



Optimal use of resources structures home ranges and spatial distribution of black bears

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Research has shown that territories of animals are economical. Home ranges should be similarly efficient with respect to spatially distributed resources and this should structure their distribution on a landscape, although neither has been demonstrated empirically. To test these hypotheses, we used home range models that optimize resource use according to resource-maximizing and area-minimizing strategies to evaluate the home ranges of female black bears, *Ursus americanus*, living in the southern Appalachian Mountains. We tested general predictions of our models using 104 home ranges of adult female bears studied in the Pisgah Bear Sanctuary, North Carolina, U.S.A., from 1981 to 2001. We also used our models to estimate home ranges for each real home range under a variety of strategies and constraints and compared similarity of simulated to real home ranges. We found that home ranges of female bears were efficient with respect to the spatial distribution of resources and were best explained by an area-minimizing strategy with moderate resource thresholds and low levels of resource depression. Although resource depression probably influenced the spatial distribution of home ranges on the landscape, levels of resource depression were too low to quantify accurately. Home ranges of lactating females had higher resource thresholds and were more susceptible to resource depression than those of breeding females. We conclude that home ranges of animals, like territories, are economical with respect to resources, and that resource depression may be the mechanism behind ideal free or ideal preemptive distributions on complex, heterogeneous landscapes.

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The home ranges and territories of animals are commonly thought to reflect the distribution of one or several limiting resources (Ebersole 1980; Hixon 1980; Schoener 1981; Powers & McKee 1994; Powell et al. 1997). The relationship between resources and territories has been investigated extensively, generally proving to be an economical balance between the benefits and costs of resource ownership (Hixon 1982; Schoener 1983; Powell et al. 1997; Powell 2000). Territory size has been shown to vary inversely with food productivity for a variety of animals (Stenger 1958; Ebersole 1980; Hixon 1980; Saitoh 1991; Powers &

McKee 1994, Both & Visser 2003). A strong linkage between food productivity, territoriality and territory size has been shown for nectarivorous birds (Gill & Wolff 1975; Carpenter & MacMillen 1976; Kodric-Brown & Brown 1978; Hixon 1980; Hixon et al. 1983; Powers & McKee 1994), voles (*Microtus* spp.: Ostfeld 1986; Ims 1987; Saitoh 1991), convict cichlids (*Archocentrus nigrofasciatus*: Prawn & Grant 1999) and carnivores (Rogers 1977, 1987; Palomares 1994; Powell et al. 1997; Gehrt & Fritzell 1998).

In contrast, the factors structuring home ranges of animals have received little attention, partly because definitions for home ranges (e.g. Burt 1943:351) are imprecise, difficult to quantify (Powell et al. 1997; Powell 2000), and do not lend themselves well to economic analyses. Although the importance of food as a limiting resource is cited in many home range studies of mammals (Lindzey & Meslow 1977; Harestad & Bunnell 1979; Lindstedt et al. 1986; Litvaitis et al. 1986; Jones 1990; Holzman

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et al. 1992; Joshi et al. 1995), particularly for females (Young & Ruff 1982; Ims 1987; Powell et al. 1997; Said et al. 2005), little is known about how a home range is structured with respect to these resources. No work has addressed whether the home ranges of animals, like territories, are optimal with respect to the spatial distribution of resources.

Similarly, a substantial body of research has explored how optimal selection of habitat can structure the distribution of animals on a landscape (e.g. Fretwell 1972; Pulliam & Danielson 1991). Optimal selection of home ranges, territories, or breeding sites among homogeneous habitat patches differing only in quality and occupancy are implicit in models designed to understand these distributions, but mechanisms of the selection process and their resulting effects in the complex, heterogeneous environments common in nature (i.e. where resources are distributed continuously and not contained in homogeneous patches) are not considered directly.

Elsewhere (Mitchell & Powell 2004), we have presented spatially explicit, individual-based models for selecting patches optimally for an annual home range. Our models predict patch selection from a landscape under different optimization strategies and constraints, and provide a mechanistic bridge between optimal use of habitat by individuals and the resulting distribution of animals on a landscape (Mitchell & Powell 2004). Key to our models is the depiction of a landscape as a continuous distribution of resources, which we depict as a grid of equally sized patches containing resources characterized by their value, V (ranging from 0, no value, to 1, high value). We have hypothesized that the benefits of patch ownership, V , to an animal are discounted for average travel costs incurred in reaching that patch from all other patches in its home range. We estimate the extent to which average travel costs reduce the value of each available patch by dividing its associated V by its distance from a point selected as the centre (i.e. core; Powell 2000) of the home range. The resulting value for each patch, V' represents the net resource value of that patch to an animal (Mitchell & Powell 2004).

Given a spatial distribution of V' , our models represent two strategies for selecting patches for a home range that balance the benefits and costs across available patches (Mitchell & Powell 2004). The first strategy is resource maximizing (model M_R), analogous to rate-maximizing models in optimal foraging (Krebs & Kacelnik 1991), which maximizes the difference between selective and random use of V' (i.e. the highest resource/area ratio possible; solid lines, Fig. 1a). This strategy might be used by animals for which survival and reproduction increase monotonically with the efficient accumulation of spatially distributed resources (i.e. a type I functional response to resource accumulation; Holling 1959). The second strategy is area minimizing (model M_A), analogous to time-minimizing models of optimal foraging (Krebs & Kacelnik 1991), which minimizes the area needed to contain the V' that an animal needs for survival and reproduction (i.e. satisficing sensu Simon 1977; solid lines, Fig. 1b). This strategy might be used by animals for which survival and reproduction asymptote with the efficient accumulation of spatially distributed resources (i.e. a type II

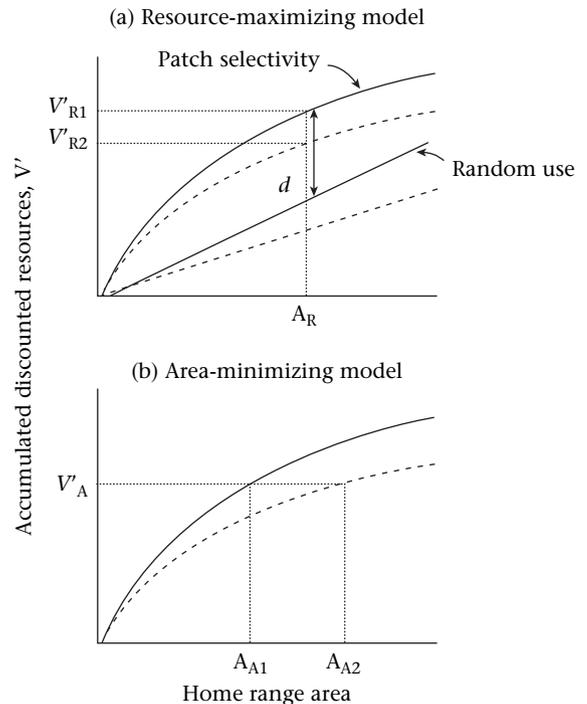


Figure 1. Conceptual models for constructing optimal home ranges based on selecting patches containing high-quality resources. In both models, an animal selects patches in order of their resource value (V'), discounted for travel costs required to reach the patches. (a) Under the resource-maximizing model, M_R , an animal stops selecting patches once the difference between random and selective use of the landscape, d , is maximized, representing the optimal balance between costs and benefits of patch ownership that can be obtained from the landscape. (b) Under the area-minimizing model, M_A , an animal stops selecting patches when the threshold necessary for survival and reproduction is reached. Thus, in (a), the home range is defined by resource accumulation $\Sigma V'_{R1}$ and area A_R , and in (b), it is defined by $\Sigma V'_A$ and area A_{A1} . Solid lines indicate resource accumulation in the absence of resource depression, dashed lines indicate accumulation when animals depress resource values within their home ranges. In (a), the point at which d is maximized does not change with proportional changes in selective and random resource accumulation, so A_R does not change with resource depression, but accumulated resources (V') decline from $\Sigma V'_{R1}$ to $\Sigma V'_{R2}$. In (b), accumulated resources (V') do not change with resource depression ($\Sigma V'_A$), but area increases from A_{A1} to A_{A2} .

functional response; Holling 1959). Both models assume that animals select patches of the highest V' available for their home ranges (Mitchell & Powell 2004).

An animal that selects a patch for its home range will consume or protect the resources that it contains, influencing how other animals will value that patch. The resulting depression of resources changes the distribution of V on a landscape, which in turn should influence how home ranges are chosen by other animals and therefore the spatial distribution of home ranges. Our models allowed the exploration of how resource depression within patches that are selected for home ranges could structure the spatial distribution of multiple home ranges created under both optimization strategies (models M_{RD} and M_{AD} ; dashed lines Fig. 1a, b).

To understand whether our home range models could provide insights into the behaviours of real animals, we compared model predictions to the home ranges of female black bears in the southern Appalachian Mountains. Black bears are good subjects for testing general hypotheses of home range optimization for several reasons. First, non-dispersing bears have well-defined home ranges that are regionally consistent in size within age, sex and breeding classes (Powell et al. 1997). Second, bears live in heterogeneous, patchy habitats and move among patches containing varying food resources on a daily and seasonal basis, but have annual home ranges that are generally stable from year to year (Powell et al. 1997). Third, food is a major limiting resource for black bears, and females in particular structure their home ranges according to the productivity of food resources (Amstrup & Beecham 1976; Alt et al. 1977; Young & Ruff 1982; Powell 1987; Noel 1993; Powell et al. 1997; Mitchell et al. 2002). Fourth, because vegetation composes the great majority of a black bear's diet, the food resources that form the basis for a home range are fixed in space and, at least seasonally, in time. Finally, energetic demands (e.g. lactation; Mauritzen et al. 2001; Moen & Boomer 2005) and the ability to sequester resources (e.g. because of social dominance based on age; Powell et al. 1997) vary among bears and should influence size and resource content of home ranges, if our hypotheses are correct.

These ecological characteristics are not unique to black bears, but represent the conditions under which many, if not most, species establish and maintain home ranges (Powell 2000). Furthermore, our home range models are not specific to bears (Mitchell & Powell 2004). Thus, using our models to evaluate the home range behaviour of bears should provide insights into how efficient use of spatially distributed resources structures the home ranges and distributions of animals in general.

Our study was part of long-term research on a free-living population of black bears in the Pisgah Bear Sanctuary (PBS) in western North Carolina, U.S.A. This research has shown that PBS bears do not use habitat in proportion to its availability (Warburton & Powell 1985) and that core home ranges of bears are located where their activities are most concentrated (Horner & Powell 1990). Furthermore, cores with the highest use are often in areas shared by multiple bears that show no spatial avoidance or territorial behaviour. The strong relationship between habitat preference and habitat quality explains the clumping of bears' activities (Powell et al. 1997), and the structure of home ranges for female bears in the PBS is determined largely by their food requirements (Seaman 1993; Powell et al. 1997). Mitchell et al. (2002) found a strong relationship between habitat preferences of PBS bears and habitat suitability index (HSI) for black bears in the southern Appalachians.

Objectives

We hypothesized that home ranges of adult female bears are efficient with respect to spatially distributed resources, balancing the resource benefits of patch ownership against the average costs of acquiring them. Bears are long-lived and reproduce slowly, so we hypothesized that adult females would show a type II response to resource

accumulation and thus pursue an area-minimizing strategy when selecting their home ranges. Energetic needs and social dominance should also influence patch selection based on resource values, so we hypothesized that variation in home range strategies among adult females would be explained in part by breeding status and age. Finally, we hypothesized that resource depression would be the mechanism underlying the spatial distribution of home ranges of adult females within our study area.

We tested these hypotheses in part by comparing home range characteristics of adult female bears in PBS to predictions generated using computer simulations performed on resource distributions of known characteristics (Mitchell & Powell 2004) as follows.

(1) If home ranges are efficient with respect to the spatial distribution of limiting resources, then mean resource content of bear home ranges should exceed average availability of resources.

(2) The spatial distribution of home ranges should depend, in part, upon the spatial distribution of resources; home ranges should be evenly dispersed where resources are evenly or randomly dispersed, and home ranges should be clumped where resources are clumped.

(3) If bears depress resources within their home ranges, then the spatial distribution of home ranges on a landscape will be more even than would be predicted in the absence of resource depletion (Mitchell & Powell 2004).

To further test our hypotheses, we performed individual-level home range simulations using our models (with and without resource depression; Mitchell & Powell 2004) for each real home range of adult female bears in the PBS; we compared similarity in patches selected by bears to those predicted under each model permutation to infer patch selection strategies. To understand the influence of energetic demands and social dominance on patch selection strategies, we evaluated the extent to which interactions between optimization strategy, resource threshold, resource depression and the breeding status and age of bears explained patterns in similarity between simulated and real home ranges.

METHODS

Study Area

The Pisgah Bear Sanctuary is the largest (235 km²) of 28 bear sanctuaries established in North Carolina in 1971 and is contained completely within the Pisgah National Forest. Elevation ranges from 650 m to 1800 m. The region is a temperate rainforest, with annual rainfall approaching 250 cm/year (Powell et al. 1997). The major forest types in the sanctuary are eastern hemlock, *Tsuga canadensis*, cove hardwoods (yellow poplar, *Liriodendron tulipifera*; magnolias, *Magnolia* spp.; birches, *Betula* spp.), oak-hickory (*Quercus* spp., *Carya* spp.) pine (*Pinus* spp.), and pine-hardwood mix. Bear hunting is illegal in the sanctuary.

Bear Trapping, Telemetry and Home Range Estimation

Bears were trapped in the sanctuary from May through early summer from 1981 through 1994 (except 1991

and 1992) using modified Aldrich foot snares (Johnson & Pelton 1980) or culvert traps. Traps were checked daily, before noon. Trapped bears were anaesthetized using either Telazol (Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, U.S.A.; 5 mg/kg dosage) or a mixture of ketamine hydrochloride (200 mg/25 kg dosage) and xylazine hydrochloride (100 mg/25 kg dosage), administered with a blow-gun or jabstick. The effects of xylazine hydrochloride, when used, were reversed using yohimbine (0.1 mg/kg dosage) administered intravenously. Bears were fitted with a self-piercing eartag (Model 1005-49; National Band and Tag Company, Newport, Kentucky, U.S.A.) in each ear; we never saw evidence that eartags impeded normal behaviour of tagged bears. A first upper premolar (a small tooth commonly lost by bears under natural conditions) was extracted using a dental elevator from each bear to estimate age from cementum annuli (Willey 1974). Most captured bears were fitted with motion-sensitive radiocollars (Telonics, Inc., Mesa, Arizona; Lotek, Inc., Newmarket, Ontario, Canada; 3M and Wildlink, both of St Paul, Minnesota, U.S.A.), weighing approximately 0.5 kg ($\leq 1\%$ body weight); we never saw evidence that collars impeded bears or increased cost of locomotion. Subadult bears were fitted with collars designed to drop off within 1 year. Fully grown adult bears were fitted with permanent collars that were changed or removed if bears were captured subsequently. Handling time of trapped bears varied from 45 to 90 min. Bears typically recovered from anaesthesia within 60–90 min. We captured and handled all bears under a special research permit issued by the North Carolina Wildlife Resources Commission and in compliance with requirements of the Institutional Animal Care and Use Committees for North Carolina State University (IACUC 96-011) and Auburn University (IACUC 0208-R-2410). We considered bears to be adult either at 3.5 years old, or at 2.5 years old, if they were known to produce cubs at age 3.

Each year from April or May until mid-December, telemetered bears were relocated from the ground. Bear locations were estimated by triangulation, generally using a minimum of three separate bearings obtained within 15 min (Zimmerman & Powell 1995). When possible, each bear was located every 2 h within 8-h sampling periods. Sampling was repeated every 32 h to standardize bias from autocorrelation within sampling periods and to minimize bias between periods (Swihart & Slade 1985; Powell 1987). Zimmerman & Powell (1995) evaluated telemetry error using test collar data (median error = 261 m; 95% of estimates were within 766 m from the true location, and error did not differ between observers).

We estimated annual home ranges for bears from location data using a fixed kernel estimator with bandwidth determined by least squares cross validation (program KERNELHR; Seaman et al. 1998). We used a minimum of 20 locations for home range estimates (Noel 1993; Seaman & Powell 1996), and a grid size of 250 m for kernel estimation to approximate median telemetry error. For analyses, we defined home range for each bear as the area containing 95% of the estimated utility distribution (Worton 1989; Seaman & Powell 1996).

Modelling Food Resources

We used the life requisite variable for food, V_F , from our HSI (Mitchell et al. 2002) to model the spatial distribution of food resources for the sanctuary for each year (1981–1994) and mapped these distributions using a GIS (IDRISI, Clark University, Worcester, Massachusetts, U.S.A.). Values of V_F ranged from 0 (poor) to 1 (excellent). We set the grain of the maps at 250×250 m to approximate the median error for telemetry locations (Zimmerman & Powell 1995).

Comparing General Predictions of Models to Real Home Ranges

We analysed home ranges estimated for adult female bears for the years 1981–2001. To determine whether resource content of bears' home ranges exceeded average availability, we compared mean V_F of real home ranges to mean V_F for corresponding neighbourhoods (the area containing 95% of the distribution of V_F ; Mitchell & Powell 2004), with respective 95% confidence intervals (CI). We concluded that the mean resource content of home ranges and of corresponding neighbourhoods differed if the 95% CIs for each did not overlap.

To determine whether the spatial dispersion of home ranges corresponded to the spatial distribution of food resources, we reconstructed the adult female bear population for each year in the PBS, including telemetered bears and untelemetered bears known to have been present. A bear was considered present each year it was alive; once contact was permanently lost, it was no longer included. We assumed that temporary loss of contact was not due to bears leaving the study area. For each bear in each reconstructed annual population, we calculated a weighted home range centre. For telemetered bears, the weighted centre was the patch with the greatest intensity of use. For untelemetered bears, we estimated the weighted centre by averaging home range centres for each bear across years when that bear was tracked, or, in the absence of tracking data, by using trap site location. We used a moving windows evaluation (Isaaks & Srivastava 1989) of home range centres to estimate the mean number of centres for the reconstructed population contained in each $20\text{-patch} \times 20\text{-patch}$ window (with 10-patch overlap of neighbouring windows) for each year. We used the ratio of mean number of centres per window to its variance as an index of spatial dispersion, D , for each year ($D = 1$, dispersal undistinguishable from random; $D > 1$, evenly dispersed; $D < 1$, clumped). Resources in PBS are clumped (Mitchell et al. 2002), so a $D < 1$ for home range centres would indicate correspondence.

To evaluate whether resource depression could affect the spatial dispersion of home ranges in PBS, we compared D for real home range centres calculated for each year to D calculated for 100 simulated home ranges generated using model M_R and maps of V_F for each year. Initial starting points for each simulated home range were selected randomly, but adaptation to the spatial distribution of resources through patch selection resulted in final centres that generally differed from starting points (Mitchell &

Powell 2004). For each year, we calculated D for both real and simulated home ranges within the smallest quadrangular area large enough to contain all real home range centres over all years in PBS (simulated home ranges with centres outside the area were discarded). We evaluated the difference between D for real and simulated home range centres by comparing mean D with 95% CIs calculated across years. Effects of resource depression are implied if home range centres are more evenly distributed than those of the simulated home ranges. We concluded a difference if the 95% CIs for each mean did not overlap.

Using Models to Approximate Patch Selection in Real Home Ranges

For each adult female bear living in PBS over our study period, we generated simulated home ranges under each of our models, (resource-maximizing model, M_R , area-minimizing model, M_A , and both models with resource depression, M_{RD} and M_{AD} , respectively; Mitchell & Powell 2004) using the map of V_F appropriate to the year in which each real home range was observed. We used the weighted centre of each real home range as the starting centre point for each model. Terrain in our study area was mountainous, so we included net change in elevation as a travel cost in our calculation of V_F values (Powell & Mitchell 1998).

Patch selection under models M_A , M_{AD} and M_{RD} requires two biological parameters, a resource threshold (M_A and M_{AD}) and the extent to which an animal depresses resources within its home range (M_{RD} and M_{AD}). No data exist to allow estimation of these parameters for black bears; therefore, we simulated home ranges under different permutations of models M_A , M_{RD} and M_{AD} . To estimate resource thresholds, we evaluated the range of summed V_F for the real home ranges of female bears living in the PBS and divided this range into six equal quantiles, representing six hypothetical resource thresholds. For each real home range, we generated six possible area-minimizing home ranges based on each threshold.

Resource depression sets a limit on the number of animals that can share a given patch of resources. Because overlap of home ranges is high in the PBS (Powell et al. 1997), we hypothesized that levels of resource depression among PBS females must be relatively low. For our simulations, we arbitrarily set -0.20 as the maximum amount that a simulated bear would depress resources within a patch included in its home range. We divided the range of resource depression values (0 to -0.20) into four equal quartiles, representing different hypothetical levels of resource depression. For each year, we used the reconstructed population of females (see above), with priority of home range construction assigned by age. For each real home range centre of bears, we generated four possible resource-maximizing home ranges with resource depression under model M_{RD} . Our area-minimizing model had six possible resource thresholds, so the incorporation of four hypothesized levels of resource depression resulted in 24 permutations of simulated home ranges generated under model M_{AD} for each real home range centre. Each simulated home range constructed under each model comprised a spatially explicit

selection of 250×250 -m patches from the map of V_F and was associated with a resource depression level (1 for models M_R and M_A , 2–5 for the other models) and, for models M_A and M_{AD} , a resource threshold (1–6).

Determining Patch Selection Strategy of Bears

We determined the spatial similarity between patches included in real home ranges and those selected under each permutation of each home range model using S , which is the average of two similarity indexes (Mitchell 1997). The first, S_A , was an index of the extent to which real and simulated home ranges shared patches:

$$S_A = \frac{\frac{P_{\text{Shared}}}{P_R} + \frac{P_{\text{Shared}}}{P_S}}{2}$$

where P_R is the number of patches in the real home range, P_S is the number of patches in the simulated home range, and P_{Shared} is the number of patches that the home ranges share in common. S_A ranges from 0 (no patches in common) to 1 (complete sharing). The second index, S_B , measured similarity between the perimeters of real and simulated home ranges (composed of boundary patches; Fortin et al. 1996):

$$S_B = 1 - \left[\frac{\left(\frac{\sum_{t_1=1}^{N_1} \min(d_{1i})}{N_1} \right) + \left(\frac{\sum_{t_2=1}^{N_2} \min(d_{2i})}{N_2} \right)}{2d_{\text{max}}} \right]$$

where $\min(d_{xi})$ is the smallest Euclidean distance for the i th patch of the boundary of home range x to a patch of the boundary of another home range, N_x is the number of boundary patches for home range x , and d_{max} is the mean distance between the perimeters of two adjacent, nonoverlapping circles with areas equal to the two home ranges. S_B ranges from 0 (strong dissimilarity between perimeters) to 1 (identical perimeters).

We used Akaike information criterion (AIC) analysis (Burnham & Anderson 2002) to assess variability in S across the 35 model permutations. We estimated annual home ranges for some bears over multiple years, so we evaluated statistical independence across observations by calculating \hat{c} . If \hat{c} exceeded 1.0, indicating lack of independence among observations, we incorporated \hat{c} as a variance inflation factor in our AIC analyses (Burnham & Anderson 2002). For all AIC analyses, we considered models with a ΔAIC value of 4 or less to be supported by the data; we analysed AIC weights (w_i) to evaluate the likelihood of each model. We evaluated evidence of importance for model parameters by summing weights (Σw_i) of each model in which each parameter was present (Burnham & Anderson 2002).

Effects of Energetic Demands and Social Dominance

We used AIC analysis to evaluate variation in S across all model permutations due to interactions between model

type (resource maximizing versus area minimizing), resource depression level (=0 for models M_R and M_A) and resource threshold (1–6 for models M_A and M_{AD} , absent for models M_R and M_{RD}), and age and reproductive status of bears.

RESULTS

From 1981 to 2001, we captured 250 bears 421 times. Of these, we located 56 radiocollared adult females with sufficient frequency (≥ 20 locations; Noel 1993) to generate 104 annual home range estimates; no home ranges could be estimated for bears in 1987, 1991, 1992 and 1998. The number of female bears tracked annually varied from 1 to 12 (Mitchell 1997). The mean \pm SD number of telemetry locations used to estimate home ranges across all bears was 114.79 ± 88.40 (Table 1).

Comparing General Predictions of Models to Real Home Ranges

Over all bears and all years, mean quality (mean V_F) of real home ranges (0.60, 95% CI = 0.59–0.61) was greater than mean quality of associated local areas (0.54, 95% CI = 0.53–0.55). Resource content of home ranges exceeded average availability.

We used capture and home range data from 68 adult female bears to reconstruct the annual PBS female bear populations (Mitchell 1997). The number of bears constituting each reconstructed population varied from 3 to 13 individuals; telemetered bears made up at least 50% of reconstructed populations in all years except 1988. We used trap site location as an estimate for the weighted home range centre point for only four bears. Over all reconstructed populations, spatial dispersion, D , for home range centres contained in each window of the moving windows analysis was 0.46 (95% CI = 0.44–0.46; home

ranges of PBS bears were clumped, similar to the distribution of resources within the PBS; Mitchell et al. 2002).

The spatial dispersion of weighted centres for real home ranges ($D = 0.46$, 95% CI = 0.44–0.46), although clumped, was more even than the weighted centres for the 100 simulated M_R home ranges that had random starting points and no resource depression ($D = 0.37$, 95% CI = 0.34–0.40), suggesting an influence of resource depression on the distribution of real home ranges.

Determining Patch Selection Strategy of Bears

We generated simulated home ranges under each of the permutations for each of the home range models to match 104 home ranges of female bears living in the PBS (Table 1). Similarity in spatial configuration of selected patches between simulated and real home ranges, S , varied across models and bears; all real home ranges, however, were reasonably approximated by a simulated home range generated under at least one model (Mitchell 1997; Fig. 2). Considering only those simulated home ranges across all models that maximized S for each real home range, mean \pm SD value of S was 0.75 ± 0.12 .

Our observations were statistically independent ($\hat{c} = 0.98$), so we did not include a variance inflation factor in our analyses (Burnham & Anderson 2002). In our AIC analysis, the resource maximization model (M_R) ranked relatively high (model likelihood = 0.96; Fig. 3, Table 2). Increasing levels of resource depression (under variations of model M_{RD}) consistently reduced the similarity between resource-maximizing home ranges and real home ranges (Fig. 3); the M_{RD} model with the lowest level of resource depression was viable, but its likelihood was low (0.18; Table 2). Four of the top models were M_A models without resource depression, including the top-ranked model (model likelihood = 1.00; Table 2) with moderate to high resource

Table 1. Summary statistics (mean and SD) for home ranges of female black bears, aged 2.5 years old or older, that were tracked in the Pisgah Bear Sanctuary in western North Carolina during 1981–2001 (no bears were tracked in 1987, 1991, 1992 and 1998)

Year	N	Age	Number of telemetry locations	Home range area (km ²)*	Home range quality†	Neighbourhood quality‡
1981	2	4.50 (0.00)	62.50 (40.31)	18.03 (4.64)	0.59 (0.02)	0.57 (0.03)
1982	2	4.00 (2.12)	176.50 (48.79)	18.63 (2.29)	0.60 (0.04)	0.57 (0.03)
1983	5	5.30 (3.03)	127.80 (49.82)	12.38 (8.65)	0.63 (0.04)	0.57 (0.04)
1984	7	6.21 (3.30)	302.86 (100.67)	10.06 (3.35)	0.62 (0.05)	0.57 (0.04)
1985	7	6.92 (3.41)	155.29 (78.44)	15.04 (4.52)	0.64 (0.05)	0.58 (0.03)
1986	3	4.83 (4.04)	178.33 (65.43)	20.25 (12.61)	0.56 (0.03)	0.58 (0.02)
1988	1	4.50 (0.00)	46.00 (0.00)	61.25 (0.00)	0.57 (0.00)	0.55 (0.00)
1989	3	4.16 (0.58)	64.00 (31.75)	15.71 (6.23)	0.61 (0.03)	0.55 (0.03)
1990	5	4.90 (2.51)	134.20 (70.76)	18.74 (12.99)	0.60 (0.05)	0.55 (0.04)
1993	7	4.36 (2.12)	233.00 (35.78)	15.18 (4.68)	0.59 (0.06)	0.53 (0.06)
1994	9	4.50 (2.00)	163.55 (35.73)	12.40 (6.45)	0.60 (0.05)	0.51 (0.06)
1995	9	4.39 (1.17)	146.44 (40.18)	9.15 (2.51)	0.59 (0.11)	0.51 (0.06)
1996	12	5.08 (1.83)	48.16 (16.72)	10.04 (4.15)	0.57 (0.05)	0.50 (0.06)
1997	1	6.50 (0.00)	26.00 (0.00)	11.94 (0.00)	0.61 (0.00)	0.52 (0.05)
1999	9	3.94 (2.01)	41.44 (15.88)	12.74 (4.70)	0.61 (0.04)	0.52 (0.06)
2000	11	5.32 (3.25)	40.82 (12.76)	15.26 (7.99)	0.61 (0.03)	0.51 (0.06)
2001	11	5.05 (1.51)	71.82 (34.11)	12.74 (8.64)	0.59 (0.04)	0.53 (0.05)

*Analyses were based on the number of 250×250 -m patches in each home range (km² \times 16).

†Mean of V_F index (life requisite variable for food, range 0–1; Mitchell et al. 2002) assigned to patches in each home range; total resources in each home range = sum of V_F values.

‡Mean V_F index for vicinity of home range.



Figure 2. Estimated optimal home range (dots) superimposed over true home range (outline) of female bear 96 in 1984, Pisgah Bear Sanctuary, North Carolina. The optimal home range was generated using resource-maximizing model M_R based on the underlying distribution of resources depicted by the V_F component of a habitat suitability index (HSI) for black bears. Home ranges are presented on the map of V_F for 1984. Dark hues represent poor food value; light hues represent high food value.

thresholds providing the best fit (Fig. 3) to real home ranges. Adding resource depression to area-minimizing home ranges (model M_{AD}) resulted in home ranges with high predictive power where resource depression was low and resource thresholds were moderate (Fig. 3, Table 2). Two M_{AD} models were viable, but their relative likelihoods were low (0.29 and 0.19). Analysis of summed AIC weights (Σw_i) for each model parameter suggested an area-minimizing strategy ($\Sigma w_i = 0.72$) was approximately 2.5 times more likely than a resource-maximizing strategy ($\Sigma w_i = 0.28$). Likelihoods of moderate resource thresholds (4 and 5, $\Sigma w_i = 0.31$ and 0.25, respectively) structuring area-minimizing home ranges were nearly equal and several times greater than those of higher or lower thresholds (3 and 6, $\Sigma w_i = 0.05$ and 0.08, respectively). The likelihood that resource depression did not influence home ranges ($\Sigma w_i = 0.84$) was approximately six times greater than the likelihood that the lowest resource depression (level 1, $\Sigma w_i = 0.16$) did.

Effects of Energetic Demands and Social Dominance

Only the interaction between breeding status and both resource thresholds of area-minimizing home ranges and levels of resource depletion (AIC = -8792.8) was important.

As levels of resource thresholds and resource depression increased, their contribution to model fit, S , remained nearly constant for lactating females but declined for breeding females (Fig. 4). Home ranges of lactating females were more strongly influenced by higher resource thresholds and higher levels of resource depression than those of breeding females. The next model in rank (an interaction between breeding status and resource depression levels) had a ΔAIC of 316.3, well beyond our decision criterion of 4. Age of bears was unrelated to any model parameters. Neither age nor breeding status influenced whether a bear pursued a resource-maximizing or area-minimizing home range strategy.

DISCUSSION

The relationship between resources and territories has been investigated extensively (Stenger 1958; Gill & Wolff 1975; Carpenter & MacMillen 1976; Kodric-Brown & Brown 1978; Ebersole 1980; Hixon 1980; Schoener 1983; Powers & McKee 1994). To date, little attention has been given to how home ranges of animals might be optimal, even though this concept is implicit in how home ranges are commonly understood (Powell 2000). To learn whether home ranges of animals might be optimal with respect to the spatial distribution of resources, and whether optimal use of these resources might structure the distribution of animals on a landscape, we compared general and explicit predictions of our home range models to annual home ranges observed for a population of black bears.

Characteristics of the home ranges of black bears in the PBS were consistent with the general predictions of our home range models (Mitchell & Powell 2004). In accordance with our first prediction, we found that female black bears in the PBS had home ranges that were efficient with respect to the spatial distribution of food resources. The availability of food resources within home ranges was greater than average availability within each bear's immediate surroundings, except for 1986 (Table 1). This anomaly was probably due to the influence of a single bear (Mitchell 1997), which did not settle into a stable home range in 1986.

In accordance with our second prediction, the home ranges of bears in the PBS were not randomly distributed on the landscape but were clumped, as are the resources available in the area (Mitchell et al. 2002). Territoriality among bears would function to distribute home ranges more evenly on the landscape. Horner & Powell (1990) found a high degree of overlap among the home ranges of PBS bears; Powell et al. (1997) concluded that female black bears in North Carolina were not territorial. The absence of territoriality suggests that the clumping of home ranges of bears in PBS is linked to the clumped spatial distribution of food resources.

Although the home ranges of female bears in PBS were clumped, they were not as clumped as would be expected based solely on the distribution of food resources. The more even spacing of the real home ranges of bears than the home ranges simulated in the absence of resource depression suggests a limit to which bears can, or will, share resources, in accordance with our third prediction. This

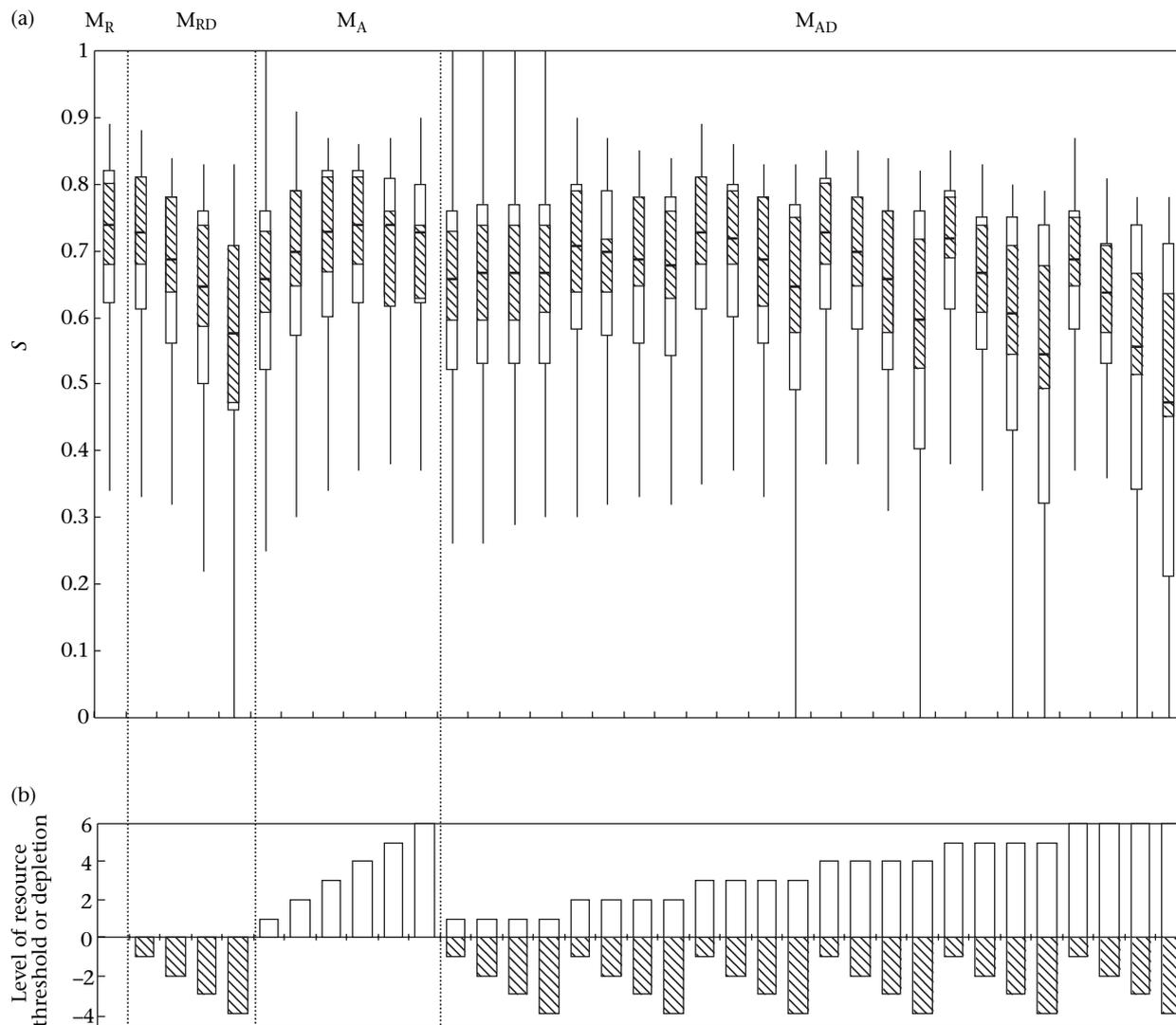


Figure 3. (a) Box plots of similarity index S , indicating the ability of different permutations of four spatially explicit home range models (M_R , M_A , M_{RD} and M_{AD}) to predict the home ranges of female bears living in the Pisgah Bear Sanctuary from 1981 to 2001. Permutations within each model differed in either the resource threshold used to establish an area-minimizing home range (six uniformly increasing thresholds for model M_A), the level of resource depletion within home ranges (four levels for model M_{RD}), or both (model M_{AD}). S ranges from 0 (poor fit) to 1 (perfect fit). Mean S for each model is represented by a dash, the white box represents mean \pm SD, the cross-hatched box represents the middle 50th percentile, and the vertical line represents the range. (b) Relative level of resource threshold (\square) and level of resource depletion (\boxtimes) for each model.

result implies the effects of resource depression, wherein the value of a patch declines with the number of bears using it, either through direct consumption or a measure of social antagonism that falls short of complete territoriality.

Correspondence of home ranges of real bears both with general predictions of our models (Mitchell & Powell 2004) and with characteristics of home ranges estimated by our models was unambiguously consistent with our hypothesis that home ranges of bears in PBS are efficient with respect to resources in much the same way that territories of other species have been shown to be (Hixon 1982; Schoener 1983; Powell 2000). Whereas home ranges of PBS bears were efficient, our study did not reveal an unambiguous distinction between efficiency strategies among the bears. Both M_R and M_A home ranges ranked high in our analyses and were thus equally viable models.

This result is possible when the resource threshold defined in M_A approximates the amount of resources accumulated through rate maximization in M_R (Mitchell & Powell 2004), making strategies difficult to distinguish. Among our highly ranked models, however, statistical evidence was strongest for an area-minimizing strategy based on moderate to high resource thresholds, suggesting that this is the most likely behavioural strategy of bears. Our hypothesis that PBS bears pursue an area-minimizing strategy in their home ranges is probably correct, although we cannot exclude the possibility of resource maximizing. Further distinguishing these strategies among PBS bears would require a change in the spatial distribution of resources such that resource thresholds of area-minimizing home ranges no longer approximate the amount of resources accumulated under a rate-maximization strategy.

Table 2. AIC analysis of similarity of simulated home ranges generated under different models for optimal patch selection and home ranges of adult female black bears living in the Pisgah Bear Sanctuary, North Carolina, during 1981–2001

Model	Resource threshold	Level of resource depression	AIC	Δ AIC	Model weight, w_i	Model likelihood
M_A	5	0	1098.095	0.000	0.25	1.00
M_R	—	0	1098.174	0.078	0.24	0.96
M_A	4	0	1098.193	0.097	0.24	0.95
M_A	6	0	1100.470	2.374	0.08	0.31
M_{AD}	4	1	1100.584	2.488	0.07	0.29
M_{AD}	3	1	1101.427	3.376	0.05	0.19
M_{RD}	—	1	1101.544	3.448	0.04	0.18
M_A	3	0	1101.987	3.891	0.04	0.14

M_R maximizes resources per unit area of a home range, given the distribution of available resources. M_A minimizes the area within a home range needed to contain a requisite amount of resources for survival and reproduction; six hypothesized levels of resource thresholds were evaluated for this model. Both models were also evaluated at five hypothesized levels of resource depression; models incorporating resource depression are denoted M_{RD} and M_{AD} . Only models with Δ AIC values at or below 4 are shown (Burnham & Anderson 2002).

Evidence for resource depression as the mechanism structuring the spatial dispersion of home ranges in the PBS was present but not strong. Although two models incorporating low levels of resource depression ranked high in our analysis, even low levels of resource depression reduced the predictive power for most of our models (Fig. 3). Although effects of resource depression did not influence the home ranges of individual bears strongly, the spatial dispersion of home ranges among bears was consistently more even than would be predicted in the absence of resource depression. These observations agree with the predictions of a home range model with low levels of resource depression, where the population of animals is small enough that animals can distribute themselves so as to minimize the effects of resource depression on their home ranges (Mitchell & Powell 2004). We cannot reject our hypothesis that resource depression structures the distribution of home ranges of female bears within PBS, but our results are suggestive of this effect. We consider it likely that the arbitrary levels of resource depression that we chose for models M_{RD} and M_{AD} exceeded actual levels of resource depression among bears in the PBS.

Home ranges of lactating females had higher resource thresholds and were more strongly influenced by resource depression by other bears than those of breeding females. Energetic costs of lactation are high (Moen & Boomer 2005), so intuitively, the resource threshold by which a lactating female chooses patches for a home range should be higher than when she is not lactating (e.g. Mauritzen et al. 2001). This would increase the number of patches needed for an area-minimizing home range, increasing overlap with home ranges of neighbouring bears, thus creating more exposure to the effects of resource depression by their occupants. This does not imply that home ranges of lactating females will necessarily be larger than those of breeding females. Whereas the home range of a female on a clumped distribution of high-quality resources may vary in size with her breeding status, it would always be smaller than that of a breeding female on a dispersed distribution of low-quality resources. Fluctuations in resource thresholds and levels of resource depression and their effects on home range characteristics should always be

relative to the spatial distribution of resources on which the home ranges are based.

The conditions under which black bears establish and maintain home ranges are common to many, if not most, animal species that show site fidelity (Powell 2000). Furthermore, the home range models that we used in our research are not specific to black bears and are applicable to any species for which the fitness value of critical resources can be mapped (Mitchell & Powell 2004). Thus, our study provides insights into how the efficient use of heterogeneous landscapes can structure home ranges and spatial distributions of animals in general. Our results suggest that home ranges are structured economically with respect to resources in much the same way that territories are (Hixon 1982; Schoener 1983; Powell et al. 1997; Powell 2000). As such, the spatial distribution of resources strongly affects home range size, structure and location on the landscape. Efficient use of spatially distributed resources by K -selected, 'slow' (Heppell et al. 2000) species is represented well by a type II, area-minimizing approach to accumulating resources through patch selection. Such home ranges contain the resources needed for survival and reproduction in as small an area as possible, but the resources that define this threshold, and therefore the size and content of the home range, will vary with the energetic needs and abilities of the animal to sequester or protect resources. Further investigation is needed to determine to what degree r -selected, 'fast' animals pursue a resource-maximizing strategy for their home ranges.

The degree to which animals depress resources within their home ranges also influences the location of home ranges on a landscape. Where resource depression is low, home ranges should be distributed largely according to the distribution of resources. Increasing levels of resource depression should result in distributions of animals that are more even than those of resources, with the highly even distributions characteristic of territorial animals (i.e. those completely depressing resources within their home ranges) representing the extreme case. Selective use of resources and resource depression should be sufficient to distribute animals on a landscape according to an ideal free distribution (Fretwell 1972). By including sequential construction of simulated home ranges for bears

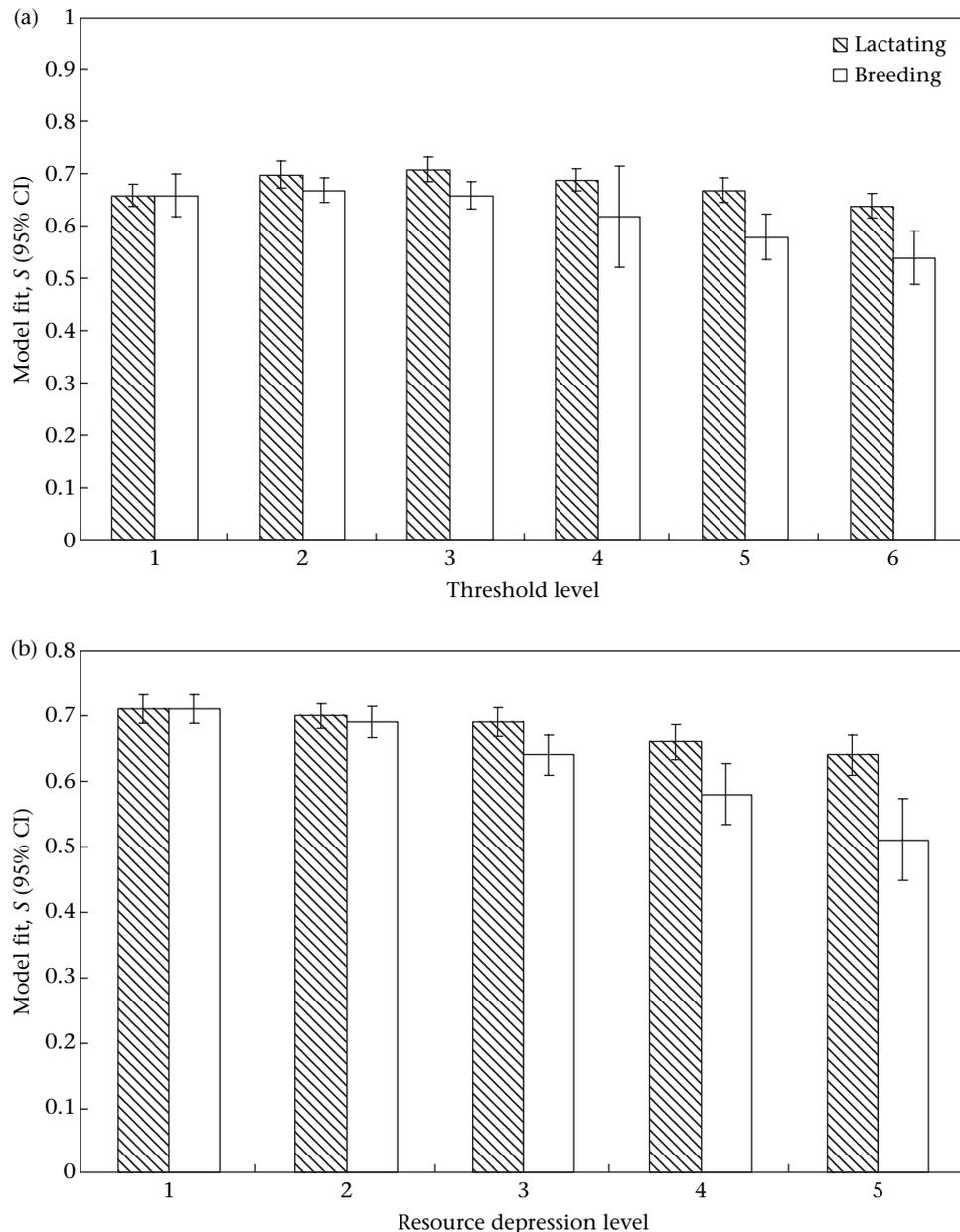


Figure 4. The extent to which (a) resource thresholds of area-minimizing home ranges and (b) levels of resource depression interacted with breeding status (lactating or breeding) to influence fit (S) of simulated home ranges to home ranges of adult female black bears living in the Pisgah Bear Sanctuary, North Carolina, during 1981–2001.

according to social dominance, we modelled the conditions necessary for an ideal preemptive distribution (Pulliam & Danielson 1991). The predictive ability of our home range models under these conditions suggests a possible mechanistic link between optimal use of resources by individual animals and the ideal free, or preemptive free distributions of animals on the complex, heterogeneous landscapes common in nature (e.g. map of V_T , Fig. 2).

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