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Simulation analyses of space use: Home range estimates, variability, and sample size

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COMPUTER SIMULATION

Simulation analyses of space use: Home range estimates, variability, and sample size

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Simulations of space use by animals were run to determine the relationship among home range area estimates, variability, and sample size (number of locations). As sample size increased, home range size increased asymptotically, whereas variability decreased among mean home range area estimates generated by multiple simulations for the same sample size. Our results suggest that field workers should ascertain between 100 and 200 locations in order to estimate reliably home range area. In some cases, this suggested guideline is higher than values found in the few published studies in which the relationship between home range area and number of locations is addressed. Sampling differences for small species occupying relatively small home ranges indicate that fewer locations may be sufficient to allow for a reliable estimate of home range. Intraspecific variability in social status (group member, loner, resident, transient), age, sex, reproductive condition, and food resources also have to be considered, as do season, habitat, and differences in sampling and analytical methods. Comparative data still are needed.

The way animals use space is of practical and theoretical interest to a wide variety of scientists, including those studying (1) relationships between behavior, age, sex, and spacing patterns, (2) resource distribution as it affects space use, (3) the relationship between metabolic requirements and home range size, and (4) space requirements for purposes of control or reintroduction of "problem" or endangered species (Altmann, 1974; Bekoff, Daniels, & Gittleman, in press; Brown & Orians, 1970; Burt, 1943; Cheeseman & Mitson, 1982; Gittleman

& Harvey, 1982; McNab, 1963; Mech, 1983; Milton & May, 1976; Powell, 1979; Rose, 1982; Sanderson, 1966; Waser & Wiley, 1979). A question that is applicable to all such studies is, "Why is the animal at a particular place at a particular time?" (Sanderson, 1966). Other questions deal with the relationship between space use and individual fitness (Parker & Knowlton, 1980; Waser & Wiley, 1979), for which there are few data and many conjectures. Regardless of field of interest, a prerequisite to studying space use and movement patterns is that they be reliably measured.

As in many other areas of research, data concerning space use and movement patterns often are easy to gather (or appear to be easy to collect) but difficult to interpret. Theoretical approaches are numerous (Anderson, 1982; Cooper, 1978; Ford & Krumme, 1979; Hayne, 1949; Heezen & Tester, 1967; Jennrich & Turner, 1969; Koeppl, Slade, & Hoffmann, 1975, 1977; Metzgar & Sheldon, 1974; Mohr, 1947; Mohr & Stumpf, 1966; Rasmussen, 1980; Schoener, 1981; Siniff & Jessen, 1969; Stickel, 1954; van Winkle, 1975), but the "correct" method of analysis is closely related to the questions being asked and to the method used to generate the data; there does not appear to be a right or a wrong way to analyze space use or movement patterns.

Numerous variables also influence the accuracy of home range size and shape estimates (Burt, 1943). These include sample size (number of locations), sampling

interval and technique, and the accessibility of subjects to direct observation, radio-telemetric study, and/or trapping (see Adams & Davis, 1967, Anderson, 1982, Hayne, 1949, Heezen & Tester, 1967, Mech, 1983, Sanderson, 1966, Sargeant, 1979, Stickel, 1954, and Waser & Wiley, 1979, for discussions of various techniques). Social status (e.g., group member, loner, resident, transient), age, sex, reproductive condition, food resources, the presence (or absence) of conspecifics and other individuals, and habitat (forest, open plains, terrain) also influence movement patterns and space use and consequently the reliability of home range estimates (e.g., Andelt, 1982; Bekoff & Wells, 1980, 1981, 1982; Bowen, 1982; Hibler, 1977; Kruuk, 1972; Laundré & Keller, 1984; Mech, 1970; Messier & Barrette, 1982; Milton, & May, 1976; Powell, 1979; Rose, 1982; Schaller, 1972; Waser & Wiley, 1979). Furthermore, as Mohr (1947) noted, large ranges usually result in reduced accuracy of movement estimates. With respect to sample size, it generally appears that as the number of locations increases, estimated home range area also increases until an asymptote is reached (Anderson, 1982; Bowen, 1982; Fritts & Mech, 1981; Jennrich & Turner, 1969; Koeppl et al., 1977; Mares, Willig, & Bitar, 1980; Metzgar & Sheldon, 1974; Odum & Kuenzler, 1955; Parish & Kruuk, 1982; Rose, 1982; Smith, Cary, & Rongstad, 1981; Stickel, 1954; Waser & Floody, 1974; Waser & Wiley, 1979; Woodruff & Keller, 1982), and additional sampling adds proportionately smaller increases in area to the estimated home range size.

The purpose of the present analysis was to study the relationship between sample size and home range estimates in order to determine a guideline that would be useful to field researchers interested in space use patterns. The relationship between number of locations and variability in estimated area also was evaluated; this aspect of space use analysis is absent in most studies of animal movement.

SIMULATION ANALYSES

Simulations were run using SPACE-OUT, a package of Hewlett-Packard BASIC graphics programs designed specifically to simulate and to analyze space use and movement patterns of animals (Bekoff, Wieland, & Lavender, 1982). One program, RAND, simulates movement patterns by randomly assigning (x,y) coordinates to a previously determined number of location points (between 10 and 2,000), each representing successive "sightings" of an individual. In addition to selecting the number of locations, one can choose the size of the study plot (10 x 10 units to 100 x 100 units), the maximum Euclidean distance that an individual is allowed to travel on each move, the (x,y) coordinate at which movements begin, and various labeling options (see Bekoff et al., 1982, for details).

The present simulations were run on a 10 x 10 plot (the maximum area covered = 100 units^2), and movements began in the center (5.00,5.00). The length of

movements was unrestricted within the boundaries of the chosen area. The total area encompassed by a plot of this size when a unit = 1 km includes home range estimates for a wide variety of mammals (recognizing that there is considerable intraspecific variability), excluding dispersal and occasional sallies outside the area of most intensive use (Bailey, 1974; Bekoff, 1982; Bekoff & Wells, 1982; Bowen, 1982; Chapman & Feldhamer, 1982; Cheeseman & Mitson, 1982; French, Stoddart, & Bobeck, 1975; Fritzell, 1978; Fuller, 1978; Georgii, 1980; Gittleman & Harvey, 1982; Harestad & Bunnell, 1979; Harvey & Clutton-Brock, 1981; Hibler, 1977; Ikeda, Eguchi, & Ono, 1979; Kruuk, 1972, 1978; Mech, 1970; Messier & Barrette, 1982; Mohr, 1947; Murray, 1982; Schaller, 1972; Schaller & Crawshaw, 1980; Sinclair, 1977; Singer, Otto, Tipton, & Hable, 1981). Ten simulations each were run for N (total locations) = 10, 25, 50, 75, 100, 200, 300, 400, and 500.

Simulation data were analyzed using 3DPOLY (Bekoff et al., 1982), a program that generates six two-dimensional, convex, percent-use polygons. The polygons represent the core areas encompassed by 25%, 50%, 75%, 90%, and 95% of the total locations (N), as well as the area defined by N (100%). Each polygon is constructed outward from a single geometric center [mean (x,y) coordinate of the total sample]. The minimum area method (Mohr, 1947) was used, and only convex polygons were constructed (Jennrich & Turner, 1969; Smith et al., 1981). We used the minimum convex polygon technique because it is the most common way in which researchers study space use, it is relatively easy to use, and it allows for a quick approximate estimate of home range size (Anderson, 1982; Rose, 1982). In some cases, this method is no less reliable than other techniques (Mares et al., 1980). However, the minimum convex polygon method is very sensitive to sample size (Anderson, 1982, and references therein; Ford & Krumme, 1979; Schoener, 1981), and for this reason, the present analyses are useful in detailing the relationship between sample size and home range estimates for scientists choosing this technique.

Although six convex percent-use polygons were generated in each simulation, we present data only for the 50% and 95% polygons (the area encompassed by 0.50N and 0.95N closest to the geometric center). The 95% area is usually used to estimate home range size (Anderson, 1982; Bekoff & Wells, 1982; Bowen, 1982; Michener, 1979) because occasional sallies and dispersal are discounted. In some cases, the 50% polygon can also be used to estimate home range area (Anderson, 1982). Data for the other percent-use polygons are available from the senior author; trends similar to those reported here were found.

RESULTS

Results are presented in Figure 1 and Tables 1 and 2. For both the 50% and 95% polygons, there was a significantly positive relationship between number of locations
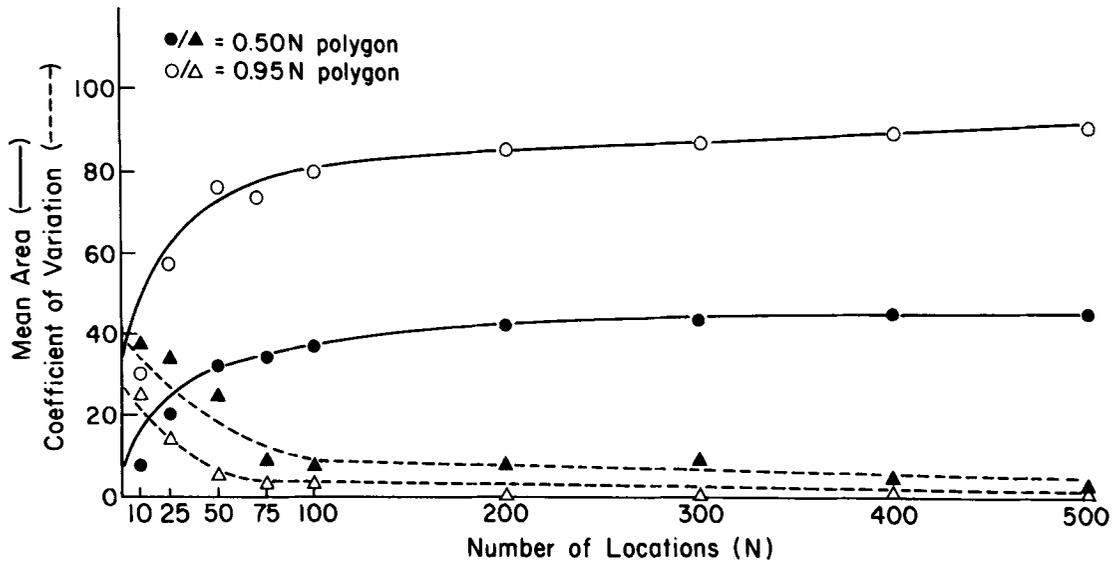
Figure 1. The relationship between estimated mean home range size (——) and variability (– – –) (coefficient of variation) and number of locations. "0.50N polygon" and "0.95N polygon" refer to the percent-use convex polygons that encompass 50% and 95%, respectively, of the total number of locations (N); see text and Bekoff et al. (1982).

Table 1
Mean Home Range Area Estimates (MHRA), Standard Deviations (SD in Parentheses), and Coefficients of Variation (CV) for
Multiple Simulations Run for 9 Sample Sizes (Total Number of Locations, N). See Text for Details.

	N	MHRA	Δ MHRA(%)*	% N = 500 MHRA Estimate	CV(%)
(a) 50% Polygon	10	7.88 (2.73)		17.24	35
	25	20.52 (7.04)	160.41	44.90	34
	50	32.55 (8.10)	58.63	71.23	25
	75	34.01 (2.96)	4.49	74.42	9
	100	36.96 (2.98)	8.67	80.88	8
	200	42.82 (3.45)	15.85	93.70	8
	300	43.83 (4.13)	2.36	95.91	9
	400	45.15 (2.15)	3.01	98.80	5
	500	45.70 (1.61)	1.22	100.00	4
ANOVA: F(8,81) = 82.90, p < .00001					
N = 10 25 50 75 100 200 300 400 500**					

	N	MHRA	Δ MHRA(%)*	% N = 500 MHRA Estimate	CV(%)
(b) 95% Polygon	10	31.61 (7.99)		34.56	25
	25	57.48 (7.97)	81.84	62.85	14
	50	76.07 (4.63)	32.34	83.17	6
	75	73.56 (2.64)	–3.30	80.43	4
	100	80.58 (2.85)	9.54	88.10	4
	200	86.72 (1.22)	7.62	94.82	1
	300	87.76 (1.25)	1.20	95.95	1
	400	89.16 (2.05)	1.60	97.49	2
	500	91.46 (1.40)	2.58	100.00	2
ANOVA: F(8,81) = 193.05, p < .00001					
N = 10 25 50 75 100 200 300 400 500					

*Percentage change in MHRA when compared with the next smaller N; all changes are positive except where noted.   **Results of analysis of variance (ANOVA); the sample sizes (N) connected with underlines (_____) represent 5 homogeneous subgroups (means for MHRA were not significantly different) identified by Scheffé's procedure.

(N) and mean home range area (MHRA) and a significantly negative relationship between N and variability (as measured by the coefficient of variation, CV = SD x 100/mean). Regression equations and other pertinent information are presented in Table 2. For all analyses, curvilinear (cubic) regressions yielded the highest coefficients of determination, r^2 (a measure of the proportion of variation of one variable that is determined by variation of the other variable; Sokal & Rohlf, 1981) and were more highly statistically significant than were linear regressions.

Analyses of variance for the MHRAs encompassed by

Table 2
Regression Equations for the Relationships Between (a) Mean Home Range Estimates (MHRA) and (b) Variability
(Coefficient of Variation, CV) and Sample Size (Total Number of Locations, N). See Figure 1.

	Polygon	Regression Equation	r^2	F	p
(a)		MHRA =			
	50%	$9.60 + 0.41N - 0.001N^2 + 0.000002N^3$	0.83*	136.34	<<.001
	95%	$37.37 + 0.65N - 0.002N^2 + 0.000003N^3$	0.83	136.62	<<.001
(b)		CV =			
	50%	$39.80 - 0.43N + 0.002N^2 - 0.000002N^3$	0.89**	13.26	.008
	95%	$23.43 - 0.32N + 0.001N^2 - 0.000006N^3$	0.87	10.82	.013

*r^2 = coefficient of determination; for the 50% polygon, r^2 for the linear regression = 0.53; for the 95% polygon r^2 for the linear analysis = 0.49.   **For the 50% polygon, r^2 for the linear regression = 0.54; for the 95% polygon, r^2 for the linear analysis = 0.38.

the 50% and 95% polygons for different Ns were highly significant, and the same homogeneous subgroups were identified using Scheffé's procedure (Table 1). For the 50% polygon, the MHRA estimate increased less than 3.01% for N > 200, when compared with the next smallest N, and N = 200-500 was a homogeneous subgroup in the analyses of variance. The difference between the MHRA estimates for N = 200 and N = 500 was 6.30%. For the 95% polygon, the MHRA estimate increased less than 2.58% for N > 200, when compared with the next smallest N, and N = 200-500 formed a homogeneous subgroup. The difference between MHRA estimates for N = 200 and N = 500 was 5.18%. For both the 50% and 95% polygons, an estimate of at least 90% of the MHRA for N = 500 was not achieved until 200 locations were used (Table 1); for the 95% polygon, the MHRA estimate for N = 100 was 88.10% of the N = 500 MHRA estimate.

DISCUSSION

The results of these simulations are consistent with the numerous studies cited above in which home range size increased asymptotically with number of locations, but provide more detailed analyses of the functional (regression) relationships between these two variables. Furthermore, as sample size increased, variability decreased among the mean home range area estimates generated by multiple simulations for the same number of locations. Coefficients of variation were <10% for N > 75 (50% polygon) and N > 50 (95% polygon). In many biological systems, coefficients of variation of <10% indicate a high degree of stability (Schleidt, 1974). Indeed, for field conditions, it might be naive to believe that it would be possible to measure home ranges with such accuracy that coefficients of variation of less than 5%-10% would be realistic estimates of the true variation that is present.

The present simulations indicate that an accurate (and cost-effective) estimate of home range size requires approximately 100 to 200 locations. When these results are compared with some of the few data available for the relationship between sample size and the reliability of home range estimates, the guideline of 100-200 lo-

cations is higher. For example, Siniff & Jessen (1969) found that in a simulation of animal movements based on 400-800 locations, 100 points were sufficient for a reliable estimate of movement patterns. For coyotes (Canis latrans), it has been suggested that about 40-50 "independent" locations [assumptions of independence are rarely if ever addressed (Anderson, 1982); see Schoener (1981) for a method for testing independence] were sufficient to estimate reliably home range size (Bowen, 1982; Messier & Barrette, 1982; Smith et al., 1981), whereas for wolves (C. lupus), 35-120 locations were needed (Fritts & Mech, 1981). Messier and Barrette (1982) considered that a home range estimate was adequate if the size of the area increased less than 10% with 20 additional daily locations. Using this criterion, our results still indicate that about 100-200 locations are needed for both the 50% and 95% polygon.

With respect to coyotes at least, our guideline of 100-200 locations is in general agreement with suggestions made by other researchers (Hibler, 1977; Laundré & Keller, 1984; Woodruff & Keller, 1982; also see Andelt, 1982). Hibler (1977) recommended that about 150 locations were necessary for an accurate estimate of home range area, and Laundré and Keller (1984) concluded that most home range estimates for coyotes were derived from insufficient sampling; they suggested that at least 100 locations were necessary. Woodruff and Keller (1982) found that a minimum of 150-175 locations were needed to estimate coyote home ranges. Undoubtedly, for coyotes and other species, sampling and analytical techniques as well as intraspecific variability in social status (e.g., group member, loner, resident, transient; it may change during the course of study), age, sex, reproductive condition, food resources, the presence (or absence) of conspecifics and other individuals, and season and habitat also need to be considered.

The size of an animal also may be an important variable to consider in the relationship between sample size and the reliability with which home range areas can be estimated. For Eastern chipmunks (Tamias striatus), Mares et al. (1980) reported that a minimum of 20 captures was necessary to estimate home range size; for lizards (Sceloporus virgatus), 18 locations seem sufficient

(Rose, 1982). Schoener (1981) suggested that, to estimate home range areas for lizards, regression equations for $N > 25$ must be used.

In general, smaller species tend to have smaller home ranges (comparative data can be found in French et al., 1975, Gittleman & Harvey, 1982, Harestad & Bunnell, 1979, Harvey & Clutton-Brock, 1981, Mace & Harvey, 1983, and McNab, 1963; also see Eisenberg, 1980, 1981). Because small home ranges are easier to estimate reliably (Mohr, 1947), it would not be surprising to find that fewer locations are needed for smaller (when compared with larger) species. Additional data are needed to determine rigorously how body size and associated factors (such as metabolic needs; Gittleman & Harvey, 1982; Harvey & Clutton-Brock, 1981; McNab, 1963) enter into the relationship between the number of locations needed to estimate reliably home range sizes for diverse species. This is not a trivial endeavor, because space use analyses form an important basis for many studies of social biology, behavioral ecology, population biology, demography, and life-history tactics.

The present analysis treats an animal's home range as though it were a static entity. In reality, a home range probably develops and changes constantly in geographic and geometric area. Thus, most schemes that sample real home ranges can only grossly represent the actual home range. For example, the mean and variation of home range areas based on 10 samples of 100 locations of an animal taken during 1 month would no doubt differ considerably from the mean and variation of 10 samples of 100 locations taken over 1 year. Nevertheless, our analysis does offer one important set of known relationships among components of the sampling scheme that biologists use to describe home ranges. In this way, it provides a useful insight into the interpretation of data based on various sampling approaches.

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