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IDENTIFYING AREAS OF CONCENTRATED USE WITHIN THE HOME RANGE

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SUMMARY

(1) Animals generally use space disproportionately within the boundaries of their home range. Areas receiving concentrated use by resident animals can be termed core areas. Identifying these core areas is an important part of understanding the ecological factors that determine use.

(2) Comparison of the observed space-use pattern with that expected from a uniform pattern of use is our basis for defining core areas. The difference in ordered cumulative distribution functions can be tested using a one-sided goodness-of-fit procedure. Core areas are delineated by enscribing those areas within the home range where use exceeds that expected from a uniform distribution.

(3) This method of estimating core areas is illustrated with a hypothetical data set and applied to radio-telemetry locations of a black bear (*Ursus americanus*, Pallas). The bear used two distinct core areas, which enclosed 34% of the total home range and included 76% of the animal locations.

(4) Patterns of core area use are demonstrated for male western tanagers (*Piranga ludoviciana*, Wilson). Although 90% home range boundaries overlap, core areas for four adjacent males are shown to closely resemble exclusive-use territories.

(5) Interspecific use of core areas of western tanagers and chipping sparrows (*Spizella passerina*, Bechstein) are compared. Core areas for chipping sparrows tended to be a larger proportion of the home range and intensity of core area use was greater for western tanagers.

(6) The size and location of core areas depend on the method of determination of home range size. Alternative home range methods may have a substantial influence on the estimation of core areas due to differences in the estimated home range boundary and underlying use distribution.

INTRODUCTION

The appropriate way to represent an animal's home range is a persistent problem (Metzgar 1973). Historically prominent methods, such as the minimum convex polygon method (Mohr 1947), the circular normal (Calhoun & Casby 1958), and the bivariate normal (Jennrich & Turner 1969), have been reviewed by Van Winkle (1975); Macdonald, Ball & Hough (1980); Voigt & Tinline (1980) and Schoener (1981). A variety of additional methods have been proposed recently (Ford & Krumme 1979; Dixon & Chapman 1980; Schoener 1981; Anderson 1982; Don & Rennolls 1983). Many of these methods calculate a utilization distribution describing the relative intensity of an animal's use of areas within a

defined space (Van Winkle 1975) and then specify the home range boundary by the contour that encompasses a selected percentage of the total space used (Anderson 1982).

The arguments over appropriate methods for estimating home ranges have focused on boundary estimation, ignoring the 'internal anatomy' of the home range (Adams & Davis 1967; Leuthold 1977). Hayne (1949) recognized that an understanding of the biological significance of an animal's home range required some knowledge of the intensity of use of various parts of the area. One approach to analysis of the interior of the home range is the concept of core area (Kaufmann 1962). This concept deserves increased consideration in the theoretical and practical development of methods to analyse patterns of space-use by animals. Our goal is to propose a standardized method for defining and identifying core areas and to illustrate the method with both hypothetical and actual location data.

CORE AREA CONCEPT

The existence of core areas within an animal's home range was suggested by Kaufmann (1962). Core areas are those areas used more frequently than any other areas and probably contain the homesites, refuges, and most dependable food sources (Burt 1943; Kaufmann 1962; Ewer 1968). Ewer (1968; p. 65) argued that 'it is not uncommon to find that while the home ranges overlap, the core areas do not'. Thus, delineating these areas of intense use may be particularly important in studying the interaction between individuals and interactions with the environment.

A variety of *ad hoc* techniques have been used to delineate core areas within a home range. Ables (1969) partitioned the home range of foxes (*Vulpes vulpes*) into grids and plotted the frequency distribution of grids containing one, two, three, etc., fixes (radio-telemetry locations). This distribution of grid use was compared to an expected geometric distribution. Ables (1969) found the tails of the observed distribution contained a larger number of fixes than expected from the geometric distribution. This clumping of fixes was attributed to intensive use of those sections of the home range. Murie & Harris (1978) considered core areas to constitute those grid cells where an individual ground squirrel (*Spermophilus colombianus*) was seen at least 25% of the days that the animals was observed. They found that males defended these areas more than other parts of the home range. Macdonald, Ball & Hough (1980) used a bivariate normal ellipse containing 62·3% of the probability distribution to designate core areas. Mohr & Stumpf (1966) defined the core of the range to include 75% of the points nearest the major and minor axes. Springer's (1982) study of movement patterns of coyotes (*Canis latrans*) found that daily locations occur in clusters. These clusters were called core areas and were composed of three or more daily locations that were within one-half the average distance of a daily move for that animal. These core areas contained 83% of the radio-locations but only 8·5% of the home range area.

Clutton-Brock, Guiness & Albon (1982) defined core areas as the number of adjacent 100 × 100 m quadrats accounting for 65% of sightings of individual red deer (*Cervus elaphus*). Their choice of 65% was based on detailed analysis of the change in home range size when increasing proportions of the outlaying observations were excluded. When 30–40% of the sightings were excluded the majority of females analysed showed an increasing curve gradient between per cent total range and per cent observations excluded. This criterion was used as an indication of transition between consistently heavily used centre portions of the home range and outer occasionally used areas. Clutton-Brock,

Guiness & Albon (1982) found that core areas were closely related to home range size and that core areas differed seasonally, between sexes in winter, in relation to habitat components, or as a result of female status (yeld or milk).

The common principle underlying all of these techniques is that animals use areas disproportionately within their home range. Alternatively, animals may use with equal intensity all areas within the home range (a uniform utilization distribution Metzgar 1973; Type A). Thus, we define core areas to be those portions of the animal's home range that exceed an equal-use pattern.

TEST PROCEDURE

Consider a hypothetical animal whose home range is based on twenty-four locations within sixteen square units (Fig. 1). If the animal uses its home range uniformly the proportion of use in each grid cell would be 1/16 or 0·063. However, the animal appears to concentrate its activity in cells AG, BG, CF, CG and DG, where proportions of use equal 2/24 (0·083), 3/24 (0·125), 5/24 (0·208), 6/24 (0·250), and 2/24 (0·083), respectively. By ordering the grid cells on the basis of these proportions of use, an ordered distribution results (Fig. 2a). The intersection of the ordered utilization distribution with the expected uniform probability (0·063) identifies the largest potential core area where all cells received greater-than-uniform use. This intensity of use of the core area is then tested for significance by comparing the value of the ordered observed cumulative distribution function (CoF, F) with that hypothesized (F_0) for the uniform distribution (Fig. 2b). By definition, the maximum difference between CDFs is at the intersection point (Fig. 2a) and may be tested by a one-sided Kolmogorov goodness-of-fit procedure (Daniel 1978). The null hypothesis may be stated as $F \leqslant F_0$. If the difference between CDFs is significant, the core area is delimited by the appropriate contour that includes only those grid cells that are ordered to the left of the intersection point (shaded area, Fig. 1). This difference ($D+ = 0{\cdot}75 - 0{\cdot}31 = 0{\cdot}44$) is significant ($P < 0{\cdot}01$, $n = 24$) for hypothetical data (Fig. 2b).

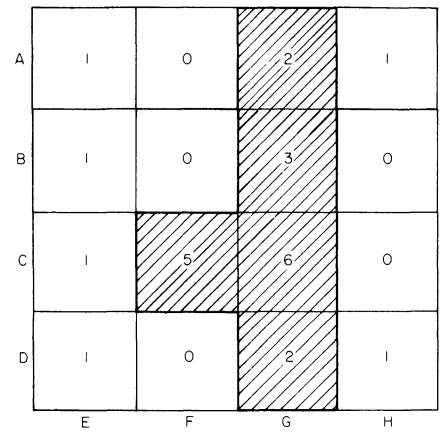

FIG. 1. Hypothetical home range based on twenty-four locations. Grid cell values represent the number of observations in each area. The shaded area represents cells receiving greater-than-uniform use.

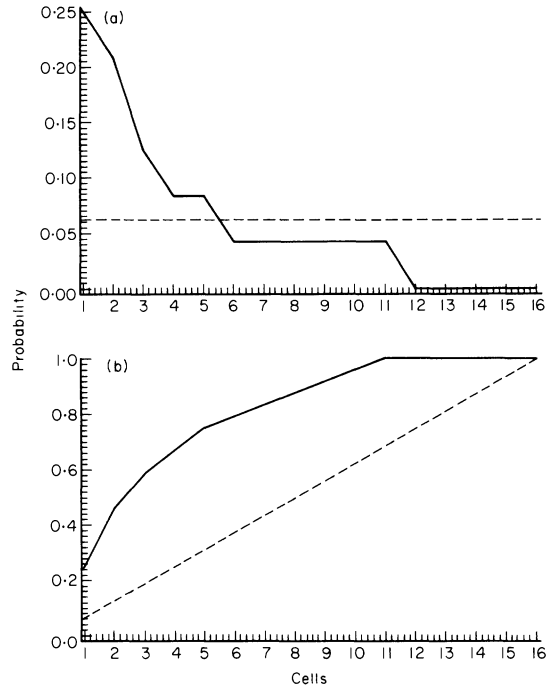

FIG. 2. Comparison of observed (——) and uniform (– – –) probabilities for hypothetical data. (a) Ordered probabilities and (b) ordered cumulative probabilities.

APPLICATION

The utilization distribution for an adult black bear (U60) in south-central Idaho during 1975 was estimated from forty-nine radio-telemetry locations (Fig. 3a) using the harmonic mean distance between locations (Dixon & Chapman 1980) as modified by Samuel *et al.* (1983). The bear was located from the ground and from fixed-wing aircraft at approximately 4-day intervals (Reynolds 1977). Grid cells from the observed utilization distribution were ordered to determine the intersection point with an expected uniform distribution. The ordered utilization distribution was used to form an ordered observed CDF (F) following the test procedures previously described. The Kolmogorov $D+$ test (Stephens 1974: Case 0) showed a significant difference ($P < 0{\cdot}05$, $n = 49$) between the uniform CDF (F_0) and F. The 95% home range area (Fig. 4) was 50·3 square kilometers. The core areas (Figs 3b and 4) contained 34% of the total home range, 52% of the utilization distribution, and 76% of the radio-telemetry locations. Notice that two distinct core areas were identified. A goodness-of-fit test of the location data for bivariate uniformity (Samuel & Garton 1985) rejected the uniform distribution ($P < 0{\cdot}01$) providing further evidence for the existence of a core area.

Core areas identified by these procedures were useful in investigating the territorial behaviour and habitat usage of male western tanagers studied on a 10 ha site in the coniferous forest of northwest Montana during 1982 (M. D. Samuel unpublished data). Birds were mist-netted and uniquely colour banded for field identification. Five males established territories on the site and were studied throughout the breeding period. Subsequent visual observations were made and recorded in 12·5 × 12·5 m quadrats

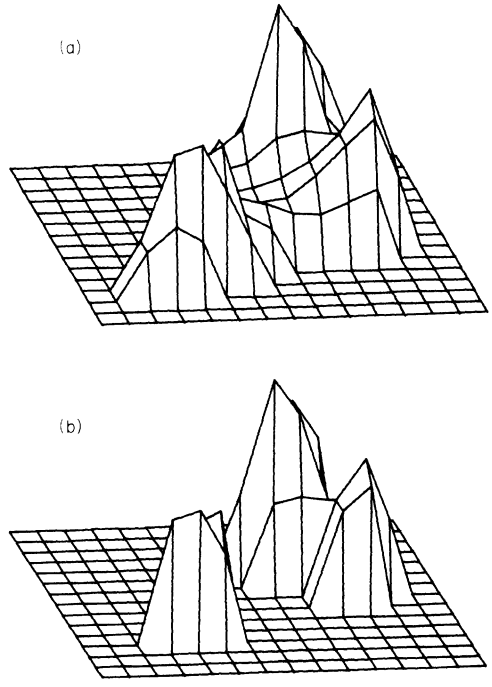

FIG. 3. Utilization distribution of black bear U60. (a) Total home range and (b) core area. Vertical axes: the proportion of the bear's total activity that occurs in each grid cell.

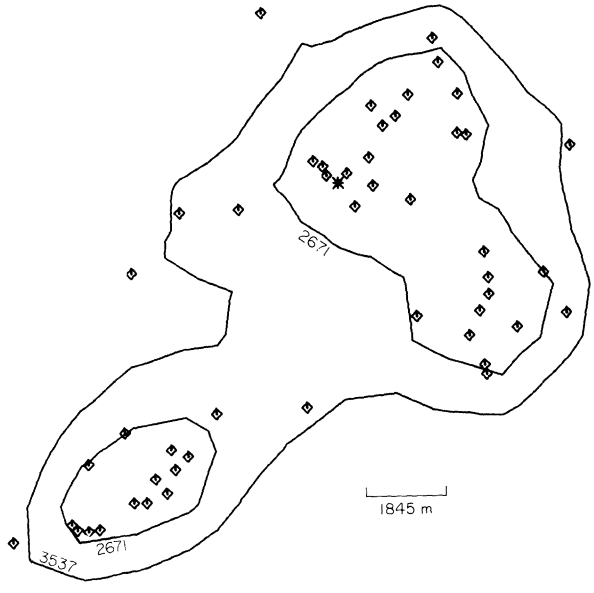

FIG. 4. Home range of black bear U60. Diamonds are recorded locations. Harmonic mean distance contours 2671 and 3537 enclose the core areas and 95% of the utilization distribution, respectively. Star (★) indicates the centre of activity.

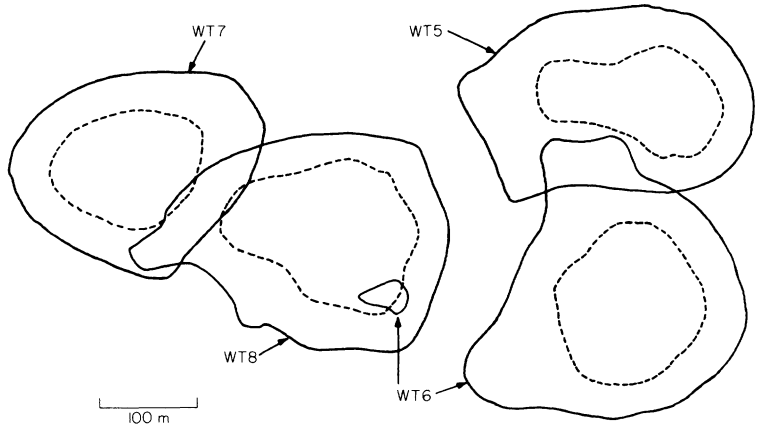

FIG 5. Male western tanager 90% (——) home ranges and core areas (– – –). Core area data presented in Table 1.

within the study site by observers walking the grid system between sunrise and 1300 h. Home ranges and core areas (Fig. 5) were determined using the harmonic distance method (Dixon & Chapman 1980) as modified by Samuel *et al.* (1983).

Four male tanagers with adjacent territories were located frequently enough to obtain a good description of their home ranges. Home range boundaries overlapped for most combinations of these adjacent males (Fig. 5). No overlap of core areas was found. However, 90% home range boundaries slightly overlapped core areas for birds 6 and 8. This resulted from a disjoint home boundary for bird 6. This male was observed in the core area of male 8 only prior to nesting and immediately following an apparent home range shift by male 8 and his mate (female 4). Nest locations were known for three of the males and all nests were contained in the respective male's core area.

We compared the home range patterns for four chipping sparrows and eight western tanagers studied at the same site in northwest Montana during 1981 and 1982. Other individuals (ten sparrows and eight tanagers) were observed an insufficient number of times (<30) to detect core areas. The core area (in ha), per cent of the home range contained in the core area (%HR), the per cent of the home range use within the core area (%USE), and intensity of core area use (INTEN = %USE/%HR) were calculated for each individual with a core area (Table 1). Data for female tanager 4 were eliminated from the analysis because its %USE value was judged to be an outlier, and it caused a non-normal distribution of the %USE variable ($P < 0{\cdot}01$; W statistic, Shapiro & Wilk 1965). The home range estimates for this female may have been adversely influenced by the shift previously mentioned. This bird was the only individual to show two distinct core areas, one surrounding the nest site and the other near the first use area. The remaining data were normally distributed ($P > 0{\cdot}05$; W statistic) and homogeneous in variance ($P > 0{\cdot}05$; F max test, Kirk 1982) for all variables.

A univariate covariance analysis (ANCOVA) was conducted for each dependent variable to test for species differences. Number of observations (n) was a significant concomitant variable for all but %USE. No evidence was found of non-linearities between n and the dependent variables, and the assumption of homogeneity of slopes was satisfied (Kirk

TABLE 1. Patterns of core area use for western tanagers and chipping sparrows

	Species	Sex	Year	n	Core Area (ha)	%HR†	%USE‡	INTEN§
1	WT	M	1981	19	0·386	20·7	58·3	2·82
2	WT	M	1981	67	0·904	33·0	60·1	1·82
3	WT	F	1982	41	0·896	27·6	61·0	2·21
4	WT	F	1982	35	0·347	24·5	50·2	2·05
5*	WT	M	1982	21	0·809	29·3	58·4	1·99
6*	WT	M	1982	57	1·104	27·4	62·7	2·29
7*	WT	M	1982	43	0·786	27·1	61·5	2·27
8*	WT	M	1982	87	1·216	33·0	61·5	1·86
9	CS	F	1981	36	0·361	27·8	57·4	2·06
10	CS	F	1981	51	0·738	35·4	62·2	1·76
11	CS	M	1982	45	0·791	30·4	54·9	1·81
12	CS	M	1982	65	1·001	36·2	58·2	1·61

* Individuals with home ranges and core areas illustrated in Fig. 5.
† %HR = per cent of the home range area within the core area.
‡ %USE = per cent of the home range use within the core area.
§ INTEN = %USE/%HR a measure of intensity of use within the core area.

1982) for all ANCOVA. Chipping sparrows had core areas that tended to occupy a greater ($P = 0{\cdot}058$) per cent of the home range than western tanagers. Western tanagers used their core areas more intensely than chipping sparrows used theirs ($P = 0{\cdot}04$). Species differences were not significant for size either of the core area ($P = 0{\cdot}154$) or per cent of use within the core area ($P = 0{\cdot}128$).

ALTERNATIVE HOME RANGE METHODS

The determination of core areas cannot be divorced from the general problem of estimating home range size. Changes in home range area will directly influence the expected uniform probability for each grid and consequently the intersection point and core area test. This point can be illustrated by reconsideration of our hypothetical example (Fig. 1). An alternative home range estimator might exclude the five cells without observations (AF, BF, BH, CH and DF) from the home range area. The new home range contains only eleven cells with an expected uniform use of 1/11 or 0·091. Consequently, the observed use of cells AG and DG is below that expected from uniform and is therefore excluded from the core area. The new core area consists of cells BG, CF, and CG. The difference between the expected uniform and observed distribution ($D+ = 0{\cdot}58 - 0{\cdot}27 = 0{\cdot}31$) remains significant ($P < 0{\cdot}01$, $n = 24$).

Detection of a core area requires comparison of the observed utilization distribution with an expected uniform distribution. This implies that the observed utilization distribution must have finite boundaries. Home range methods that require unbounded utilization distributions, such as the bivariate normal or Fourier transform method (Anderson 1982), have small utilization probabilities even at infinite distance. A corresponding unbounded uniform model is not available for comparison. This boundary problem might be overcome by choosing a limit to the home range, such as the 95% probability contour. Unfortunately, the appropriate boundary choice is not easily specified and can tremendously influence the core area size. In addition, the presence of extreme locations in the data may have a substantial effect on estimates of home range size (Anderson 1982; Samuel & Garton 1985) and subsequent core area determination.

DISCUSSION

Considerable effort has been focused on the problem of estimating the home range area and boundary. In contrast, the internal distribution of areas of animal activity has been virtually ignored. The home range is not typically a piece of land with resources distributed evenly within the boundary. More often it is a heterogeneous environment with certain areas rich in resources scattered throughout areas poor in resources (a coarse-grained environment). Studies of a variety of species have shown that animals use certain areas within their home range more frequently and for different reasons than other areas (Adams & Davis 1967; Van Ballenberghe & Peek 1971; Metzgar 1973; Leuthold 1977; Inglis *et al.* 1979; Dixon & Chapman 1980; Georgii 1980; Whitten 1982; Springer 1982).

Recent developments in home range analysis using techniques that estimate a utilization distribution from the observed data are presumably more realistic in representing animal space-use patterns. These techniques facilitate the development of methods for analysis of internal home range use. The identification of core areas within the home range is one type of analysis that identifies areas selected by the animal. The next step should be examination of environmental and behavioural processes that result in the disproportionate use of these core areas.

Intensive analysis of the internal space-use patterns of a home range leads to certain recommendations for data collection procedures. An important goal is to obtain unbiased and serially uncorrelated samples of animal utilization distributions. The probability of detecting an animal in any part of its home range should adequately represent the proportion of use in each area. Radio-tracking animals from the ground in inaccessible areas or sampling during only a small portion of the diurnal cycle are two approaches that may produce biased estimates. Similarly, researchers may be tempted to oversample areas where animals are easiest to locate (e.g., nest and den sites). While many locations are obviously desirable, the tendency to sample frequently should be tempered by the necessity to reduce the biases associated with sampling procedures. Locating an animal repeatedly during a short interval of time and subsequently obtaining fixes at more reasonable intervals could lead to erroneous identification of core areas. Although completely random designs are often impossible, the analysis of data which indicate strong dependence between successive observations should be avoided.

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