BLACK BEAR HOME RANGE OVERLAP IN NORTH CAROLINA AND THE CONCEPT OF HOME RANGE APPLIED TO BLACK BEARS

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Abstract: Theoretical and empirical research indicates that territoriality is related to habitat productivity. Female black bears (*Ursus americanus*) exhibit intrasexual territoriality in northern North America where habitat productivity is low. However, telemetry studies show that adult female black bears in the Southern Appalachian Mountains, where productivity is higher, exhibit considerable home range overlap. This overlap was quantified using an index that weighs home range overlap by the extent that 2 bears share parts of their home ranges. Home range of adult females overlapped extensively during each year and season. Females who reached sexual maturity established home ranges close to their mothers or took over their mothers' home ranges if their mothers had died. The importance of sample size and statistical and biological independence of bear locations to home range analysis is unclear.

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Burt (1943) clarified the terms territory and home range as applied to mammals. He defined a mammal's home range as "the area . . . over which the animal normally travels in search of food" (1943:351), and defined territory as "any defended area" (1943:346). Since then, home range analysis has become important to field research on mammals, especially carnivores, and home ranges have been studied from many approaches (e.g., Waser and Jones 1983, Bekoff and Mech 1984, Harrington and Mech 1984, Hemker et al. 1984, Laundre and Keller 1984, Liberg 1984, Lima 1984, Stamps 1984). However, because an animal's home range is easier to conceive than to map and because different researchers have had different interests, researchers have used a variety of definitions more precise than Burt's to facilitate mapping and description. Not all of these definitions are equivalent, and some may even be inappropriate for methodological or statistical reasons (Bekoff and Mech 1984, Laundre and Keller 1984, Swihart and Slade 1985).

The concept of territory has undergone even more evolution than has that of home range. In general, an individual or a group of animals is now considered to be territorial when it has exclusive use of an area or resource with respect to other members of its species. The potential effects of territoriality on population regulation have received considerable theoretical attention (Brown 1969, Fretwell and Lucas 1969, Watson and Moss 1970, Maynard Smith 1974) and territory size appears to be the most critical factor. A predominant determinant of territory size is food and in general increased availability of food leads to decreased territory size (Ebersole 1980, Hixon 1980, Schoener 1983). Under some conditions, increased food availability affects territory size indirectly through increased trespassing (Myers et al. 1979). Increased food availability may also lead to a breakdown of territorial behavior altogether (Carpenter and MacMillan 1976) in areas with significant habitat patchiness.

The predicted inverse relationship between food availability and territory size has been observed in controlled field manipulations (Kodric-Brown and Brown 1978, Hixon 1980, Miller 1980, Hixon et al. 1983, Stimson 1973). A striking feature of such tests is that they have all been done on small vertebrates (birds, lizards, fish) or on a few invertebrates. Though a large number of mammals exhibit territorial behavior (Crook et al. 1976), including several carnivores (Peters and Mech 1975, Erlinge 1977, Kruuk 1978, Powell 1979), effects of food availability on territory size have not been investigated in mammals.

Two studies have found that adult female black bears are territorial toward other adult females, though these females may exhibit tolerance of their own immature female offspring (Rogers 1977, Ruff and Kemp 1980). Intrasexual territoriality among females (Powell 1979) implies that some limiting resource is being defended. The studies by Rogers (1977) and Ruff and Kemp (1980) were conducted in boreal/northern-hardwood-hemlock and boreal forests, which have low primary productivity (Cronquist 1961). The bears in these northern habitats responded dramatically to yearly changes in food supply and in years with poor food supplies exhibited reproductive failure and increased mortality (Rogers 1976). This indicates that territoriality in female black bears is a response to limited food resources.

Since 1981 I have been studying black bears in the Southern Appalachian Mountains to test the hypothesis that increased habitat productivity leads to decreased territorial behavior in adult female black bears. To quantify territoriality, a method of quantifying home range overlap is needed. Simply measuring the area of home range overlap between 2 adult female black bears is inadequate because bears do not treat all areas of their home ranges equally. Therefore, home range analysis must incorporate bears' use of different parts of their home ranges. Because convex polygons (Mohr 1947) do not weigh home ranges in this manner, they are inadequate for analyzing home ranges. Harmonic mean methods of determining home ranges (Dixon and Chapman 1980, Spencer and Barrett 1983) provide isoclines of animal use of different parts of a home range, but these methods are highly biased when an animal's home range is skewed, is unevenly used, or has several centers of activity (Spencer and Barrett 1983). This bias occurs because home range use does not meet the method's underlying assumption of use declining in a harmonic manner at distances farther and farther from the center of activity. Probability ellipses and other methods of determining home ranges (Hayne 1949, Jennrich and Turner 1969, Koepple et al. 1975) also assume that animal behaviors follow particular probability distributions. Black bear home ranges generally are skewed and have multiple centers of activity, which precludes the use of these methods. In this paper I present another method of determining the probability of a bear using a particular part of its home range and use this method in an index of home range overlap borrowed from niche theory. I also discuss conceptual problems caused by statistical autocorrelation of radiotelemetry locations of black bears.

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STUDY AREA

This research was conducted on the 220 km^2 Pisgah Bear Sanctuary (PBS), Pisgah District, Pisgah National Forest, western North Carolina, where bear hunting is illegal. The Blue Ridge Parkway (BRP), also a sanctuary, forms part of the western border of the PBS and bisects the northern portion of the PBS. Elevation ranges from 650 to 1,770 m. Major forest types include hemlock (*Tsuga canadensis*)-northern hardwood, cove hardwood, mixed oak (*Quercus* spp.), mixed pine (*Pinus* spp.), and pine-hardwood. Oak associations comprised nearly 90% of the forest types. Eighty percent of the timber area was in the 40–80 year age class, 17% over 80 years, and only 3% under 20 years.

METHODS

Field work was conducted from May 1981 to December 1984. Black bears were captured with modified Aldrich foot snares (Johnson and Pelton 1980) and were immobilized with a 2:1 mixture of ketamine and rompun. Standard data were collected from all bears and bear ages were estimated from annuli on premolars.

Bears 2.5 years or older were outfitted with activity monitoring radiocollars (Telonics, Inc., Mesa, Ariz.) and some 1.5-year-old bears received eartag transmitters (Servheen et al. 1981). Locations of bears were estimated by triangulation using an 8-element yagi antenna mounted on the roof of a pickup truck and occasionally using a 2-element "H" antenna. By driving the BRP, researchers could locate bears almost any place in the PBS. No locations were accepted if the 1st and last compass bearings used to locate an active bear were taken more than 15 minutes apart if the triangle formed by 3 compass bearings exceeded 0.2 km^2. Estimated triangulation error for accepted locations was $\pm 5°$ and no locations were accepted if their error polygons exceeded 0.25 km^2 (Warburton 1984). For telemetry data collection, each day was divided into 12 2-hour periods. During most weeks of the bears' active seasons, bears were located in each period on 2 different days. Additional unscheduled locations led to some bears being located up to 30 times each week.

To quantify home ranges, telemetry locations were considered to be an incomplete sample of all locations actually used by bears during the period of study. The study area was divided into 0.25-km^2 blocks to match telemetry error; for each bear the number of locations per block was determined. Using SAS-Graph (Anon. 1985) procedures developed from research by Akima (1978), Harder and Desmarais (1972) and Meinguet (1979) to interpolate missing values for surfaces in 3-dimensional space, the true relative use of each 0.25-km^2 block was estimated for each bear. Then for each bear, the use of each block was divided by total estimated use of the study area to obtain the proportional use of each block. Because the proportional uses calculated for all blocks add up to exactly 1 for each bear, the proportional use of any block can be used as the estimated probability that a given bear will be found in that block at any given time.

Note that this method does not assume that animal movements follow any underlying statistical distribution. One might say that the animals are allowed to determine their own probability distributions of home range use.

I quantified home range overlap between 2 bears using Pianka's (1974) index of niche overlap:

$$O = \left[\sum_k p_{ik} \times p_{jk}\right] \Big/ \left[\left(\sum_k p_{ik}^2\right)\left(\sum_k p_{jk}^2\right)\right]^{0.5}$$

where p_{ik} and p_{jk} are the probabilities that bears i and j will be found in block k. O is thus an index of home range overlap that incorporates differential use of overlap areas by different bears. When the home ranges of 2 bears overlap little, O is small. It is small when the area of overlap (no matter how large) is used little by both bears. When very small home ranges overlap extensively in areas of intensive use by both bears, O approaches unity.

For each year, O was calculated for every pair of adult females with overlapping home ranges for that year. Home ranges were defined as overlapping if at least 1 location for 1 bear was within the convex polygon of locations for the other. O was also calculated for overlap during each season for which there were sufficient data (100 locations per bear, Bekoff and Mech 1984). Seasons were defined by bear biology and plant phenology as spring: emergence from dens-14 June; breeding: 15 June-13 July; early fall: 1 August-30 September; late fall: 1 October-den entry.

Schoener's t^2/r^2 (Schoener 1981, Swihart and Slade 1985) was used to calculate the time interval between telemetry locations necessary for independence for 2 bears followed in 1984.

RESULTS

Six bears were followed in 1981, of which 2 were adult females (bears 11, 23). In 1982 there was only 1 adult female (bear 28) among 14 bears followed; in 1983 4 adult females (bears 1, 5, 61, 70) among 18 bears; and in 1984 5 adult females (bears 1, 61, 87, 98, 106) among 12 bears. During these 4 years some bears were located over 400 times per year and all bears were located over 100 times a year except in 1981. In 1981 and 1982 there may have been adult females in the central part of the study area who had not been outfitted with transmitters; however after 1983 no new adult females were trapped in the central part of the study area and most bears were recaptured at least once, suggesting that all adult females were carrying transmitters.

In all 3 years when 2 or more adult female black bears were followed, females had broadly overlapping home ranges (Figs. 1–3). In 1981, bears 11 and 23 had home ranges that almost completely overlapped. In 1983 and 1984, the home ranges of bears 1 and 61 broadly overlapped and also overlapped with the home ranges of other adult females. There was no

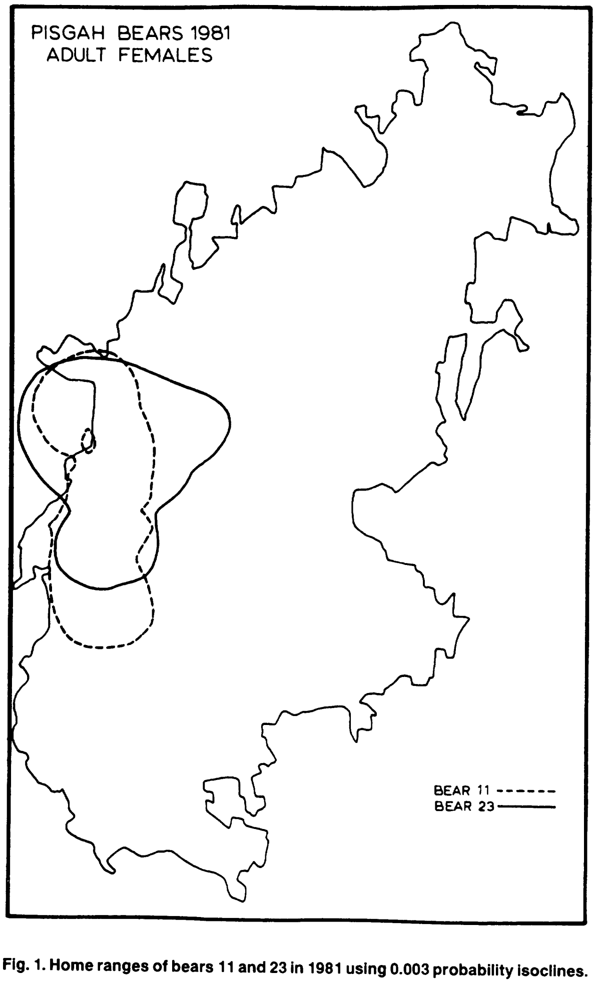

Fig. 1. Home ranges of bears 11 and 23 in 1981 using 0.003 probability isoclines.

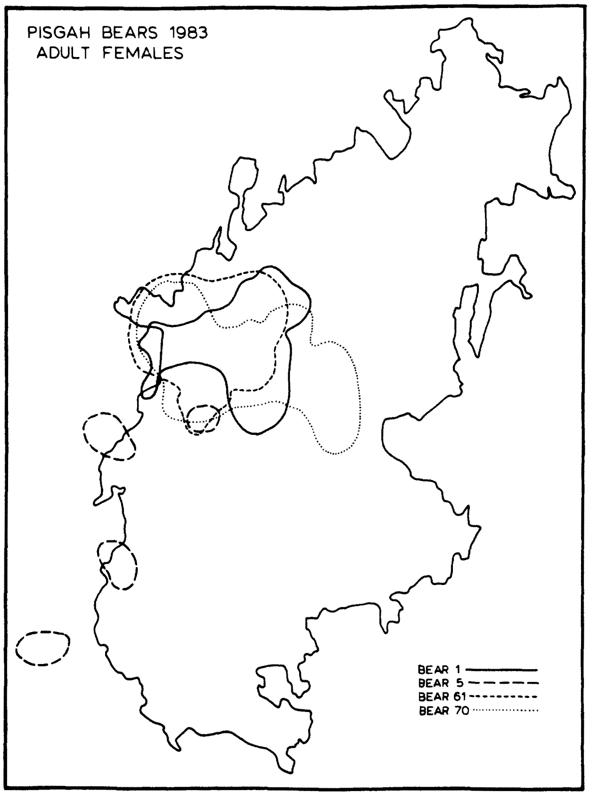

Fig. 2. Home ranges of bears 1, 5, 61, and 70 in 1981 using 0.003 probability isoclines.

indication of exclusive use of any part of any bear's home range.

The probability isoclines for the bears' use of their home ranges showed home range shapes and use considerably better than would convex polygons or other methods (Fig. 4). The probability isoclines exhibited irregular shapes and multiple centers of activity for bears whose home ranges were obviously irregular as seen from simple plots of telemetry data (Fig. 4). Bears with large home ranges tended to have low probabilities for being in any 0.25-km^2 block in their home ranges (Fig. 5), whereas bears with small home ranges tended to have higher probabilities of being in the blocks in their home ranges (Fig. 4). Bear 5, whose 1983 home range is shown in Figure 5, traveled over a large area and therefore had a low probability of being in any particular 0.25-km^2 block. Figure 5 shows few isoclines, and those isoclines are for low probability levels.

The 2 adult females (11, 23) followed in 1981 had broadly overlapping home ranges (Fig. 1), with centers of activity that were located very close together. These 2 females were born in 1977 and could have been sisters. In all seasons of 1983 and 1984, females 1 and 61 had broadly overlapping home ranges with centers of activity that were close (Figs. 2 and 3). These 2 females were born in 1976 and 1974, respectively, and therefore could not have been mother and daughter; however, they could have been half-siblings with the same mother. These females' home ranges also overlapped with that of female 70 in 1983 and females 87 and 98 in 1984 (Figs. 2 and 3). Female 70 was born in 1980, female 87 in 1977, and female 98 in 1981. The relationships of these bears to other bears are unknown.

Females 87 and 106 (born in 1976) had home ranges that overlapped moderately in 1984, the only year that both bears were followed (Fig. 3). Bear 106's home range did not extend to those of bears 1, 61, or 98. Female 5 in 1983 and female 78 in 1984 occupied almost exclusive home ranges (Figs. 2 and 3).

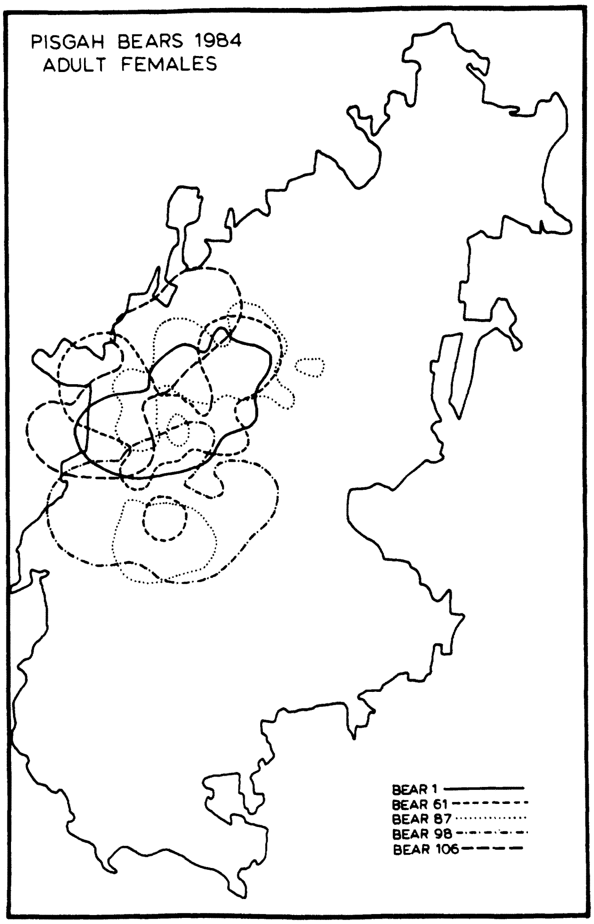

Fig. 3. Home ranges of bears 1, 61, 87, 98, and 106 in 1981 using 0.003 probability isoclines.

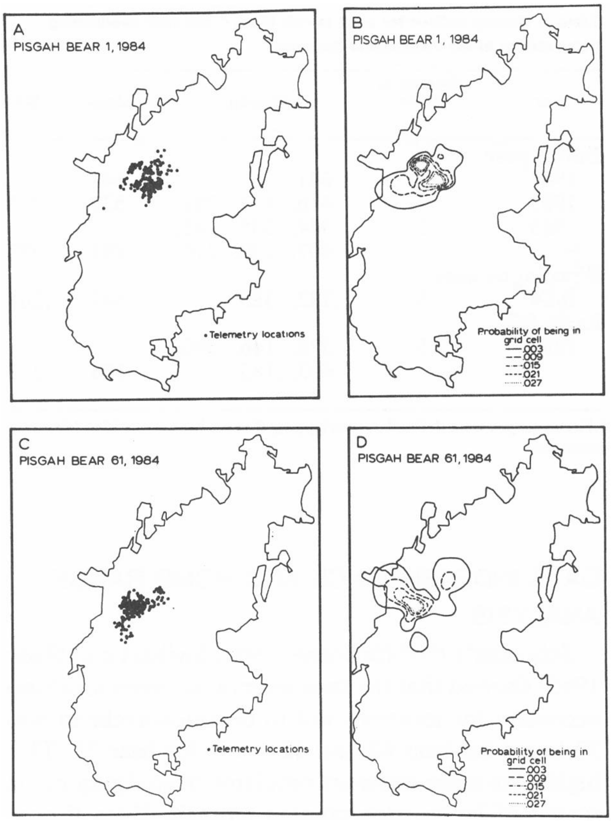

Fig. 4. Plots of telemetry locations and home range probability isoclines for bears 1 and 61 in the Pisgah Bear Sanctuary during 1984. A. Plots of telemetry locations for bear 1's home range in 1984. B. Probability isoclines for bear 1 in 1984 with lowest isocline set at 0.003. Note the irregular shape and the multiple activity centers, which correspond to the telemetry plot in Figure 4A. C. Plots of telemetry locations for bear 61 in 1984. D. Probability isoclines for bear 61's home range in 1984 with lowest isocline set at 0.001. Note the irregular shape and the multiple activity centers, which correspond to the telemetry plot in Figure 4C.

Female 5 was female 11's daughter and became sexually active in 1983. She was legally killed just outside the PBS in November of that year. Female 78, female 1's daughter, was 2.5-years-old in 1984 but became sexually active in 1985 and occupied the same home range until she was apparently illegally killed in July of that year. These 2 females had essentially the same home ranges, which were in the part of the study area used by bears 11 and 23 in 1981. Both of these bears were illegally killed in the fall of 1981. Thus bear 5 settled into the home range of her mother after her mother's death whereas bear 78 settled into a home range that did not overlap with her mother's and her mother was still alive. All of the female bears that settled in this part of the study area were illegally killed. It may be that the level of poaching in this area hinders long-term occupancy by bears, and therefore it may be rare that enough bears establish home ranges in the area to have them overlap.

In 1984 there were sufficient data to examine home range overlap during the breeding season and early fall. During both seasons overlap was extensive but for fewer bears. Bears 1 and 61 overlapped extensively during both these seasons, as they did during all seasons throughout 1983 and 1984. Bear 1 also overlapped with bear 98 during the breeding season and early fall 1984. Bear 98 was born in 1981, and her relationships to other bears are unknown. During early fall, when the bears were foraging mostly for berries but also for acorns, there were more cases of overlap. Bear 87 moved south into the home ranges of bears 1 and 61 during early and late fall, and this move was responsible for much of the overlap for the whole year as well as for early fall.

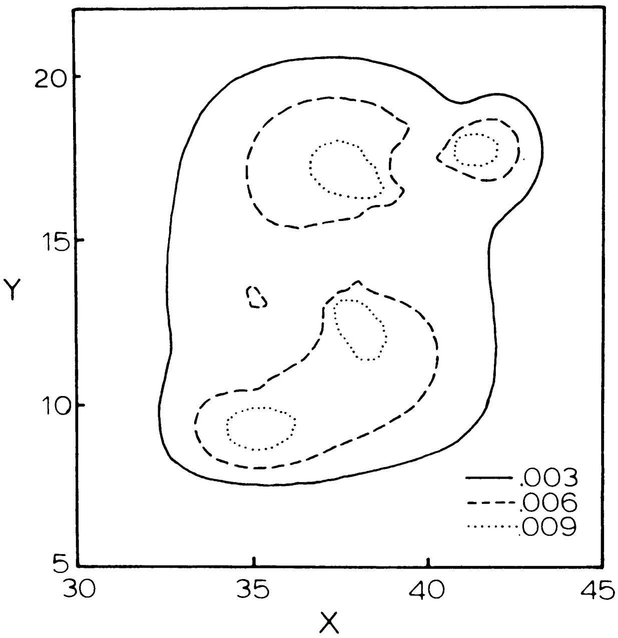

Fig. 5. Probability isoclines for bear 5's home range in 1983 with lowest isocline set at 0.003. Note the few isoclines compared with Figures 4B and 4D. This bear had a large home range and hence low probability of being in any particular place.

The mean indices for home range overlap of adult female bears with overlapping or adjacent home ranges are shown in Table 1. For comparison with O values for overlapping home ranges, females with convex polygon home ranges that did not overlap but were close together had low O values (bears 1 and 5 in 1983: 0.055; bears 98 and 106 in 1984: 0.044), whereas those bears whose home ranges overlapped extensively had high O values (bears 11 and 23 in 1981: 0.641; bears 1 and 61 in 1983: 0.416, and in 1984: 0.344). Depending on year and season, the mean index for those bears whose home ranges overlapped ranged from 0.295 to 0.641, whereas O values for bears with non-overlapping home ranges exceeded 0.29 only 3 times ($N = 16$).

Table 1. Overlap indices for adult female black bears with overlapping home ranges in the Pisgah Bear Sanctuary.

Year	Number of bears	Overlap	Mean	SD
Entire year				
1981	2	.641	.641	—
1983	4	.416, .415, .781	.537	.211
1985	5	.344, .335, .245, .407, .230, .210	.295	.078
Breeding season				
1984	5	.782, .380	.581	.284
Early fall				
1984	5	.376, .146, .390, .693, .185	.358	.217

[a] Home ranges were defined as overlapping if bears have embedded telemetry locations.

DISCUSSION

Adult female black bears in the Pisgah Bear Sanctuary in the western North Carolina mountains exhibited broadly overlapping home ranges. They did not maintain exclusive use of any part of their home ranges and, thus, cannot be considered territorial. Home ranges did not have regular shapes and had multiple centers of activity (Fig. 4) but were stable from year to year (Figs. 2 and 3; bears 1, 61). It is possible that some of the bears with overlapping home ranges were siblings or half-siblings (bears 11 and 23 in 1981, bears 1 and 61 in 1983 and 1984), but this is not possible for all cases of overlap (bears 87 and 106 in 1984) because birth years for these bears do not differ by 2 years or more. Given the number of bears showing extensive home range overlap, it is unlikely that they were all related. One must conclude that extensive home range overlap is possible for bears that are not closely related and that adult female bears in the Pisgah Bear Sanctuary are not territorial.

Pianka's index for niche overlap may be useful for quantifying home range overlap because it weights the amount of area overlapped and the intensity of use of that area. This quantification shows that the adult female bears in the PBS had extensively overlapping home ranges that often overlapped in the areas most intensively used by the individual female bears. However, the index was not always consistent and sometimes gave higher index levels for bears with nonoverlapping home ranges than for bears with slightly overlapping home ranges. Another index may be more appropriate, such as summed probabilities of bears being in the same grid cell at the same time.

DATA INDEPENDENCE AND HOME RANGE ANALYSIS

Schoener's t^2/r^2 (Schoener 1981, Swihart and Slade 1985) showed that the time interval between locations necessary for locations not to be autocorrelated was 30 hours for bear 68 and 32 hours for bear 78. This highlights some inherent problems of studying home ranges of large, wide-ranging animals. Even if conditions for data collection are perfect, an individual bear can provide at most 120 independent locations per year. This is barely more that the absolute minimum number of locations necessary to yield an accurate estimate of the outer limits of an animal's home range (Bekoff and Mech 1984). Given that bears often do not cooperate with researchers and that field logistics often break down, it may be impossible to collect a sufficient number of statistically independent locations on a population of bears to analyze yearly home ranges.

Field observations in my study area indicate that the problem may be even more complicated. I believe that no locations of any resident bear in my study area are independent. Bears are intelligent animals, as are all carnivores, and may well possess the ability to have conscious thought (Griffin 1984). Resident bears appear to have cognitive maps of their home ranges (Peters 1978) and to be able to travel to any particular place at any time they wish. It is obvious that bears do not move at random, and even telemetry locations that are not autocorrelated are not expected to resemble Brownian movement. Thus every movement and every telemetry location of a bear depends on the bear's past experiences in its home range and on its knowledge of where particular resources exist, whether those resources are berries, acorns, members of the opposite sex, or whatever. Therefore no 2 telemetry locations can ever be truly independent, even though they may not be autocorrelated.

In addition, the bears in my study area have exhibited the ability to travel over 4 km in less than 2 hours and this distance is larger than the radii of the convex polygon home ranges of all adult females. Thus the adult females discussed in this report had the ability to travel to any parts of their home ranges between any 2 telemetry locations but chose not to do so. At those times when the bears moved long distances, they chose to move those distances just as they chose not to move at other times. Thus one might ask if bears moving long distances quickly should have statistically independent locations after shorter times than slowly moving bears. And if independence is determined for a mean or "normal" speed, do the statistical tests consider fast movements abnormal? Finally, because using Schoener's t^2/r^2 ratio to test for independence requires choosing an arbitrary percentage of the ratio values that must exceed a set value, choosing a different limiting arbitrary (though defendable, Swihart and Slade 1986) value leads to a different time interval for independence of locations. Depending on the power one chooses for the test, considerably shorter times for independence will be found for my data.

Because of these considerations about independence of bear locations, my knowledge of bears' home ranges, and the bears' abilities to move, I have used all acceptable telemetry locations of my female bears and have chosen not to limit location data to those locations that are not autocorrelated.

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