Topographical constraints and home range quality

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The topography of an area affects the animals that live in it. Using digitized topographic maps of our mountainous study area in North Carolina, USA, and using radio telemetry data for locations of black bears *Ursus americanus*, we tested the hypotheses that topography influences home ranges of black bears and that topography affects access to resources by black bears. Use of space by bears correlated positively with steepness of slope but negatively with relative elevation. The perimeters of bears' home ranges aligned with ridges and valleys more than expected by chance and home ranges were oriented on major topographic features, such as watersheds and basins. Bears' home ranges had lower resource values than was optimal for their home range locations and access to resources was limited by topography. Ignoring topography may lead researchers to misunderstand the ecology and behavior of animals that live in mountainous areas.

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The physical structure of an area affects the animals that live in it. Topography affects costs of locomotion for mammals (Stamps 1995). Reef structure influences territories and behavior of resident fish (Ehrlich 1975). Topographic complexity of territories affects mating success in pupfish (Kodric-Brown 1983) and topography and vegetation affected by topography can affect territory boundaries for generations of birds (Reid and Weatherhead 1988). Nonetheless, since Burt (1943) defined the concept of a 'home range' with respect to mammals, the concept of home range has been associated mostly with resources available within a mammal's home range and not with constraints such as topography, which can limit or enhance access to resources.

Black bears *Ursus americanus* establish their home ranges to take advantage of available resources (Mitchell 1997) and adjust their home ranges in response to annual variation in food (Noel 1993, Powell et al. 1997). Nonetheless, home ranges of bears do not correspond perfectly to the patchy distributions of resources, even when resource depletion by other bears is considered (Mitchell 1997). Reid and Weatherhead (1988) found that territories of Ipswich sparrows

Passerculus sandwichensis did not conform optimally to available resources but were influenced by local topography and unfavorable habitat. We tested whether the home ranges of adult female black bears in the Southern Appalachian mountains are influenced significantly by the local mountain topography. We also tested an hypothesis related to the one posed by Reid and Weatherhead: that topography constrains inclusion of resources within home ranges.

Methods

After developing a computer graphic relief image of our study area, the Pisgah Bear Sanctuary (Fig. 1) in the Southern Appalachian Mountains of western North Carolina, USA, we calculated and then superimposed home ranges for black bears on the relief image. We were intrigued that boundaries for home ranges of some adult females, which we have studied since 1981, appeared to coincide with major ridges (Fig. 2). Before examining the home ranges of many females, we developed the hypothesis that major topographic features
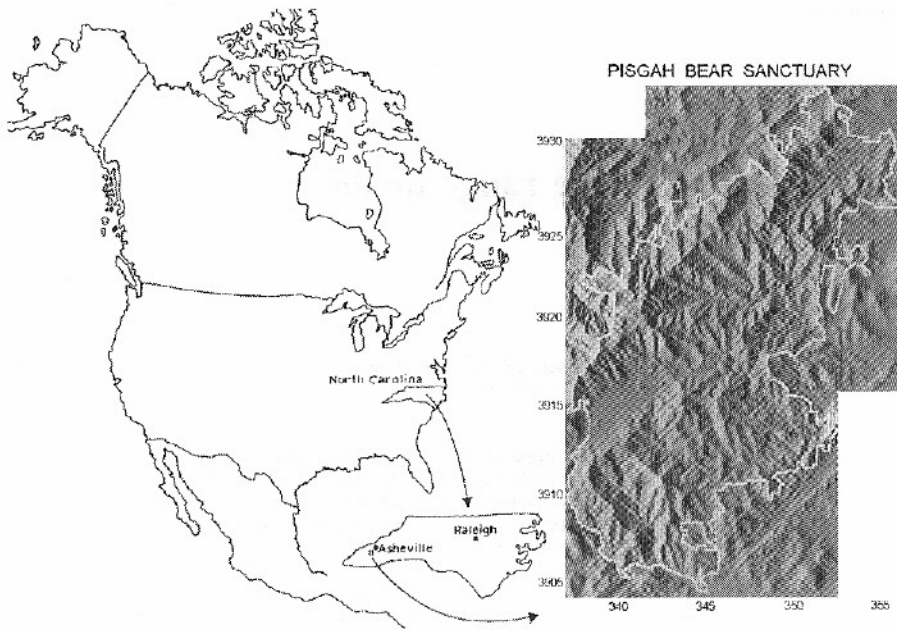
Fig. 1. Relief image of the Pisgah Bear Sanctuary, its location in the US, and its UTM (Universal Transverse Mercator) coordinates (km). The rugged topography of the study area is evident in the relief image.

affected the boundaries for home ranges of adult females. To test this hypothesis, we did the following.

To estimate home ranges of adult female bears we used estimates of bears' locations obtained from radio telemetry (see Powell et al. 1997 for details of data collection) and the computer program KERNELHR (Larkin and Halkin 1994, Seaman and Powell 1996). KERNELHR depicted home ranges as 95% utilization distributions using a cross validated, fixed kernel estimator. Cross validated, fixed kernel estimators are the best estimators of home ranges available and do a good job of reconstructing animals' utilization distributions from samples of the size we have for bears (100–200
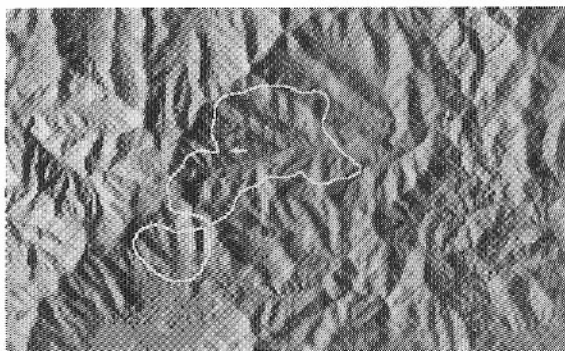

Fig. 2. Home range of bear 61 in 1985. This image stimulated the inquiry into the effects of topography on home ranges. Note that Big Pisgah Ridge runs from NE to SW across the image, forming a rough NW border on 61's home range. Also note the the 'notch' in the NW border to 61's home range (arrow) corresponds to Little Pisgah Ridge, a particularly steep, rugged ridge, that bear 61 appeared to avoid.

location estimates for most bears; Seaman and Powell 1996, Powell et al. 1997). We superimposed a grid of 250×250 m cells over the Pisgah Bear Sanctuary (cell size chosen from estimates of telemetry error [Zimmerman and Powell 1995, Zimmerman 1992, Powell et al. 1997]) and, from the bears' utilization distributions, we assigned to each cell the probability of each bear using that cell.

From digital elevation maps (US Geological Survey), we assigned to each cell its slope (in degrees) and calculated the distance to the nearest water (m) using Idrisi GIS. Distance to nearest water in mountainous terrain is a measure of relative elevation; it represents the elevation of a point above the valley or cove nearest to that point. From these values, we developed indices for slope and relative elevation. Each index was the slope or relative elevation as a proportion of the maximum for the study area. Hence, the indices for both slope and relative elevation ranged from 0 to 1. An index value of 0 for the slope index represented flat ground, while a value of 1 represented the steepest slope in the study area. An index value of 0 for the relative elevation index represented low relative elevation, while a value of 1 represented the highest relative elevation in the study area.

Hypothesis 1: For our first test of the general hypothesis that topography affected use of space by black bears, we tested the hypothesis that use of cells in the study area by bears was correlated with indices for slope and relative elevation for the cells (PROC CORR, SAS 1990). Because each cell had the same area, we did not have to adjust by relative availability.

For our second test, around the center of each bear's home range we created a circle with area equal to the home range. We then tested for differences in mean slope and relative elevation between these circles and the associated home ranges (PROC GLM, SAS 1990, blocked by bear and year). The circle provided a measure of the topography available to a bear and the bear's home range showed the topography the bear chose to use.

Hypothesis 2: Next, using SAS and Idrisi (Eastman 1997), we tested the hypothesis that the boundaries of bears' home ranges were influenced by topography. We placed the outline of each female's home range upon the relief image of the study area. Then we rotated the home range around a random angle and randomly replaced the rotated home range on the relief image. We now had two home range images for each bear, one true and the other manipulated, so we hid the identities of the true and manipulated home ranges. For each home range, without knowing its identity, we measured the portions of the perimeter that did or did not align visually with topographic features (major ridges or valleys) and calculated the proportion that did align with topographic features. Visual alignment was subjective but unbiased between true and manipulated home ranges because we did not know the identity of any home range while measuring perimeters. Visual alignment meant that a section of the home range perimeter generally followed a topographic feature closely ($\pm 15°$) and was within 250 m of the feature for > 750 m. We also recorded whether home ranges with two disjunct pieces were split by a major ridge and whether each entire home range was associated visually with large scale features such as large basins, watersheds, or large, associated ridges.

We tested whether true and manipulated home ranges differed in the proportion of home range perimeter that aligned with topographic features (PROC GLM, SAS 1990 blocked by bear and year); we tested whether true home ranges were more likely than manipulated home ranges to be split into two disjunct pieces by a ridge (PROC GLM, SAS 1990); and we tested whether true home ranges were more likely to be situated over a major topographic feature (PROC CATMOD, SAS 1990).

Hypothesis 3: To test the hypothesis that topography constrains inclusion of resources within home ranges, we built home ranges for each bear that made 'optimal' geographic use of home ranges (Mitchell 1997) and compared true to optimal' home ranges with respect to resources included and with respect to topography. Zimmerman (1992) and Powell et al. (1997) presented a Habitat Suitability Index Model and showed that bears prefer areas with high Habitat Suitability Index (HSI) values and avoid areas with low HSI values. Mitchell (1997) tested the HSI Model

with more data than used by Zimmerman and confirmed the predictive value of the HSI Model with regard to bear use of habitat. We, therefore, used HSI as a measure of habitat quality for bears and assigned to each grid cell in the study area its HSI value. Mitchell (1997) developed and tested an algorithm (a set of rules for making calculations) for optimal choice of a home range given an underlying distribution of critical resources. To build the optimal home range for each bear in our study area for each year, we ran Mitchell's algorithm starting at the weighted center of each bear's home range (mean arithmetic center with each cell weighted by its HSI value). We tested whether optimal and estimated true home ranges differed in mean HSI and whether optimal and true home ranges and the circles around each home range had different mean indices for slope and relative elevation (PROC GLM, LSD means test among treatments, $\alpha = 0.05$, SAS 1990).

Results

The bears' utilization distributions correlated positively with steepness of slope (Pearson correlation coefficient = 0.084, $p < 0.0001$, N (number cells) = 17 206) but correlated negatively with relative elevation (-0.013, $p < 0.085$, N = 17 206).

The mean slope ($p < 0.0001$, $p = 83.71$, DF = 507) and mean relative elevation ($p < 0.0001$, $p = 46.5$, DF = 507) varied significantly among 1) bears' estimated home ranges, 2) circles centered on those home ranges and 3) optimal home ranges. Bears' home ranges had steeper slopes and lower relative elevation than did the circles or optimal home ranges ($p < 0.05$, for both slope and relative elevation), while circles and optimal home ranges did not differ.

A larger proportion of the perimeters of bears' home ranges aligned with major ridges or valleys (0.68 ± 0.23, mean $\pm$ SD) than did the perimeters of randomly placed and rotated home ranges (0.39; $p < 0.0001$, $p = 40.58$, DF = 1) but home ranges with 2 disjunct pieces were not more likely to be separated by a ridge than randomly placed and rotated home ranges ($p = 0.27$). Bears' home ranges were more likely to be oriented on a major topographic feature such as a watershed or set of ridges ($p < 0.0001$) than were randomly placed and rotated home ranges.

Bears' estimated home ranges averaged significantly lower for mean HSI value (0.59 ± 0.07) than did optimal home ranges at the same site (0.64 ± 0.06; $p < 0.0006$, $p = 12.65$, DF = 1). And bears' home ranges aligned with topographic features (0.68 ± 0.23) more than did optimal home ranges (0.23 ± 0.18; $p < 0.0001$, $p = 109.00$, DF = 1).

Discussion

The home ranges of the black bears we, studied were affected by the local topography, although low correlation coefficients indicate that many other factors also affected their home ranges, as expected. The best estimates of the bears' actual utilization distributions had significantly steeper slopes and lower relative elevation than were available in the local area (circles of equal area centered on the bears' centers of activity). The bears we studied appeared 1) to seek steep slopes, 2) to avoid high ridge tops, 3) to align their home range boundaries with ridges and valleys, and 4) to orient their home ranges around major topographic features, such as watersheds and basins. The best estimates of the bears' utilization distributions correlated positively with steep slopes but marginally negatively with high ridges. The boundaries of their home ranges aligned with ridges and valleys more than expected from random placement of home ranges. And their home ranges were oriented with major topographic features, such as basins and watersheds, more than expected from random placement of home ranges.

The orientation of the bears' home ranges with topographic features appears to have affected the bears' access to some nearby resources. The mean HSI value for bears' estimated home ranges was significantly lower than the mean HSI for optimal home ranges at the same place. We can surmise how using ridges as boundaries to their home ranges could lead bears not to have optimal home ranges with respect to distribution of foods. The bears' home ranges had lower average habitat quality (HSI values) than did optimal home ranges with the same centers of activity. Ridge sides in our study area often have stands of huckleberry *Gaylusaccia* spp., greenbriar *Smilax* spp. and or blackberry *Rubus* spp. in the understory, hence these stands of berries are separated by ridge tops. Because topography appears to constrain home ranges, only 1 of 2 adjacent huckleberry patches separated by a major ridge might be included in a bear's home range.

One good explanation for the effects of topography that we observed also relates directly to resources. That berries (huckleberries, blackberries, greenbriar) are often found on ridge sides may explain the attraction for steep slopes shown by adult female black bears. Our HSI Model devalues food sources by their distance, values steep slopes as escape cover, and devalues sites that are distant from water. Apparently the HSI Model does not weight these topographic features heavily enough and does not incorporate the difficulty of travel over rough topography. The energetic cost of travelling over a high ridge top to a nearby berry stand might make that berry stand not worth visiting. Berries in a patch do not all ripen at the same time, so to use a berry patch a bear must visit it several times during a season. Frequent visits to a berry patch that is over a high ridge cost more than a single visit. The benefits to a bear of incorporating a berry stand into its home range must outweigh the costs, and energetic costs of going over a big ridge may be high. We suggest that bears avoid some nearby food sources because of the energetic cost of reaching them. Bears appear to devalue distant foods by the distance and the height of ridges that must be travelled to reach those foods

Another possible explanation of our results relates to bears and humans. Bears avoid humans in our study area and humans are the major source of mortality for bears (Powell et al. 1996). Steep slopes may be important to black bears as escape cover, while ridge tops may be avoided because many have maintained hiking trails. Black bears avoid roads (Powell et al. 1996), presumably to avoid people, and roads tend to be built in valleys and not on steep slopes. Stamps (1995) suggested that animals maintain home ranges to develop "site-specific serial motor programs" (near reflex movements associated with specific sites) that increase their chances of escape from predators. Black bears' home ranges are too large and their interactions with humans too few for bears to establish such site-specific behaviors. Nonetheless, familiarity with areas of steep topography and dense vegetation should enhance escape from humans when humans are encountered.

Reid and Weatherhead (1988) documented an effect of topography on territories of Ipswich sparrows, surmising that territory boundaries set by topography could constrain the numbers of nest sites and the amount of food in a territory. A major point of Reid and Weatherhead's discussion was that topography could affect mating patterns. They hypothesized that topographic constraints could lead to reduced coupling of territory quality with male quality. In contrast, Kodric-Brown (1983) documented that topographic features were the critical features of high quality territories of male pupfish *Cyprinodon pecosensis* and were tightly coupled with mating success. Many reef fish are similarly affected by local topography (Ehrlich 1975). We have documented that topographic constraints on home ranges of female black bears affect access to resources but we doubt that these constraints affect mating patterns. Male black bears have large home ranges that overlap with home ranges of several females (Carlock et al. 1983, Garshelis and Pelton 1981, Powell et al. 1997, Reynolds and Beecham 1977), while home ranges of females in our study area overlap extensively (Horner and Powell 1990, Powell 1987, Powell et al. 1997). It is possible that topographic constraints on home range boundaries might affect reproduction by females, by limiting access to resources, but topography is unlikely to affect mating.

Topographic constraints appear to be an important factor structuring the home ranges of black bears; the bears we studied preferred areas with steep slopes but appeared to avoid high ridge tops. Future analyses of

home ranges of black bears in mountainous areas must include topography in addition to factors that are traditionally considered, such as habitat, access to mates, and home range overlap. We expect that topography affects home ranges of many mammals. Topographic features have the potential to affect an animal's perception of habitat, food resources, access to mates and other important aspects of its ecology. Ignoring topography may lead researchers to misunderstand the ecology and behavior of animals that live in mountainous terrain.

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