

Foraging optimally for home ranges

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Economic models predict behavior of animals based on the presumption that natural selection has shaped behaviors important to an animal's fitness to maximize benefits over costs. Economic analyses have shown that territories of animals are structured by trade-offs between benefits gained from resources and costs of defending them. Intuitively, home ranges should be similarly structured, but trade-offs are difficult to assess because there are no costs of defense, thus economic models of home-range behavior are rare. We present economic models that predict how home ranges can be efficient with respect to spatially distributed resources, discounted for travel costs, under 2 strategies of optimization, resource maximization and area minimization. We show how constraints such as competitors can influence structure of home ranges through resource depression, ultimately structuring density of animals within a population and their distribution on a landscape. We present simulations based on these models to show how they can be generally predictive of home-range behavior and the mechanisms that structure the spatial distribution of animals. We also show how contiguous home ranges estimated statistically from location data can be misleading for animals that optimize home ranges on landscapes with patchily distributed resources. We conclude with a summary of how we applied our models to nonterritorial black bears (*Ursus americanus*) living in the mountains of North Carolina, where we found their home ranges were best predicted by an area-minimization strategy constrained by intraspecific competition within a social hierarchy. Economic models can provide strong inference about home-range behavior and the resources that structure home ranges by offering falsifiable, a priori hypotheses that can be tested with field observations.

Key words: area minimization, black bear, distribution, habitat quality, home range, optimality, resource depression, resource maximization

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DOI: 10.1644/11-MAMM-S-157.1

Economic models assume that behaviors that are consequential for an animal's fitness have been shaped by natural selection to maximize benefits over costs. The home ranges of animals, and the spatial distribution of animals within a population, are commonly thought to reflect an economic use of resources distributed on a landscape (Ebersole 1980; Hixon 1980; Mitchell and Powell 2004; Powell 2000; Powell et al. 1997; Powers and McKee 1994; Schoener 1981). The relationship between resources and territories (i.e., that part of an animal's home range where conspecifics are excluded [Ostfeld 1990; Powell 2000; Powell et al. 1997; Wolff 1993, 1997]) has been investigated extensively (Brown 1969; Carpenter and MacMillen 1976; Ebersole 1980; Gill and Wolff 1975; Hixon 1980; Kodric-Brown and Brown 1978; Powers and McKee 1994; Schoener 1983; Stenger 1958), primarily using economic analyses of fitness trade-offs between benefits gained from resources and costs of defending

them. In contrast, the costs and benefits structuring home ranges of animals have received less attention, in part because definitions for home ranges are imprecise. Burt (1943:351) described a home range as "... that area traversed by an individual in its normal activities of food gathering, mating, and caring for the young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range."

Burt's definition is conceptually complete but difficult to evaluate analytically because it contains terms that are vague and difficult to quantify in terms of costs or benefits (Mitchell and Powell 2004; Powell 2000; Powell et al. 1997). Intuitively, though, economic use of resources should structure home



ranges as they do territories, if perhaps under less-stringent constraints. Although the importance of food as a structuring resource is cited in many home-range studies (Garshelis and Pelton 1981; Harestad and Bunnell 1979; Holzman et al. 1992; Jones 1990; Joshi et al. 1995; Kelt and Van Vuren 2001; Lindstedt et al. 1986; Lindzey and Meslow 1977; Litvaitis et al. 1986; Trombulak 1985), particularly for females (Ims 1987; Mitchell and Powell 2003; Powell et al. 1997; Reynolds-Hogland et al. 2007; Young and Ruff 1982), little is known about how a home range is structured with respect to these or any resources (e.g., escape or thermal cover, denning resources, etc.); historically, researchers have had to assume that an animal's life requisites are satisfied by the resources available within its observed home range. Indeed, most home-range studies are attempts to infer post hoc how resources structured observed home ranges. Because home ranges based solely on accumulating as many resources as possible would be limitless in size, it is clear that animals with defined, finite home ranges accumulate spatially distributed resources under limiting constraints. Home ranges, therefore, like territories, should be a function of the benefits of accruing limiting resources, given their availability and distribution, limited by the costs of resource acquisition.

Research on home ranges inherently assumes that animals are behaving nonrandomly with respect to their environment, choosing to live where their fitness is maximized within the constraints imposed by their environment, conspecifics, competitors, mobility, and predators. Thus, economic models that evaluate optimal balances between such benefits and costs offer a priori, mechanistic explanations of why animals exhibit the home-range behavior they do (as opposed to the inferentially weaker approach of deriving such explanations post hoc from field data). Economic models of home ranges are, nonetheless, very rare. In this paper, we provide an overview of economic models we developed for home ranges (Mitchell and Powell 2004, 2008) and review what we learned from applying these models in a study of black bears (*Ursus americanus*—Mitchell and Powell 2007). We provide a conceptual outline that deals explicitly with how benefits (i.e., resource values) and costs (i.e., travel costs and resource depression by conspecifics) can be balanced in the selection of home ranges to maximize their value under 2 alternative, fitness-maximizing strategies (Mitchell and Powell 2004). We show how this approach was used to predict the home ranges of adult female black bears living in the southern Appalachian Mountains. We illustrate potential pitfalls in understanding home ranges if an economic approach is not used, and we address the overarching importance of the currency chosen for economic analyses of home ranges.

ECONOMIC MODELS

The primary tool for exploring trade-offs between costs and benefits within given constraints is optimality modeling, based on the Darwinian logic outlined by Krebs and Kacelnik (1991: 105) that “selection . . . is an iterative and competitive process,

so that eventually it will tend to produce outcomes (phenotypes) that represent the best achievable balance of costs and benefits.” Optimality modeling had its beginning in foraging theory (Emlen 1966; MacArthur and Pianka 1966) and under a variety of approaches it has been used to test hypotheses about prey choice (Charnov 1976a), patch residency time (Charnov 1976b), diet composition of herbivores (Belovsky 1978, 1981), and movement (see Pyke et al. 1977), all based on balancing costs and benefits within sets of constraints. From these beginnings, optimality theory has been used to model territoriality (see above), parental investment (see Clutton-Brock and Godfray 1991), sexual selection (see Harvey and Bradbury 1991), predator-prey interactions (see Endler 1991), and mating systems (see Davies 1991; Powell et al. 1997:134), and it has the potential to develop models for testing hypotheses about coevolution, community structure, and population dynamics (Pyke et al. 1977).

Optimality theory has come under considerable criticism (Gould and Lewontin 1979; Lewontin 1978, 1979, 1983; Pierce and Ollason 1987), and not without justification. These critics assert that an optimization approach to studying organisms too often promotes an adaptationist agenda and that the infinite number of evolutionary possibilities necessary to allow any animal to become truly optimal with respect to its environment do not exist; limits on optimality are imposed by phylogeny and the adaptive compromises required by conflicting selective pressures. Optimization approaches to research can be viewed as tautological (Ollason 1980) because assumptions made by optimality models are often inherently untestable, and, when predictions and observations fail to agree, faulty assumptions often are assumed to be the cause (instead of the potential invalidity of the model [Pyke 1984]).

Krebs and Kacelnik (1991) attributed these criticisms to a consideration limited primarily to naive examples of optimality modeling, and with Stephens and Krebs (1986) advocated the usefulness of optimization theory for developing testable alternate hypotheses. Pulliam (1989) further contended that optimality modeling does not attempt to prove that evolution maximizes fitness, rather if one assumes that animals do not choose among available options at random, optimality modeling allows the prediction of how those choices will be made.

Benefits

An appropriate currency for economic models of home ranges comprises the resources that contribute to the fitness of animals, particularly those that are limiting. The traditional components of habitat (food, water, and escape cover) are obvious candidates, but some species might require broader thinking (see Powell and Mitchell 2012). For example, suitable den locations structure home ranges of coyotes (Moorcroft et al. 1999), the distribution of female black bears structures home ranges of males (Powell et al. 1997), and habitat features that provide safe transit between food patches structure home ranges of prey species; each of these can rightfully be

considered resources that contribute wholly or in part to the optimization of a home range.

Realistically, fitness of most animals depends on multiple resources (see Moorcroft 2012); should these resources be evaluated separately in an economic model, optimal solutions to the diversity of trade-offs can become highly complex. Two simplifying solutions can address this problem. First, select a currency common to all resources of interest; energy (e.g., kilocalories expended versus kilocalories gained) is an intuitive and commonly used currency for optimal foraging models (Pyke et al. 1977). Energy is a clearly preferable currency where food resources are concerned (and energetic needs and expenditures of an animal can be understood), but can be limiting for resources such as escape cover, den sites, potential mates, and so on, that have no clear energetic value but can nonetheless be critical to an animal's fitness. Alternatively, the cumulative value of all resources (i.e., energetic and non-energetic) potentially contributing to an animal's fitness can be modeled as an index (see Powell and Mitchell 2012), wherein the relative contribution of all resources can be combined based on a common scale (e.g., 0–1).

However currency is defined, its distribution on a landscape must be depicted to understand how it contributes to selection of home ranges. With the aid of geographic information systems and remote sensing, opportunities to depict the distribution of resources on a landscape are abundant, although we recommend extreme discernment in assuming relationships between mapped information (often based on vegetative community) and the resources that actually contribute to the survival and reproduction of animals (Mitchell and Hebblewhite 2012; Mitchell and Powell 2002). To be an effective currency for economic home-range analyses, mapped resource values should represent the potential, gross benefit or value to an animal's fitness, V , of each patch on a landscape to an animal that includes that patch in its home range, on the same scale of measurement. This requires some hard biological thinking, which can be no small endeavor in its own right. In the absence of this effort, though, a currency is of questionable value and can lead to misleading insights, even where economic models are otherwise used appropriately, as we will discuss later.

Costs

Costs of acquiring resources within a patch reduce the patch's value, V . Identifying costs may not always be clear. Obviously, being killed by a predator is an ultimate cost, but one that could only be modeled probabilistically (i.e., the "landscape of fear" [Laundré et al. 2001]); thus, risk of predation could be considered a cost (i.e., reduction in V within patches varies depending on modeled predation risk) or a constraint (i.e., reduction in V within patches is a constant function of predation risk; see below) that affects V . Similarly, foraging costs, or handling time, can be very specific to variable resource conditions (e.g., productivity and distribution within a patch) and, absent highly detailed observation, can only be understood probabilistically or as an average condition.

Perhaps more tractably, a large and unavoidable cost for any nonsessile animal is energy expended during travel, which is a function of Euclidean distance and may or may not include other factors such as topography (Taylor 1973), and can influence strongly the efficient use of spatially distributed resources (Stamps and Eason 1989). For example, a modestly productive food patch that is nearby may be more valuable to an animal than a richly productive patch far away (Getz and Saltz 2008).

We depict the value of a patch that has been discounted for costs as V' , that is, the potential, net benefit of a patch on a landscape to an animal that includes it in its home range. In one approach to modeling V' , we modeled the costs of including a patch in a home range as a function of the average distance that must be traveled to reach the patch (Mitchell and Powell 2004). Because most animals spend much of their time in core areas within their home ranges (Powell 2000; Powell et al. 1997; Samuel and Green 1988; Samuel et al. 1985; Seaman and Powell 1990), we used the distance of a patch from the center of the core to approximate the average distance traveled over time to reach that patch from all other patches within a home range (Smith 1968), if the patch were included. We discounted the value of resources in a patch for the average cost of traveling to that patch from all other patches in the home range as:

$$V' = V/(aD), \quad (1)$$

where V' is potential net resource value, D is distance of patch from home-range core, and a scales D to the animal being studied and V . Because V' is undefined for $D = 0$ under this definition, we set D equal to one-half the patch width for the center patch.

Alternatively, V' could be modeled using energetics:

$$V' = V - cD, \quad (2)$$

where c is a constant relating energy expenditure to distance traveled. Unfortunately, c is unknown for most animals.

Importantly, the value of critical nonfood resources (e.g., escape cover) is not addressed in a purely energetic model; thus, how V will lose value with distance is unknown. Further, nonenergetic, comprehensive indexes of habitat quality exist for many species. Most are easy to depict spatially and can be evaluated readily using equation 1, whereas the estimation of c and the conversion of V and D to a common currency (e.g., kilocalories) needed for equation 2 can be problematic (Mitchell and Powell 2004).

Constraints

Other factors such as predation, social interactions (e.g., territoriality and hierarchical antagonism), and competition (e.g., consumption of foods, causing prey to be vigilant, and occupation of den sites) can affect the ability of an animal to experience the benefits or to pay the costs associated with a patch (see Powell and Mitchell 2012). Constraints effectively depress the perceived value of resources or raise the costs

associated with a patch and, thereby, affect patch selection by an animal establishing a home range. Risk of predation, for example, might limit the time a forager spends in patches or increase the cost of foraging and handling food. The value, V , of such patches in economic models can be reduced proportional to risk, time lost, or the increase in foraging energy. In the case of social interactions or competition, V of a patch should depend on the quantity and quality of resources, the number of conspecifics and other competitors using that patch, and the extent to which conspecifics or predators depress the value of resources in those patches (see Spencer 2012). Thus, use of a landscape by an animal modifies the distribution of resources available to other animals; as the number of animals using a landscape increases, the distribution of V available to successive animals changes, and therefore, the distribution of home ranges on the landscape also should change (Mitchell and Powell 2004).

Optimization

We have hypothesized (Mitchell and Powell 2004) that an animal optimizes resource accrual within its home range through the selection of resource-bearing patches, analogous to optimal foraging for food items in a diet (Charnov 1976a; Krebs and Kacelnik 1991; Stephens and Krebs 1986). This view of the home range differs from the notion that a home range is the sum of an animal's movements (Bascompte and Vilà 1997; Gautestad and Mysterud 1993, 1995; Lewis and Murray 1993; Loehle 1990; Worton 1987); our focus is on the spatially distributed resources that structure those movements (i.e., its cognitive map—Peters 1978 [see Powell and Mitchell 2012; Spencer 2012]).

Our models were spatially explicit, individual-based models for selecting patches for a home range optimally from a landscape comprising resource-bearing patches (Mitchell and Powell 2004). Each model assumed that animals select the best available patches. We modeled the benefit of a patch to be the value of resources contained in the patch, V , set to range from 0 (low value) to 1 (high value). We hypothesized that animals select patches for their home ranges based on potential net value V' . We modeled this selection by 1st establishing a center point for a home-range core on a distribution of V ; functionally, this can be done randomly, according to the values of V (e.g., selecting the greatest value or cluster of values for V), or based on some known properties of home ranges for the species of interest (e.g., geographic centers for observed animals). We used that center point to calculate V' across the landscape, and then selected patches sequentially for inclusion within the home range, from highest to lowest V' . Our models differed in the point at which patch selection would stop, that is, when resource accumulation within the home range was sufficient. We modeled 2 alternative strategies for determining when patch selection should end: maximizing resources within a home range over random use of patches (i.e., resource maximization), and accumulating resources sufficient to satisfy a preset minimum threshold (i.e., area minimization). The 1st strategy maximizes the difference between selective and

random use of resources on a landscape and is optimal with respect to the resources themselves. The 2nd strategy minimizes the area needed to satisfy a resource threshold sufficient for an animal's survival and reproduction and is optimal with respect to this biological threshold. These strategies are, respectively, directly analogous to the energy-maximizing and time-minimizing strategies of optimal foraging (Charnov 1976a, 1976b; Krebs and Kacelnik 1991; Mitchell and Powell 2004; Stephens and Krebs 1986). Home ranges selected under each of these strategies are influenced differently by constraints such as resource depression (Charnov et al. 1976); therefore, we also created variants for each that incorporated effects of resource depression.

Model M_R , resource maximization.—Animals that use patches randomly will, on the average, accrue resources within a home range equal to the mean availability of resources on a landscape. A selective animal could choose high-quality patches so as to exceed mean availability of resources as much as possible, until adding more patches begins to reduce this difference. A home range that maximizes the density (V'/area) of resources within a home range can be modeled as one maximizing the difference (Fig. 1A, difference d) between accumulated resources, V' , within its home range (Fig. 1A, *Patch Selectivity* line) and random use of the landscape (Fig. 1A, *Random Use* line).

Model M_A , area minimization.—Home ranges of animals might contain only the minimum resources necessary to survive or to reproduce successfully. Thus, an optimal home range would be one that meets this minimum in as small an area as possible. We modeled such survival or reproductive thresholds as a constant (Fig. 1B). The point at which the resource accumulation curve of a selective animal meets the minimum resource threshold represents the home range that satisfies the resource needs of the animal in as small an area as possible (Fig. 1B).

Models M_{RD} and M_{AD} , effects of resource depression.—Resource values on a landscape are depressed proportionate to the number of animals occupying the landscape and their per capita influence on resources. Thus, as more animals establish home ranges on a landscape both the *Patch Selectivity* lines and the *Random Use* lines become shallower, changing predicted home ranges (e.g., Fig. 2). For resource-maximizing home ranges, the point at which d is maximized does not change with proportional changes in the curves, thus home-range area, A_R , does not change with resource depression, but accumulated resources (V') decline (from $\sum V'_{R1}$ to $\sum V'_{R2}$ in Fig. 2A). For area-minimizing home ranges, accumulated resources (V') do not change with resource depression ($\sum V'_A$), but area increases (from A_{A1} to A_{A2} in Fig. 2B).

APPLICATION OF MODELS

Simulations.—We evaluated how spatial distribution of resources and optimization strategies could interact to structure home ranges of animals by performing individual-based, spatially explicit computer simulations using each

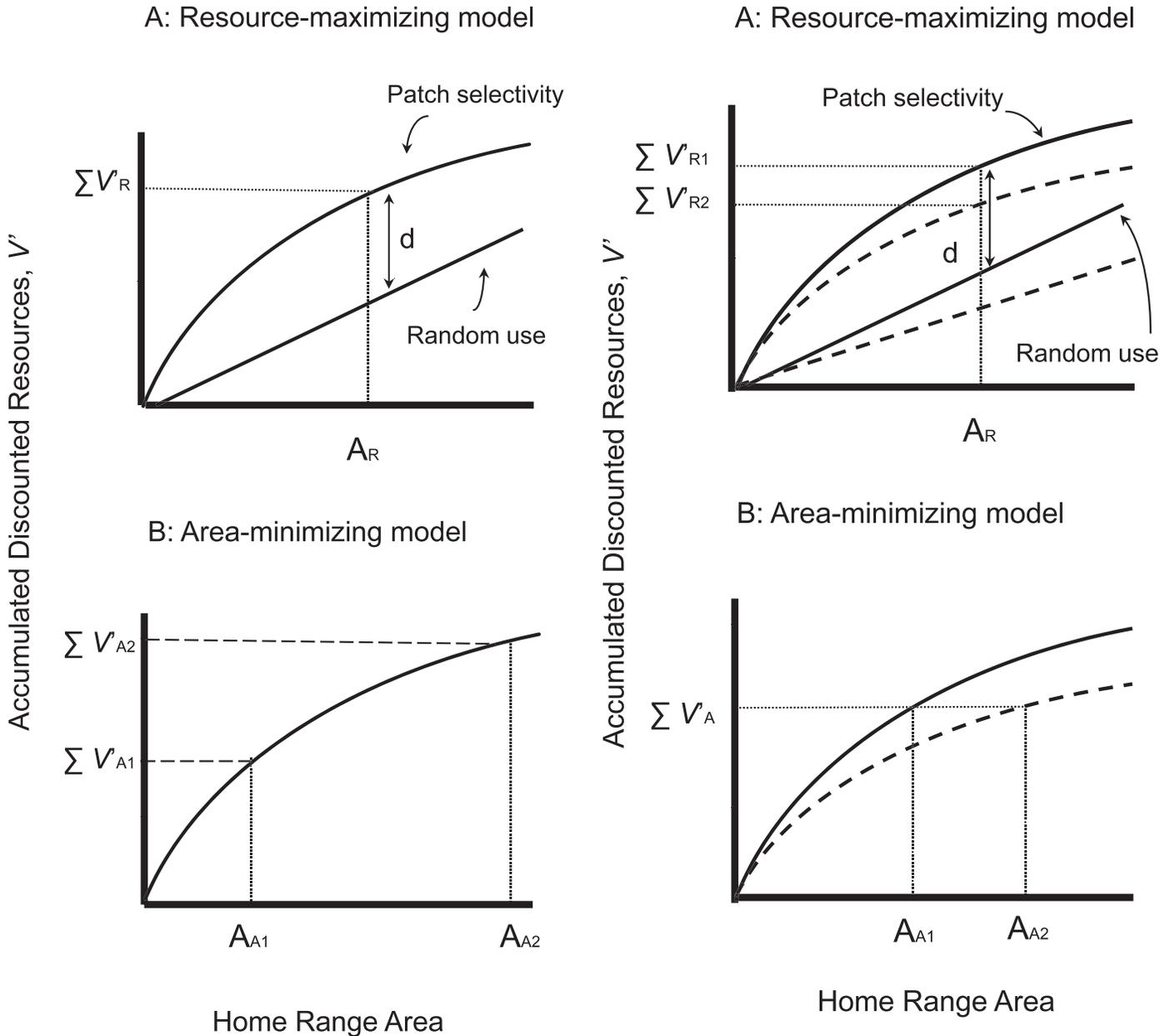


FIG. 1.—Conceptual models for home ranges that are optimal with respect to spatially distributed patches containing resources. In both models, an animal selects patches in order of their resource value discounted for travel costs (V'). A) Under model M_R , patch selection stops once the difference between random and selective use of the landscape, d , was maximized, representing the maximum density or resources per area obtainable from the landscape. B) Under model M_A , patch selection stops when a minimum threshold necessary for survival and reproduction is reached. Panel A shows the resource-maximizing home range defined by resource accumulation $\sum V'_R$ and area A_R . Panel B shows 2 possible area-minimizing home ranges, defined by $\sum V'_{A1}$ and area A_{A1} and $\sum V'_{A2}$ and area A_{A2} , respectively, based on meeting 2 different resource thresholds (from Mitchell and Powell 2004).

FIG. 2.—Conceptual model for how resource depression by animals affects home ranges under 2 models of optimal patch selection. The *Patch selectivity* line in panels A and B indicates how a selective animal would accumulate resources by choosing patches for its home range in order of their resource value discounted for travel costs (V'). The *Random use* line in panel A indicates how an animal using the landscape randomly would accumulate resources. Dashed lines indicate resource accumulation for selective and random use prior to resource depression, and solid lines indicate resource accumulation after resource depression (from Mitchell and Powell 2004).

model on simulated landscapes. We devised 5 landscapes that each comprised a grid of uniformly sized patches with values of V that ranged from 0 to 1; these landscapes differed only in the spatial continuity of V among patches (from overdispersed to clumped—Mitchell and Powell 2004). On each of the landscapes we sequentially placed randomly located centers of 100 home ranges and selected patches for each under each of

our models, modeling V' using equation 1 and setting $a = 1$. After patch selection for each simulated home range was complete, we compared geographic center for the home range to the geographic center weighted for V within the home range. If the 2 centers differed, we set the geographic center weighted for V as the new home-range center, recalculated V' , and reselected patches. This allowed patch selection to be adaptive to the distribution of V , resulting in home ranges that locally maximized accumulation of V within the home range. Because home ranges incorporating resource depression fundamentally changed the distribution of V , as a computing expediency we used a moving windows analysis of V for each landscape to select the areas of highest mean V for placement of each home-range center for models M_{RD} and M_{AD} ; this results asymptotically in the same distribution of home ranges as would random placement of centers with unlimited time for reiterations of patch selection. After patches were selected for a home range developed under models M_{RD} and M_{AD} , values of V were reduced in patches selected for that home range by 0.15 to emulate the effects of resource depression, with a minimum value of 0 set per patch.

From our simulations, we found the most important factor determining size, shape, and location of home ranges was the extent to which resources were clumped on a landscape. As designed, characteristics of resource-maximizing home ranges were determined only by the distribution of resources, and differed from those of area-minimizing home ranges depending upon the resource thresholds used; an increase in resource threshold increased area and total resource content for area-minimizing home ranges, but did not change their quality (which we defined as summed V) or efficiency (which we defined as mean V for the home range – mean V for the landscape [Mitchell and Powell 2004]). Adding resource depression to our models resulted in home ranges that differed little in configuration and landscape interactions from those without, except that they were distributed more evenly on the landscapes and overlapped each other less. Predictably, as the number of home ranges on a landscape increased, resource distributions declined in quality and heterogeneity, and home ranges became larger, less efficient, and of lower quality. Our results suggested that, in addition to landscape configuration, the extent to which animals depress resources included in their home ranges should determine the evenness of spatial dispersion, overlap, and home-range structure, especially where animals pursue an area-minimizing strategy and their density is high (see Spencer 2012). Because resource depression sets a limit on the number of home ranges a landscape can support, our models allow estimation of carrying capacity of a landscape for a species of interest (Mitchell and Powell 2004).

An interesting outcome of our simulations was to show that some resource distributions resulted in highly fragmented patch distributions for home ranges (Mitchell and Powell 2008); although perhaps intuitive, what was interesting was that such home ranges did not differ in quality or efficiency from more contiguous home ranges. This raises a potentially problematic

question for the interpretation of empirical estimates of home ranges that are commonly used to infer habitat relationships (see Fieberg and Börger 2012). Because such estimates are generally contiguous, the resource-bearing patches selected by an animal from a fragmented distribution of patches are difficult to discern; unselected patches included in the home-range estimate would thus bias estimates of habitat relationships. To address the potential for this bias, we simulated home ranges where selected patches were spatially disjunct, including interstitial, unselected cells most likely to be traveled by an animal moving among selected patches (Mitchell and Powell 2008). We compared characteristics of simulated home ranges with and without interstitial patches to evaluate how insights derived from field estimates might differ from actual characteristics of home ranges, depending on patchiness of landscapes. We found that contiguous home-range estimates could lead to misleading insights on the quality, size, resource content, and efficiency of home ranges, proportional to the spatial discontinuity of resource-bearing patches. We concluded that the potential bias of including unselected, largely irrelevant patches in the field estimates of home ranges of animals can be high, particularly for home-range estimators that assume uniform use of space within home-range boundaries (Mitchell and Powell 2008). Thus, choosing home-range estimators (e.g., minimum convex polygons) or smoothing parameters for estimators (e.g., kernel estimators—Kie et al. 2010) to purposefully represent home ranges of animals as contiguous could be misleading for animals occupying patchy landscapes; as conceptually satisfying as contiguous depictions of home ranges might be, the inclusion of inconsequential or irrelevant patches into a home-range estimate can strongly bias post hoc assessments of habitat selection. Where empirically based statistical home-range estimates are needed for animals inhabiting fragmented landscapes, the synoptic model presented by Horne et al. (2008) accounts for the spatial distribution of resources and can produce appropriately fragmented home-range estimates.

Home ranges of black bears.—We used our home-range models to evaluate the home ranges of female black bears living in Pisgah Bear Sanctuary (35°17'N, 82°47'W) in the southern Appalachian Mountains (Mitchell and Powell 2007). To model resource values, V , for our study area, we used the food component of a habitat suitability index (HSI) developed for black bears in the southern Appalachian Mountains (Mitchell et al. 2002; Powell et al. 1997; Zimmerman 1992; Table 1; Fig. 3A). The HSI ranged from 0 (poor quality) to 1 (high quality) and strongly predicted habitat use by black bears in our study area (Mitchell et al. 2002). Based on this model of V (modeling V' using equation 1) we tested general predictions of our models using 104 observed home ranges of adult female bears in Pisgah Bear Sanctuary, North Carolina (1981–2001) that were estimated from telemetry data using a fixed kernel home-range estimator (Mitchell and Powell 2007). We also used our models to simulate home ranges for each observed home range under a variety of strategies and constraints (resource-maximizing, area-minimizing, and both strategies

TABLE 1.—Habitat components used to calculate the food component of a habitat suitability index (HSI) for black bears living in the southern Appalachians (summarized from Mitchell et al. [2002], Powell et al. [1997], and Zimmerman [1992]). The food component of the HSI ranged in value from 0 (poor quality) to 1 (high quality) and was used to model resource values, V , for modeling optimal home ranges of black bears in Pisgah National Forest, North Carolina, by Mitchell and Powell (2007). GIS = geographic information system.

Habitat component	Relationship to fitness of bears	Method of sampling
No. fallen logs/ha	Abundance of colonial insects	Field sampling
Anthropogenic food source	Availability of food from human point sources	Aerial and ground survey
Distance to anthropogenic food source	Costs of traveling to human food source	GIS
Distance between anthropogenic food source and escape cover	Risk of acquiring food from human sources	Topographic maps
Distance to perennial water	Abundance of grasses and forbs in spring	GIS
% cover of <i>Smilax</i> spp.	Availability of fruit in fall	Field sampling
% cover in berry species	Availability of fruit in summer	Field sampling
Presence of red oak species	Availability of squaw root in summer	Forest inventory data and GIS
Forest cover type	Availability of hard mast in fall	Forest inventory data and GIS
Age of stand	Productivity of hard mast	Forest inventory data and GIS
No. grape vines/ha	Availability of fruit in fall	Field sampling

with resource depression) and compared simulated to observed home ranges. Our models were able to predict, accurately and a priori, the observed home ranges of bears (Mitchell and Powell 2007; Fig. 4).

We defined resource thresholds used to model area-minimizing home ranges for bears we observed relatively, on a scale from minimum to maximum accumulated V' in observed home ranges; in the absence of data on resource depression, we also arbitrarily defined a range of 4 equal quartiles between 0 and -0.20 . Our models allowed us to show that the home ranges of female bears were efficient with respect to the spatial distribution of resources and on the average were explained best 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, because the lowest levels we modeled had limited support we concluded that levels of resource depression among the bears we sampled were too low to quantify accurately. We found that home ranges of lactating females had higher resource thresholds and were more susceptible to resource depression than those of nonlactating females. We ultimately concluded 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 (Mitchell and Powell 2007). Indeed, simulating home ranges on a landscape using our models can produce predicted distributions of home ranges that vary from ideal free to ideal despotic (Fretwell 1972; Fretwell and Lucas 1970) depending on the degree of resource depression used (i.e., absent to complete, respectively).

Our finding that female bears living in Pisgah Bear Sanctuary pursued, on the average, an area-minimizing strategy with low levels of resource depression has strong ecological implications because resource depression sets a maximum to the number of home ranges a landscape can support. In this case, our models can be used to estimate carrying capacity. We evaluated this possibility by sequentially adding simulated, area-minimizing home ranges to a fitness landscape for the sanctuary comprising the food component of Zimmerman's

(1992) HSI (Mitchell et al. 2002). The resource thresholds and resource depression defining each home range were the same as those found to be most predictive for female black bears in the sanctuary (Mitchell and Powell 2007). Results of these simulations showed an increase in home-range area as the simulated population grew (Fig. 5), to a point where no new home ranges could be added that satisfied the resource threshold. Our results suggested that carrying capacity for adult female black bears in Pisgah Bear Sanctuary was approximately 52 (Fig. 5), which is a credible number for a 235-km² area in the southern Appalachian Mountains (Mitchell and Powell 2007). To derive a comprehensive estimate of carrying capacity for the sanctuary that included all age and sex classes using our models would require the use of home-range parameters and possibly alternative fitness surfaces appropriate to each class.

A caveat about currency.—Much of the success of our models in predicting the home ranges of female black bears was due to the selection of a good, biologically credible currency on which the models accurately parse the home-range strategies of the bears (Powell and Mitchell 2012). As our currency, we used the food component from an HSI developed by Zimmerman (1992; Mitchell and Powell 2007; Mitchell et al. 2002; Powell et al. 1997) that explicitly depicted fitness relationships between black bears and components of their habitat and minimized assumptions about how habitat features convenient to human measurement and mapping actually depict important habitat relationships (Mitchell and Hebblewhite 2012). A map of this index for our study area showed a continuous distribution of the potential contribution of each point in space to the survival and reproduction of black bears (Fig. 3A). A test of the HSI using independent data showed it was strongly predictive of habitat selection by female black bears living in Pisgah Bear Sanctuary (Mitchell et al. 2002; see Fieberg and Börger 2012).

Alternatively, we could have used a more commonly considered, if biologically less meaningful, depiction of resources for our currency such as forest cover type. To illustrate how model predictions under this currency would differ, we compared the best-fitting home range of bear 96 in

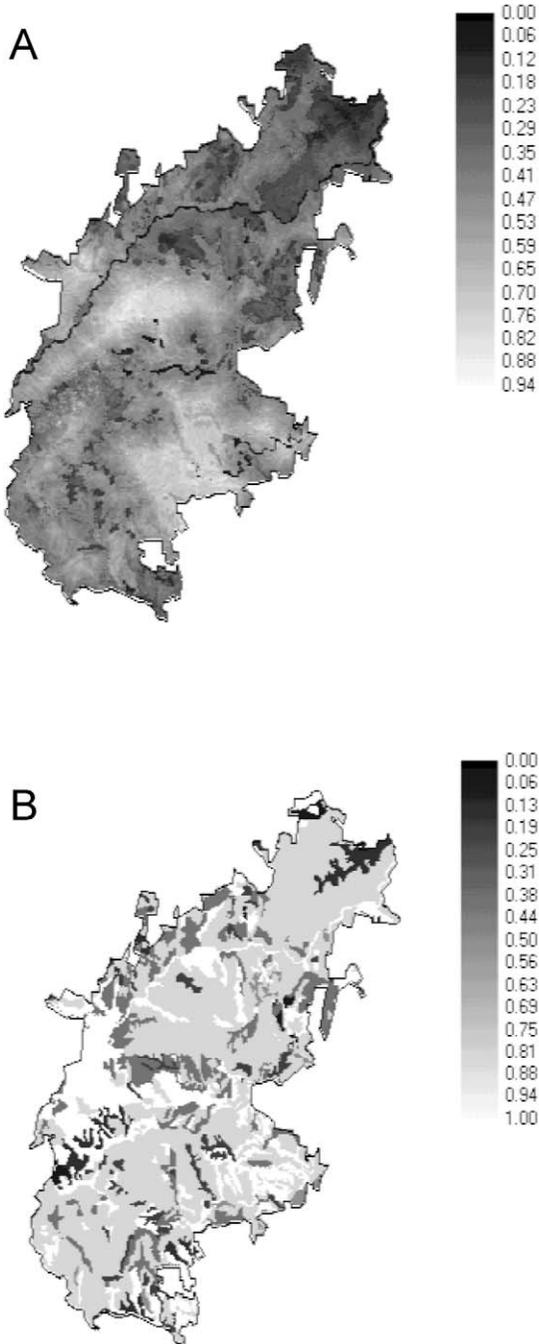


FIG. 3.—Two potential models of resource value, V , that can be used for predicting the home ranges of female black bears in Pisgah Bear Sanctuary, North Carolina, 1981–2000. A) The food component of a habitat suitability index (HSI) for black bears in the southern Appalachians (Mitchell et al. 2002; Zimmerman 1992). B) The forest cover component of the HSI. Values for both currencies range from 0 (poor quality) to 1 (high quality [from Mitchell and Powell 2002]).

1984 (Fig. 4) estimated using the resource-maximizing model based on the food component of Zimmerman’s (1992) HSI to one estimated using the same model based on just the forest cover component of Zimmerman’s HSI (ranking forest cover types from 0 to 1 based on Zimmerman’s [1992] review of

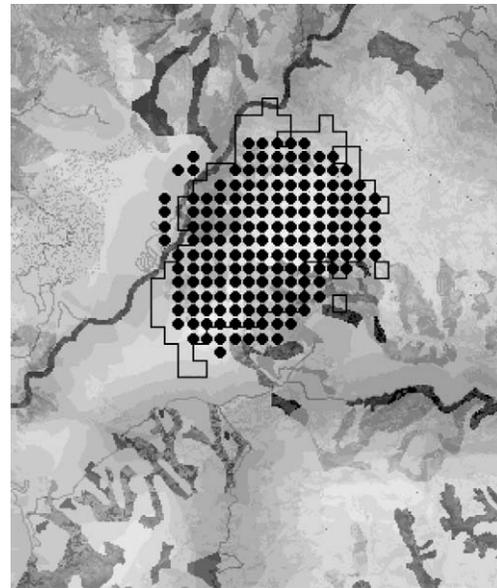


FIG. 4.—Simulated optimal home range (dots) superimposed over observed home range (line; estimated from telemetry data using kernel estimator) for female bear 96 in 1984, Pisgah Bear Sanctuary, North Carolina. The optimal home range was generated using resource-maximizing model M_R based on the underlying distribution of resources depicted by the V_F component of a habitat suitability index (HSI) for black bears. Home range is presented on the map of V_F for 1984; dark hues represent poor food value, and light hues represent high food value (from Mitchell and Powell 2007).

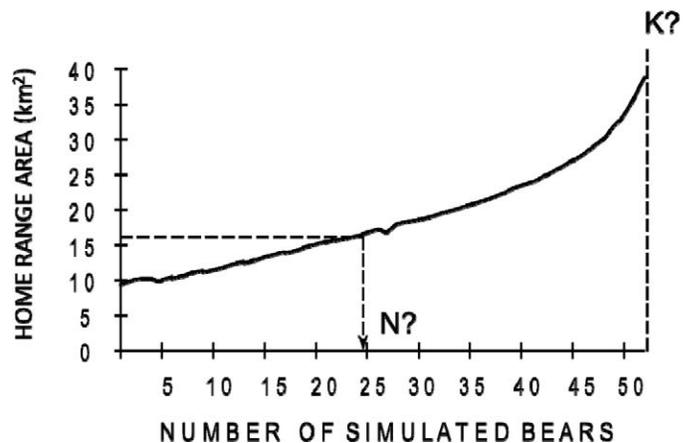


FIG. 5.—Change in area of simulated, area-minimizing home ranges for female black bears in Pisgah Bear Sanctuary, North Carolina, as the population increases. Simulations were of sequentially established optimal home ranges constructed under an area-minimizing strategy with moderate resource thresholds and low resource depression (Mitchell and Powell 2007), and based on the food component of a habitat suitability index (HSI) for bears in the southern Appalachians. As more home ranges are added to the sanctuary, area of home ranges increased in size, suggesting that area of home ranges may be useful for understanding population size (N). Eventually, no new area-minimizing home ranges could be added to the sanctuary, resulting in a maximum of 52, the estimated carrying capacity (K) for Pisgah Bear Sanctuary.

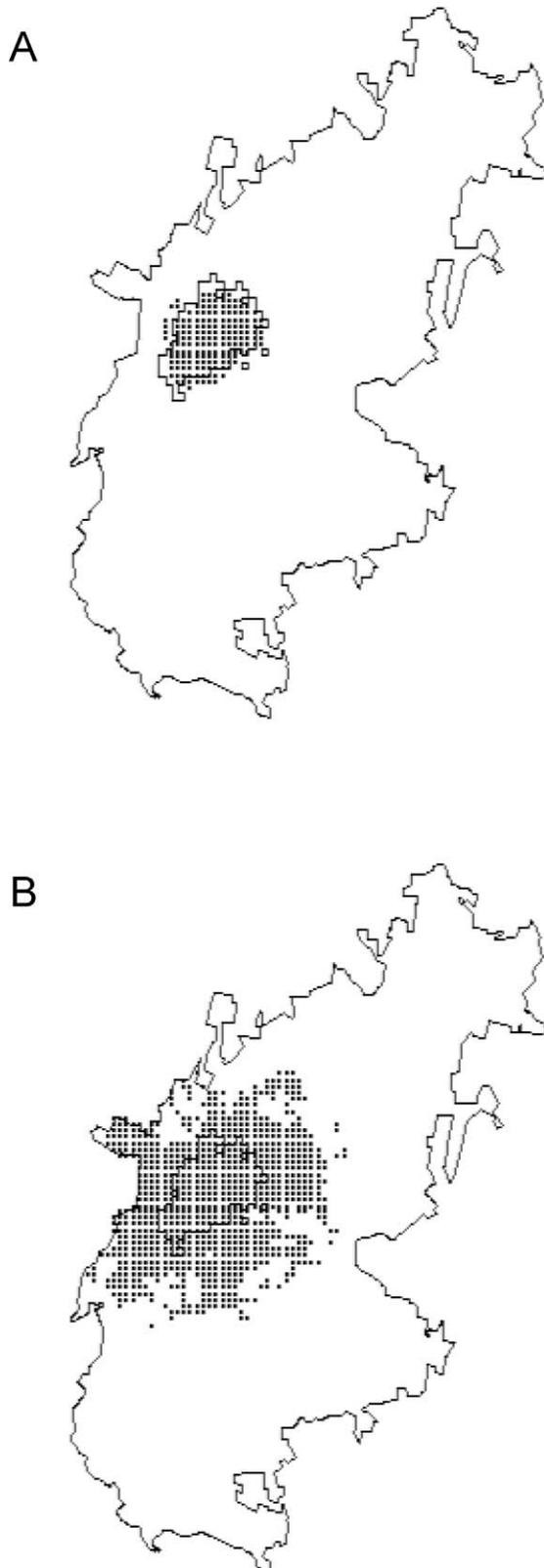


FIG. 6.—Simulated optimal home range (dots) superimposed over observed home range (line; estimated from telemetry data using kernel estimator) for female bear 96 generated using the resource-maximizing optimization model with the 2 alternative currencies depicted in Fig. 4 in Pisgah Bear Sanctuary (outline), North Carolina,

published findings [Fig. 3B]). The difference between what was predicted using the full food component of the HSI instead of just the forest cover component is dramatic. The former estimate accurately depicts the behavior of bear 96 (Fig. 6A), whereas the latter reveals very few similarities or useful insights (Fig. 6B).

The merits of a good currency for optimization analyses closely track those of rigorous definitions of habitat (Hall et al. 1997; Mitchell and Hebblewhite 2012; Morrison 2001; Sinclair et al. 2005); ignoring such considerations could result in a “garbage in, garbage out” modeling exercise. Zimmerman’s (1992) HSI was particularly useful for modeling optimal home ranges for black bears in our study area because it was developed a priori from biological 1st principles (i.e., what do bears eat, when and where are such resources available, and what are their relative values to bears?) and empirical precedent, was explicit with respect about the value of resources to bears (e.g., within the food component of his HSI, the value of berry-producing plants to bears, F_{su1} , was modeled: $F_{su1} = (0.027 + 0.005n)x$, for $(0.027 + 0.005n)x < 1.0$, or $F_{su1} = 1.0$, for $(0.027 + 0.005n)x \geq 1.0$, where n = number of berry genera present and x = percent cover in berry plants), and was then tested rigorously on independent data. Sensibly, any model designed to predict habitat selection (e.g., HSIs, resource selection functions, etc.) should be an excellent candidate for modeling V , provided the biological reasoning behind its components is sound; a model need not be as complex or detailed as Zimmerman’s (1992) HSI (which, although highly predictive, wins no awards for parsimony), provided its predictive capacity can be shown rigorously. We suggest the best approach to developing a currency might look like this:

1. Start with a basic question or hypothesis about how resources structure home ranges;
2. Based on ecological and behavioral theory, a review of previous research, expert opinion, and so on, make a list of resources, costs, and constraints that, a priori, should be important to the species of interest;
3. Determine if these resources can be adequately measured, or alternatively, if surrogate measurements are available and appropriate;
4. Build a model (or better still, alternative competing models) for V that captures the combined resources in (3);
5. Predict a priori how V should influence space-use patterns, and then test these predictions with empirical data; and
6. Revise the model and retest with independent data as present and new questions dictate.

Finally, although many uninformative or misleading currencies exist, as we point out elsewhere in this Special Feature

←

1984. A) The home range simulated using the food component of a habitat suitability index (HSI) for bears in the southern Appalachians. B) The simulated home range using just the forest cover component of the HSI (Zimmerman 1992 [from Mitchell and Powell 2002]).

(Powell and Mitchell 2012), no single, “right” currency exists. Choice of currency depends on the questions being asked (see Fieberg and Börger 2012): even a biologically meaningful currency can yield uninformative answers to poorly matched questions about optimal behaviors.

Although we evaluated our models using black bears and a currency suitable for them, we emphasize that our models are general and are not limited to bears or ecologically similar species. On the contrary, they could be used to generate testable predictions for any species exhibiting home-range behavior. Along those lines, we suggest that the greatest potential for learning offered by economic models and their accompanying currencies is when they fail to predict well, because failure requires consideration of new variables and alternative models (Thomas et al. 1989). This approach is the logical essence of maximizing inferential strength through falsification of hypotheses. As a means of proposing and testing falsifiable, alternative hypotheses, economic models offer the opportunity to ask and to answer critical questions about the home ranges of animals, the resources that structure them, and the mechanisms behind this relationship, with a logical rigor unachievable through more traditional, post hoc analyses.

ACKNOWLEDGMENTS

We thank M. Reynolds, L. Brongo, J. Sevin, J. Favreau, G. Warburton, P. Horner, M. Fritz, E. Seaman, J. Noel, A. Kovach, V. Sorensen, T. Langer, D. Brown, and F. Antonelli; more than 40 undergraduate interns, technicians, and volunteers; and approximately 400 Earthwatch volunteers for their help with data collection. Our research received financial and logistical support from Auburn University’s Peaks of Excellence Program, Auburn University’s Center for Forest Sustainability, B. Bacon and K. Bacon, J. Busse, Citibank Corp., the Columbus Zoo Conservation Fund, the Geraldine R. Dodge Foundation, Earthwatch—The Center for Field Research, Environmental Protection Agency Star Fellowship Program, Federal Aid in Wildlife Restoration Project W-57 administered through the North Carolina Wildlife Resources Commission, Grand Valley State University, McNairs Scholars Program, International Association for Bear Research and Management, G. and D. King, McIntire Stennis funds, the National Geographic Society, the National Park Service, the National Rifle Association, the North Carolina State University, Port Clyde and Stinson Canning Companies, 3M Co., the United States Department of Agriculture Forest Service, Wildlands Research Institute, Wil-Burt Corp., and Wildlink Inc. We thank J. Horne, J. Fieberg, P. Moorcroft, and an anonymous reviewer for constructive reviews of earlier versions of this paper. Use of commercial names does not imply endorsement by the United States Government.

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Special Feature Editor was Janet L. Rachlow.