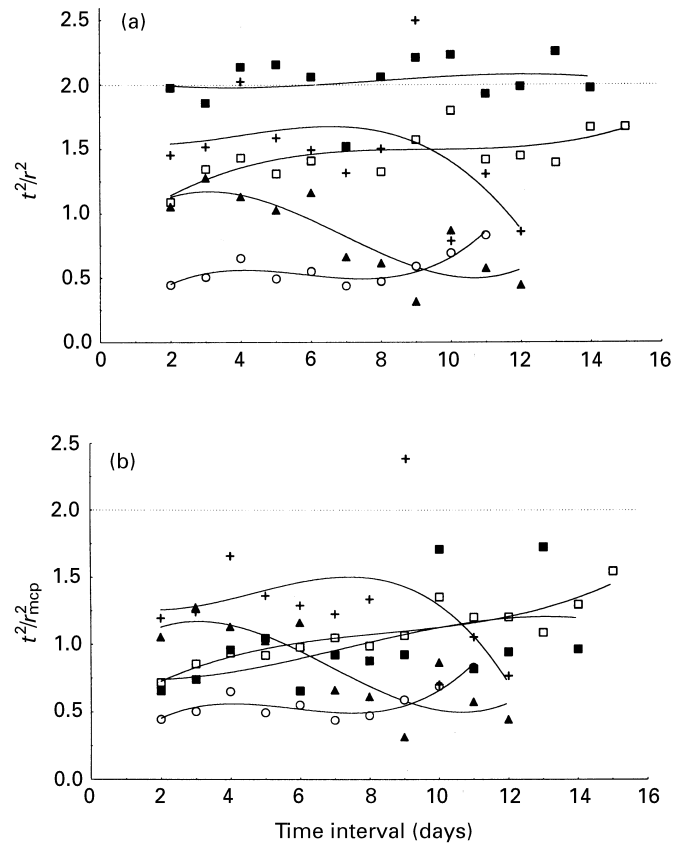
Fig. 5. Relationship between t^2/r^2 and t^2/r^2_{mcp} with time interval between observations. (a) Polynomial regression of t^2/r^2 and time interval of four antler flies. (b) Polynomial regression of t^2/r^2_{mcp} and time interval of four antler flies.

Hansteen, Andreassen & Ims (1997) also found that using the shortest time interval with the highest degree of autocorrelation, reduced the bias of kernel-based home range estimates of root voles (*Microtus oeconomus*). Swihart & Slade (1997) stated that the cost of using moderately autocorrelated data with kernel estimates was low and exclusive use of independent observations was unnecessary, although autocorrelation still slightly increased bias. It has been stated that equivalent levels of autocorrelation (Swihart & Slade 1985a), sample size (Harris *et al.* 1990) and spatial resolution (Hansteen *et al.* 1997) are required before some home range parameters can be compared among different animals. We suggest that the time interval has to be the same among animals to correctly compare home range estimates, although this means that the sample sizes have to be the same as well if the total sampling period is to remain the same.

At all time intervals, our estimates of the simulated home ranges were over-estimated. Worton (1995) suggested multiplying the h estimated by LSCV by 0·8, which would reduce the home range size and thus reduce the bias. It appears that this correction factor should be inversely proportional to the time interval, where a correction factor should be considerably smaller than 1 at larger time intervals, and approach 1 at small time intervals.

Our conclusions are different than those of either Swihart & Slade (1985a) or Cresswell & Smith (1992). First, we did not find any relationship between home range size and t^2/r^2_{mcp} from our field data, and although we found a negative relationship between t^2/r^2 and home range size from our simulation, the home range estimates were less biased with stronger autocorrelated observations. Swihart & Slade, (1985a) used a Monte Carlo simulation to model the effect of autocorrelation on home range size, in which they forced the sample size to be constant and the total sampling time period to be proportional to the time interval between observations. We do not dispute their results that sampling within a shorter time frame would reduce the size of the home range estimate, but we disagree with their conclusion that the auto-correlation is the cause. If we had used a shorter total sampling period, our home range estimates would also have been smaller. Instead, we interpret their results as suggesting that the total sampling period should be as long as possible, so as to minimize the risk of any information loss, as well as to incorporate the entire home range behaviour of the animal.

FIELD STUDIES

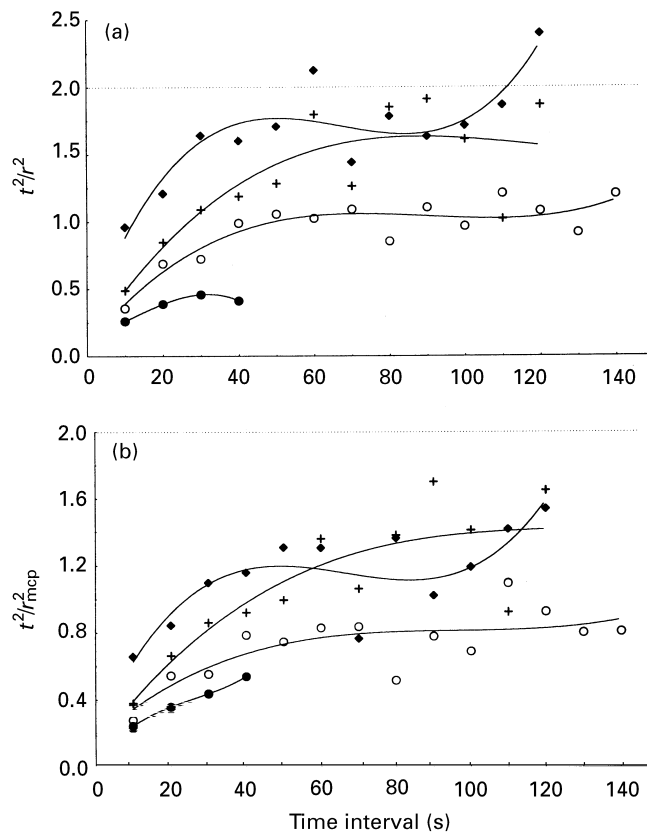Increasing the time intervals between observations failed to generate consistently independent data sets

Fig. 6. Relationship between t^2/r^2 and t^2/r^2_{mcp} with time interval between observations. (a) Polynomial regression of t^2/r^2 and time interval of five snapping turtles. (b) Polynomial regression of t^2/r^2_{mcp} and time interval of five snapping turtles.

for either antler flies or snapping turtles. The degree of autocorrelation cannot be reduced by increasing sample size because sample size could only be increased by reducing the time interval between samples. Antler flies defend territories for only a short time before they are overcome by competitors or leave to copulate. Because their territories are so transient the only way to significantly increase sample size is by reducing the time interval between observations. The sampling regime used to estimate snapping turtles home ranges encompassed almost the entire annual active season, so again sample size could only be increased by reducing the time interval between observations.

Increasing the time interval between observations of antler flies or snapping turtles did not reliably reduce autocorrelation. If the main cause of autocorrelation is due to short-term movements, we would expect that, as the time interval between observations increased, t^2/r^2_{mcp} would also increase. The initial increase in independence arising from increasing the time interval was likely due to the elimination of short-term dependence between observations, but independence was not reached even after long time intervals. Observations may remain autocorrelated if the time interval approaches an integer multiple of the period length for animals with cyclical behaviour, the animal shifts

its home range, or moves along a path in a temporally predictable manner (Swihart & Slade 1985b; Hansteen *et al.* 1997). Although we did not find evidence of periodicity in the relationship between t^2/r^2 or t^2/r^2_{mcp} and time interval, an asymptote was reached, where further changes in the time interval did not strongly affect autocorrelation. Much of the autocorrelation present, particularly at the longer time intervals, is likely to be an intrinsic property of the home range behaviour.

Antler flies defend a stable territory, but use short range search patterns to detect rivals or potential mates. Patrolling for mates or intruders should entail short, but frequent visits by the resident animal (Sherwin & Nicol 1996). Similarly, the areas in which the turtles spent prolonged periods of time were also sites to which they frequently returned, suggesting that these areas were refuges from which the turtle would occasionally venture. Any autocorrelation present at longer time intervals, while statistically dependent, were likely biologically independent (Lair 1987). The assumptions of homogeneous spatial and temporal sampling of the t^2/r^2 statistic is violated when animals move systematically in a temporally predictable manner, habitat use is constrained by spatial heterogeneity or there are shifts in the animals activity pattern (Minta 1992). The relevance of a repeated behav-
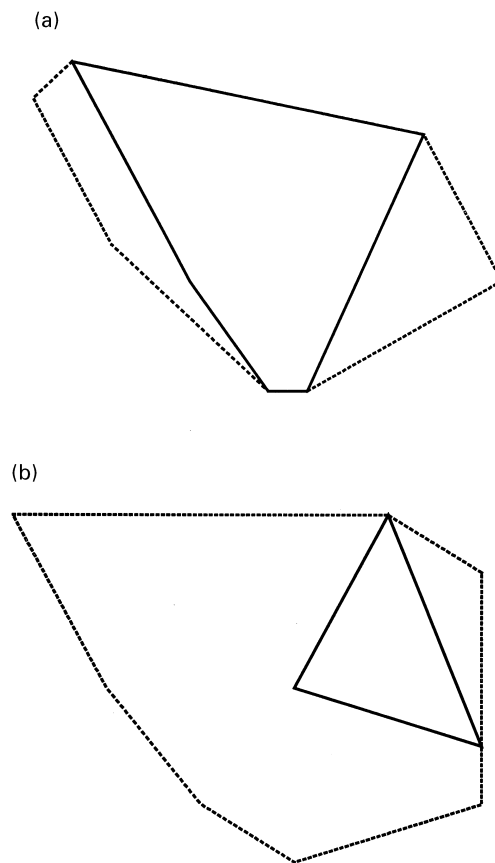
(a)

(b)

Fig. 7. Comparison of MCP home range of (a) male antler fly (all observations, $n = 43$; independent, $n = 10$) and (b) snapping turtle (all observation, $n = 138$; independent, $n = 9$) for all observations, and first statistically independent (t^2/r^2) subsample. The dotted lines represent all observations and the solid lines represent subsampled observations.

iour would be under-estimated by eliminating autocorrelation, not over-estimated by incorporating it in the analyses.

As expected, as the time interval between antler fly observations increased, the relationship between the number of observations and the corresponding probability density weakened. Although the relationship was still significant, at 70-s intervals only 71% of the variation in the probability density was explained by the number of observations, as opposed to 98% at 10-s intervals. Yet even at 70-s intervals, independence was not achieved and was reached only sporadically at a 160-s interval for t^2/r^2, and not at all for t^2/r^2_{mcp}. With such a long time interval, there were only 21 observations or 15·7% of the total observations taken. Similarly, the relationship between the number of observations and the corresponding probability density weakened as the time interval between snapping turtle observations increased. At 8-day intervals, only 56% of the variation in the probability density was explained by the number of observations. Independence was only erratically achieved at 15-day intervals, at which point there were only 17 observations or 30·4% of the initial number of observations taken. Home

range analyses cannot accurately estimate the home range size with so few observations (Harris *et al.* 1990; White & Garrott 1990).

The primary reason that the home range size, using minimum convex polygons, of snapping turtles did not decline with subsampling as much as did the antler flies (e.g. Figure 7a,b) is that snapping turtles spent most of their time buried in the mud along the periphery of the home range and occasionally foraged in the open water in the centre of the home range, while antler flies had a more even distribution. The proportion of observations that lay on the periphery of the home range is higher for snapping turtles than antler flies, so subsampling eliminated a higher proportion of peripheral observations of flies than turtles.

Our results support Reynolds & Laundre's (1990) conclusion that increasing the length of time intervals between observations under-estimates the true distance travelled. The estimate of total distance travelled by antler flies decreased precipitously as sampling rate was increased from 10 to 50-s intervals, then slowly reached an asymptotic minimum. There was a similar decline in the estimate of total distance travelled by snapping turtles, from 2- to 8-day intervals. Shorter time intervals than those used here would result in higher estimates, although at the expense of reducing independence between observations.

t^2/r^2_{mcp} appears to be better than t^2/r^2 as an index of autocorrelation as the length of time intervals increases because it is not as susceptible to sampling errors, especially at smaller sample sizes. Due to sampling error, observations from small sections of the home range were over-represented. Estimating t^2/r^2 using a static centre of activity would detect autocorrelation present when all or most of the observations were centred around a subsection of the home range. Clumping of observations at certain intervals suggests repeated activity, such as those associated with foraging, mating, resting, or similar activities (e.g. Swihart & Slade 1985b). Using a variable centre of activity to estimate autocorrelation might not detect a lack of independence amongst observations and so would reduce the ability to detect cyclical behaviour. We used the corners of a minimum convex polygon to derive a static centre of activity; however, other methods of estimating the centre of activity may also be appropriate. Lair (1987), for example, found the harmonic mean centre (Dixon & Chapman 1980) to have advantages over the arithmetic mean centre (Hayne 1949) and bivariate median centre (Neft 1966).

GENERAL COMMENTS

TTI is supposed to estimate the time required by the animal to traverse its home range, where its current position at time t is a function of home range use, rather than a function of its position at $t-1$ (Swihart, Slade & Bergstrom 1988). However, this index of statistical independence is not the same as biological
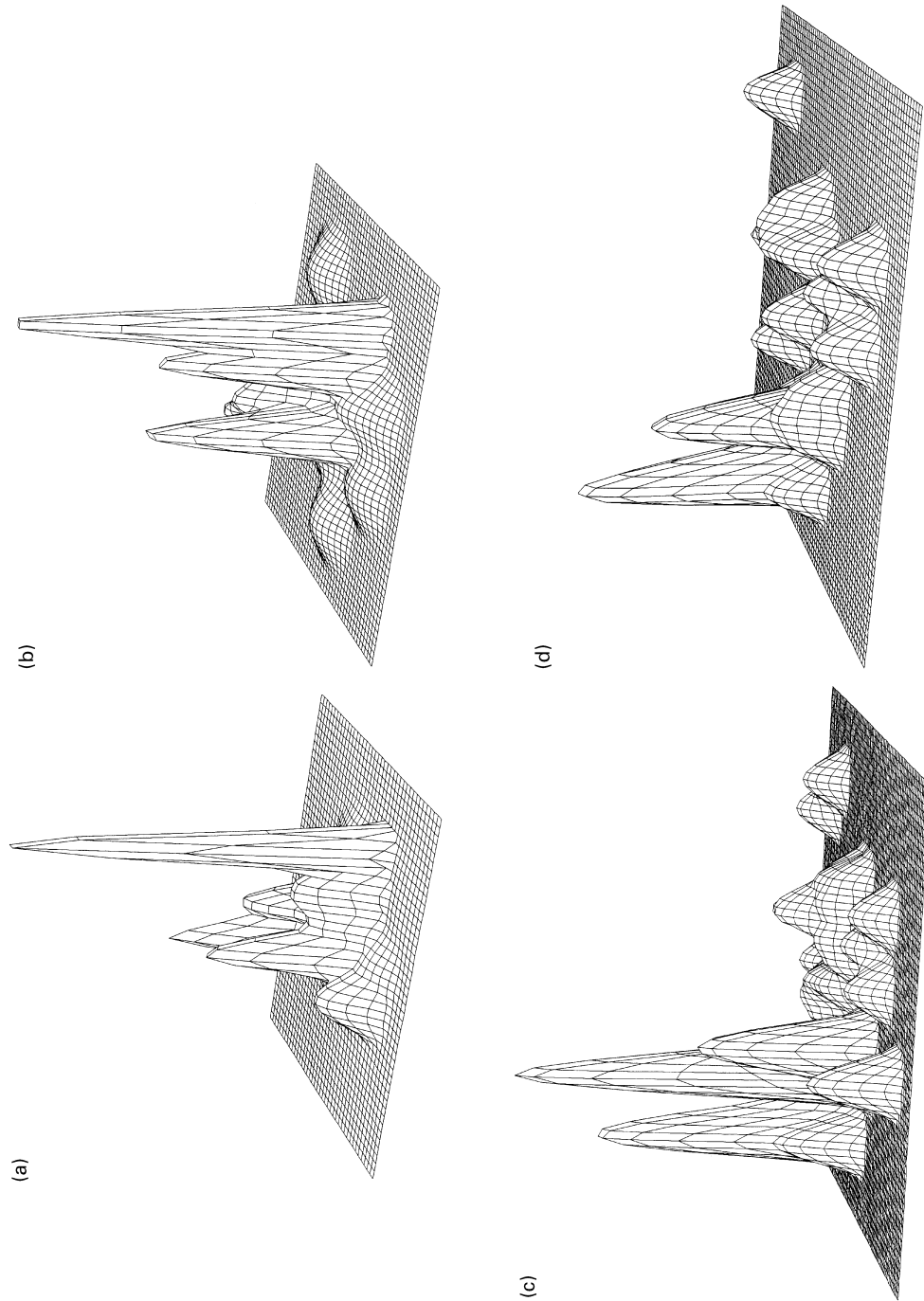
Fig. 8. Adaptive kernel density estimates. (a) Antler fly home range with 10-s intervals between observations ($h = 2\cdot6$, $n = 143$). (b) Antler fly home range with 60-s intervals between observations ($h = 2\cdot6$, $n = 24$). (c) Snapping turtle home range with 2-day intervals between observations ($h = 1\cdot2$, $n = 43$). (d) Snapping turtle home range with 6-day intervals between observations ($h = 1\cdot2$, $n = 17$).

Table 1. Regression summary of number of observations within each grid cell with the respective probability density, for each time interval for the male antler fly

Time interval	t^2/r^2_{mcp}	No. of observations	Adj. r^2	F	P-value	Sample size
10	0·5743	134	0·9793	4642·41	<0·0001	99
20	0·8370	67	0·9439	1482·19	<0·0001	89
30	0·8483	45	0·9137	721·091	<0·0001	69
40	1·0819	34	0·9129	619·489	<0·0001	60
50	1·0423	27	0·8690	266·371	<0·0001	41
60	1·1254	24	0·8494	259·405	<0·0001	48
70	1·1329	21	0·7106	106·597	<0·0001	44

Table 2 Regression summary of number of observations within each grid cell with the respective probability density, for each time interval for the male snapping turtle

Time interval	t^2/r^2_{mcp}	No. of observations	Adj. r^2	F	P-value	Sample size
2	1·097	43	0·9308	1170·92	<0·0001	88
3	1·235	33	0·8111	434·65	<0·0001	102
4	1·318	29	0·8454	460·28	<0·0001	85
5	1·301	23	0·8169	384·68	<0·0001	87
6	1·361	20	0·7512	244·19	<0·0001	79
7	1·431	17	0·6319	129·75	<0·0001	76
8	1·370	15	0·5609	94·25	<0·0001	74

Table 3. Regression of home range size and time interval of four antler flies

	Adj. r^2	Slope	F	Sample size	P-value
Fly 1	0·1786	−0·1523	3·826	14	0·0742
Fly 2	0·8433	−0·1620	17·143	4	0·0537
Fly 3	0·4501	−0·1335	10·002	12	0·0101
Fly 4	0·7785	−0·3935	39·662	12	0·0001

Table 4. Regression of home range size and t^2/r^2_{mcp} of four antler flies

	Adj. r^2	F	Sample size	P-value
Fly 1	−0·0818	0·0168	14	0·8989
Fly 2	0·8244	15·08	4	0·0568
Fly 3	0·0816	1·978	12	0·1900
Fly 4	0·0389	1·445	12	0·2570

independence, because the animal may choose to move in a non-independent fashion (Lair 1987). Antler flies could traverse the length of their home ranges within seconds, and often did. Similarly, snapping turtles at Cootes Paradise could traverse the pond which contains their entire home range within minutes. That they usually did not is probably a better reflection of their pattern of home range use than is TTI.

It has generally been assumed that autocorrelation is caused by short time intervals (Swihart & Slade 1985b; Worton 1987; Harris *et al.* 1990; White & Garrott 1990), rather than an inherent pattern of home range use. At shorter time intervals than TTI, observations may not be statistically independent, but their position at *t* may not be a function of their position at *t* − 1. Instead, the positions at *t* and *t* − 1 may both be a function of a third factor. TTI is generally considerably longer than the length of time required for the animal to travel between any two points within the home range (this study; Lair 1987). It should not be surprising that areas with autocorrelated observations are often associated with important resources (e.g. Swihart & Slade 1985b; Lair 1987; Weatherhead & Robertson 1990).

Autocorrelation among consecutive observations is analogous to the problem of pseudoreplication, which is often defined as the use of inferential statistics to test for treatment effects using replicates that are not statistically independent (Hurlbert 1984). The lack of independence among observations generally inflates the degrees of freedom for most statistical tests (Legendre 1993; Lombardi & Hurlbert 1996) and prohibits us from knowing the actual α value (Hurlbert 1984). However, using non-independent replicates or observations is not invalid, as long as the replicates are pooled to estimate a mean value for an experimental unit, and the correct degrees of freedom describing the number of experimental units, are used (Hurlbert 1984). Replication of samples within treatments increases precision by reducing 'noise' or random error (Hurlbert 1984). Individual observations in home range analyses are not treated as independent replicates to compare treatment effects, but rather a single value, home range size, is estimated by using the observations as replicate samples. Each home range can be then treated as a single experimental unit if the treatment is specific to each animal or, if the treatment is specific to certain sites, the home ranges of each animal are also pooled to compare mean home range sizes among sites. In either case, the number of observations used to estimate each home range are not used to represent the degrees of freedom for inferential statistics to test for treatment effects. Increasing the number of observations used to calculate home range size or shape increases the accuracy of the home range estimate, but does not inflate the degrees of freedom used for inferential statistics. Consequently, the assumption of independence among sequential locational observations for non-parametric home range analyses, such as kernel estimators, is not relevant.

There is an important exception to our conclusion about autocorrelation. As long as the time interval between successive observations remain relatively constant, autocorrelation should not reduce the validity of home range estimates. However, uneven sampling does bias home range estimates. 'Bursts' of sampling, where clusters of observations are closely spaced in time, but are separated from other clusters by a long time interval, will over-estimate the probability distribution at any area associated with the bursts. Sample size should not necessarily be maximized at the cost of grossly unequal sampling intervals.

We recommend that the number of observations be maximized for home range or time budget analysis using constant time intervals, even at the expense of increasing autocorrelation between observations. Our findings demonstrate that shorter time intervals better estimate parameters, such as the accuracy and precision of home range size estimates, time partitioning and distance moved. Furthermore, including autocorrelation in valid statistical models is a preferable way to deal with autocorrelation rather than to attempt to eliminate it by restricting data prior to analysis (Griffith 1992; Legendre 1993). Even if it was desirable to remove autocorrelation, this study shows that it may not always be possible to do so. This stresses the importance of combining models and empirical data to examine home range characteristics. Field studies may reveal patterns not discernable from simulations, while simulations allow proper replication. We are not arguing that tests for independence are unimportant, because they can be used to infer movement patterns; however, eliminating autocorrelation reduces statistical power, reduces the accuracy of home range analyses and destroys biologically relevant information. Few animals move in a random or temporally-independent fashion (but see Loreau & Nolf 1993), so autocorrelated data are required to sufficiently model animal movement and space use. Finally, if the prime concern of the researcher is to estimate time partitioning within the home range, then the lack of spatial independence among observations does not violate assumptions of home range analyses.

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