



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

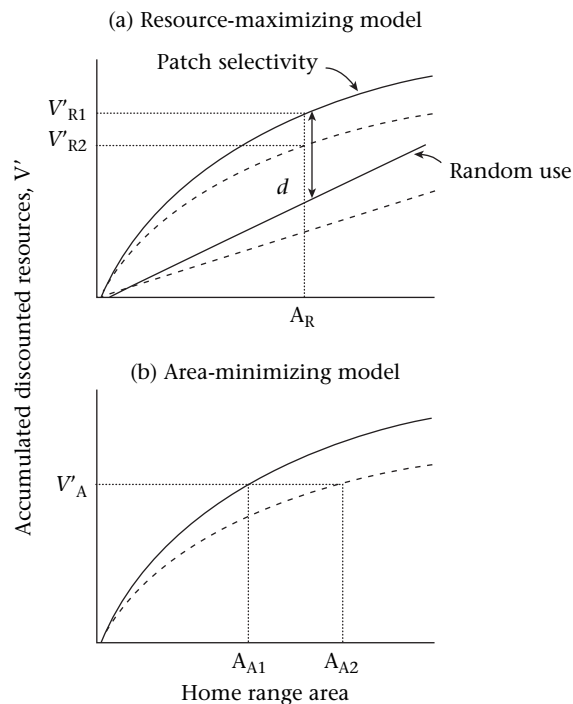


Figure 1. Conceptual models for constructing optimal home ranges based on selecting patches containing high-quality resources. In both models, an animal selects patches in order of their resource value (V'), discounted for travel costs required to reach the patches. (a) Under the resource-maximizing 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).

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