

## Carnivore habitat ecology: integrating theory and application

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Few terms in wildlife ecology and conservation biology enjoy jargon status more than the word “habitat.” The ubiquity of the word in popular, scientific, and administrative literature suggests a universal definition, yet the diversity of contexts in which it is used clearly indicates little consensus. This conceptual imprecision has strong, but generally unacknowledged, implications for understanding and managing populations of wild animals, particularly for those where human-caused changes to ecosystems threaten viability. Few vertebrate groups better epitomize such populations than carnivores. Yet efforts to quantify what makes places habitable for carnivores are strongly compromised when poorly considered or biologically meaningless definitions of habitat are used.

We agree with Morrison *et al.* (1992), Hall *et al.* (1997), and Sinclair *et al.* (2005) that a definition of habitat must explicitly consider the resources that contribute to an animal’s fitness. Describing habitat simply as the places or prevailing conditions where an animal is found is tautological, precluding robust knowledge and effective conservation. Nonetheless, descriptive definitions are overwhelmingly prevalent in the habitat literature. Why? We hypothesize three possible explanations. First, so little is known about an animal’s habitat that only the initial steps of the scientific method are available to investigators: observe and hypothesize, the essence of description. Such cases are surely much rarer than the prevalence of descriptive habitat definitions suggests. The second explanation is that scant critical thought has been given to defining habitat because of the challenges of employing the entire scientific method (i.e. testing of hypotheses). In the absence of careful thought, over time such traditions become paradigms by weight of representation, irrespective of their limited scientific or biological merits. A final explanation is that data sufficient for developing rigorous, resource-based definitions of habitat are unavailable. This real-world constraint does sometimes

limit the application of even the best of habitat definitions, requiring the careful use of surrogates (e.g. using proportion of hardwoods in the over story as a surrogate for the specific hardwoods that produce hard mast); indeed, every habitat definition we know relies on surrogates. Nonetheless, the uncritical use of surrogates, particularly given the rapid growth of remotely sensed land-cover data, computing power, and the use of sophisticated analytical techniques, has produced a large number of studies whose definition of habitat would seem to be “throw a bunch of conveniently available environmental variables into the statistical hopper and see what pops out.”

The prevalence of descriptive habitat definitions not linked to fitness suggests both biological and scientific shortcomings in how we understand and study habitat. Describing *where* animals live is not informative science; for robust understanding that can lead to effective management and conservation, we need to know *why* animals live where they do (Gavin 1991). For many species, including a large and growing number of threatened carnivores, the consequences of poor understanding or misguided conservation are real and strongly negative. Knowing why an animal lives where it does is not just an academic exercise; we must bring the best science possible to bear on problems that may ultimately prove insoluble if we do not.

This chapter outlines our understanding of how to bring the best possible science to bear on discerning why carnivores live where they do. We discuss the concept of habitat, particularly as it applies to carnivores, whose resources contributing to fitness are often mobile. And we will discuss how habitat for carnivores can be quantified and its use interpreted. Finally, we discuss a study design that uses sound logic and robust analysis to maximize strength of inference. We then review some of the recent advances linking carnivore habitat to populations. We suggest a way of thinking about, and studying, carnivore habitat that will improve the efficiency of learning and the efficacy of conservation.

## 10.1 What is habitat?

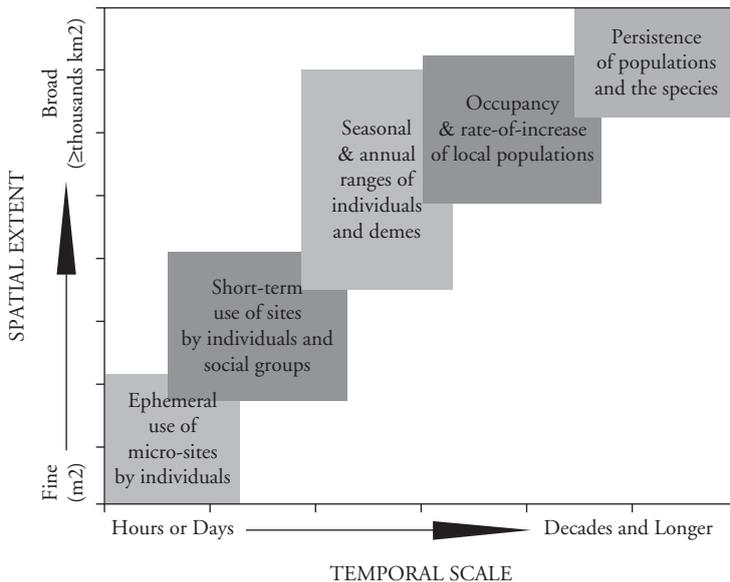
The habitat definitions of Hall *et al.* (1997), Morrison (2001), and Sinclair *et al.* (2005) are based on the classic notion of the ecological niche, whereby animals select the resources and conditions that increase fitness (hence resource selection is distinct from habitat selection). Individuals, populations, and species have habitat and, consequently, habitat cannot occur without the animal. As with habitat, many definitions of the niche exist but Grinnell's original concept includes all subsequent definitions. The niche is a property of a species, includes abiotic and biotic components, is related to fitness, and includes long temporal and large spatial

scales. Niche-based modeling has spurred recent investigation into explicit linkages between the niche concept and use of habitat by animals (Pulliam 2000; Soberon 2007; Hirzel and Le Lay 2008). Another important contribution of niche theory to habitat ecology is the distinction between fundamental and realized niches (Hutchinson 1957). An important consequence is that, unless we use experiments (MacArthur 1967), as empiricists we almost always describe the realized niche, or habitat, of a species. Under niche theory, populations have habitat but in Figure 10.1 we can see clearly that habitat is hierarchical from populations to individual foraging decisions by an animal. The concept of the niche is a good starting point for understanding habitat in a way that can be applied across scales.

### 10.1.1 Potential, sink, quality, source, suitable, or critical?

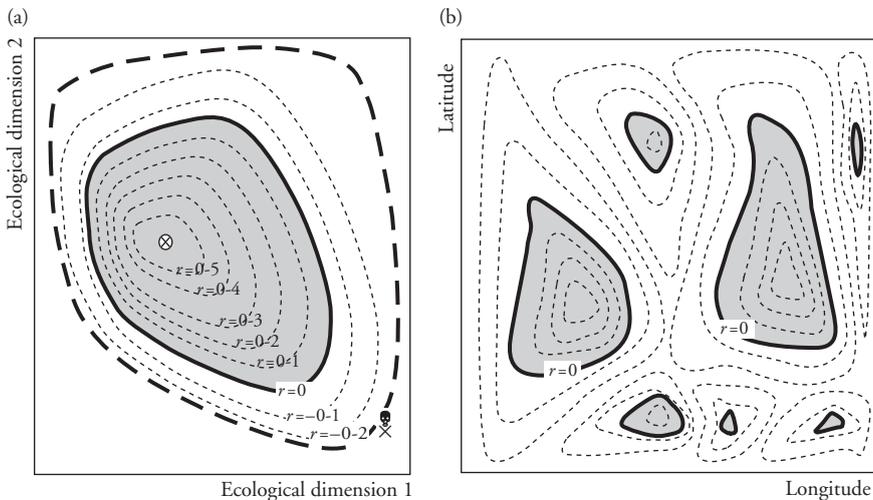
#### What kind of habitat is it?

Following from the niche-based definition of habitat, habitat cannot just be a geographical description of an area or piece of land. Certain conditions must be



**Fig. 10.1** Habitat occurs at multiple temporal and spatial scales; at the 1st order, habitat selection scale of the persistence of the species, equivalent to the species' niche; the 2nd-order, growth of local populations and seasonal and annual ranges of individuals; 3rd order (short-term use of sites by individuals and social groups) and finally; at the 4th order scale, where individuals make microscale foraging or selection decisions. Source: Mayor *et al.* (2009)

present for a species to survive and to reproduce. Hirzel and Le Lay (2008) illustrated the relationship between habitat and its distribution in geographic space (Figure 10.2). This approach to habitat helps us define several confusing terms, such as source habitat, sink habitat, potential habitat, habitat quality, suitable habitat, and critical habitat (Garshelis 2000; Pulliam 2000; Hirzel *et al.* 2002, Soberon 2007). First, presence of animals in an environment does not define habitat because presence alone does not consider survival and reproduction. Thus, environments where animals can occur, but where potential for survival is low and reproduction absent, are sink habitats, and environments with sufficient resources to support high survival and reproduction are source habitats (Figure 10.2). Note that a sink habitat can be critical to a species if residents of a sink habitat emigrate to a source habitat when a source population is low for reasons other than habitat. Environments where members of a species could occur, but presently do not, are



**Fig. 10.2** Conceptual diagram of the relationship between habitat as defined by Sinclair *et al.* (2005) and the geographic distribution of that habitat in space adapted from Hirzel and LeLay (2008). (a) represents the relationship between intrinsic population growth rate ( $r$ ) and two ecological dimensions (such as lichen abundance, or snow pack). Shaded areas indicate source habitat where population growth ( $r$ ) is  $>0$  (i.e. the population is growing), and the area inside the solid dashed line is considered sink habitat where species can persist, but only through immigration from an adjacent source. The skull and crossbones represent areas where the species cannot persist. (b) Represents this environmental space translated to geographic space given spatial measurements of the same resources for caribou in space. Shaded areas again represent source habitat where the conditions present are favorable for species persistence. Note that  $r$  here assumes density independence.

potential habitats. Similar to the fundamental niche, measuring a potential habitat well in field studies is almost impossible.

A habitat is of high quality (i.e. suitability) if individuals can experience high survival and reproduction and, thus, the population has the potential for a high growth rate. Note, however, that neither high nor low rates of survival and reproduction are necessarily reliable indicators of habitat quality where vital rates are density dependent; survival and reproduction could be high in poor habitat that is sparsely populated and low in excellent habitat occupied by a population near carrying capacity. Also, under the niche-based definition, the term “unsuitable habitat” has no logical meaning: all habitat, by definition, is of various degrees of suitability. “Non-habitat” is outside the solid dashed lines in Figure 10.2a, where a species cannot persist. Under this definition, only habitat (where populations can exist, with immigration for sink habitats) and non-habitat (where populations cannot persist) can exist.

Finally, no stand-alone, *biological* definition of critical habitat exists because “critical” implies importance for a specific goal or objective function. For endangered species, the goal is most often making the species non-endangered by reaching some recovery goal, but the target is a socially or politically defined goal. Heuristically, however, we can imagine some smaller subset of the shaded area in Figure 10.2 as being high-quality habitat that is sufficient for maintaining a specific population size, given a geographic area and species’ life-history.

### 10.1.2 A fitness-based definition of habitat

The best understanding of habitat will explicitly relate resources to the survival and reproduction of an animal. This is a conceptually satisfying understanding of habitat because it proceeds from first principles, providing the mechanism that explains why an animal does what it does. If we can understand the potential contribution of each point in space to an animal’s fitness based on the resources found there, we can evaluate the decisions an animal makes in its day-to-day activities (i.e. the behaviors that we perceive as habitat use). Mitchell *et al.* (2002) presented such an approach, originally developed by Zimmerman (1992) for black bears (*Ursus americanus*) in the southern Appalachian mountains, presenting habitat as a “fitness landscape” (Box 10.1). The fitness landscape proved highly robust for predicting habitat selection of black bears (Mitchell *et al.* 2002), effects of forest management on habitat use by bears (Mitchell and Powell 2003a), and optimal selection of home ranges based on the spatial distribution of resources (Mitchell and Powell 2007). Mosser *et al.* (2009) linked a fitness surface to habitat variables for long-term studies of lions (*Panthera leo*) in the Serengeti and showed a disconnect between habitats with high lion density and habitats selected because they contributed the most to adult female survival and

**BOX 10.1** A habitat suitability model for black bears in the Southern Appalachians

Black bears obtain most of their nutrition from seasonally available vegetation, augmented by colonial insects, carrion, and rare acts of predation. In the southern Appalachian Mountains of North Carolina during spring, black bears eat predominantly grasses, forbs, and a saprophytic parasite of red oaks (*Quercus* sp.), squaw root (*Conophilus americanus*); berry-producing plants during summer; and hard-mast producing trees during fall. Bears in the region eat anthropogenic foods but suffer high rates of mortality near roads.

Zimmerman (1992; Mitchell *et al.* 2002) approached modeling habitat for black bears in the region based on first principles, attempting to quantify those resources and environmental attributes that contributed strongly to survival and reproduction. Zimmerman's approach was based on the habitat suitability index paradigm (Brooks 1997) but departed from it in some important respects. Drawing on published literature, Zimmerman modeled a priori the values of 15 food, denning, and escape resources important to bears (Table 10.1) and combined them into a

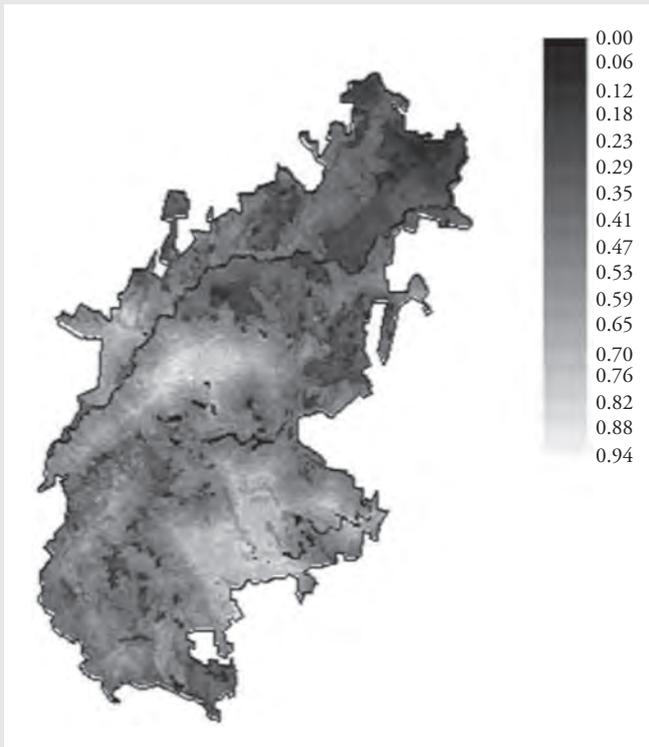
**Table 10.1** *Habitat components used to calculate a Habitat Suitability Index for black bears living in the Southern Appalachians.*

Habitat Component	Relationship to Fitness of Bears	Method of Sampling
Number of fallen logs/ha	Abundance of colonial insects	Field sampling
Anthropogenic food source	Availability of food from human point sources	Aerial/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
Percent cover of <i>Smilax</i> spp.	Availability of fruit in fall	Field sampling
Percent 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/ GIS
Forest cover type	Availability of hard mast in fall	Forest inventory data/ GIS
Age of stand	Productivity of hard mast	Forest inventory data/ GIS

(continued)

**Table 10.1** *Continued*

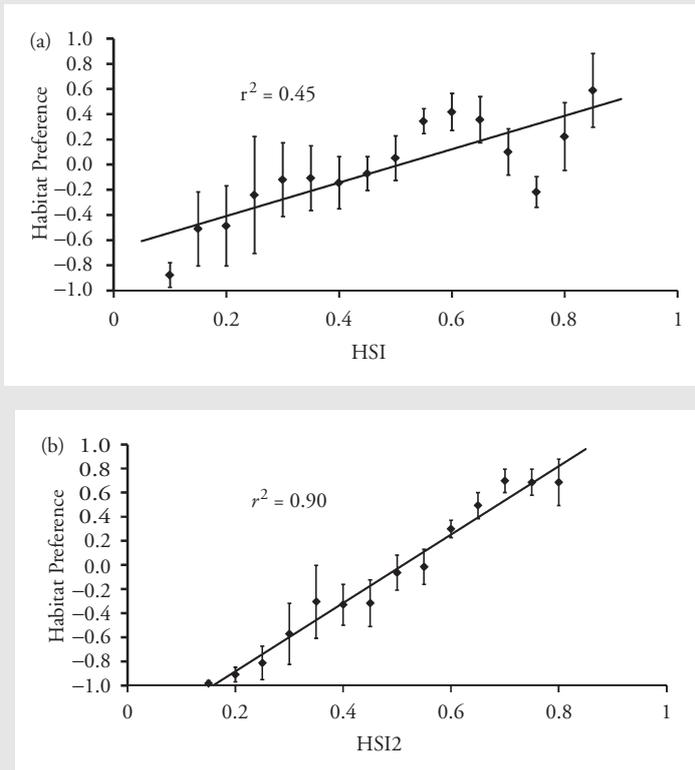
Habitat Component	Relationship to Fitness of Bears	Method of Sampling
Number of grape vines/ha	Availability of fruit in fall	Field sampling
Distance to nearest road	Risk of encountering humans	GIS
Area of conterminous forest not bisected by roads	Risk of encountering humans	GIS
Percent closure of understory	Escape cover	Field sampling
Slope of terrain	Escape cover, availability of caves for denning	GIS
Area in <i>Rhododendron</i> spp. or <i>Kalmia</i> sp.	Availability of thickets for denning	Aerial photo
Number of trees $\geq 90$ cm DBH/ha	Availability of large trees for denning	Field sampling



**Fig. 10.3** Zimmerman's habitat suitability index (HSI) for black bears in the Southern Appalachians depicted as a fitness landscape for the Pisgah Bear Sanctuary in western North Carolina. HSI values range from 0, poor quality, to 1, high quality.

**BOX 10.1** *Continued*

model that indexed habitat suitability on a scale from 0 (poor) to 1 (good; Figure 10.3). In a test of the model using independent data, the index predicted strongly habitat selection by 81 telemetered bears, especially when escape resources were removed (Figure 10.4), and helped to elucidate complex responses of bears to habitat changes caused by forest management (Mitchell and Powell 2005). Used as a currency for individual-based, optimal home-range models, the index facilitated accurate prediction of the home ranges of 100 adult female bears (Figure 10.5; Mitchell and Powell 2004, 2007). Winning no awards for parsimony, the index nonetheless has yet to be improved; sensitivity analyses showed that no variable or suite of variables dominate its predictions and no attempts to reduce the model have resulted in improved predictiveness. The explicit linkages between resources and their value to bears likely contributed strongly to the robustness of model predictions across a variety of applications, making the map of model predictions a “fitness



**Fig. 10.4** Relationships between habitat use and Zimmerman’s HSI (a) and the HSI without escape resources (b) for black bears in the Pisgah Bear Sanctuary, Pisgah National Forest, North Carolina.

**BOX 10.1** *Continued*

landscape,” i.e. the potential contribution of each point in space to the survival and reproduction of black bears (Powell 2004). The explanatory value of Zimmerman’s model, beyond describing habitat selection by bears, highlights the merits of testing hypotheses about fitness-based definitions of habitat.



**Fig. 10.5** Estimated optimal home range (dots) superimposed over true home range (outline) of female bear 96 in 1984, Pisgah Bear Sanctuary, North Carolina. Shades of gray depict Zimmerman’s HSI values (dark is low quality, light is high quality) that served as the currency for home range optimization.

cub production. This result emphasizes the long-understood, but seldom addressed, flaw in equating density to quality (Van Horne 1983), i.e. where habitat quality is high, a population has the potential to have high density but this potential may not be realized for a number of reasons.

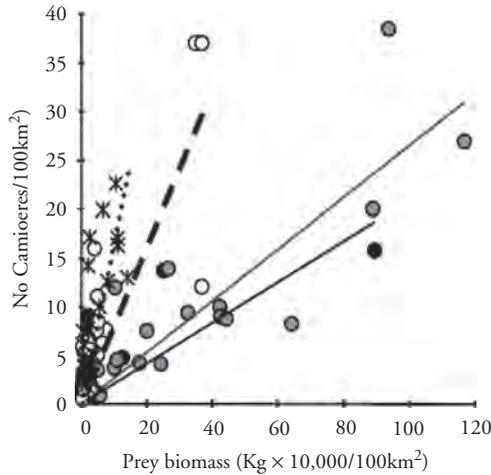
The notion of habitat as a fitness landscape, where the contribution to survival and reproduction of resources at each point in space is made explicit, has conceptual appeal, but in practice can prove a daunting challenge. More often than not, resources, such as specific food types, are difficult to observe or model over the large landscapes that carnivores use, necessitating the use of surrogates. Thus, even in

Zimmerman's (1992) model (Box 10.1), few resources were measured directly. For example, the model used percent cover of berry-producing species as a surrogate for productivity of berries. The use of these surrogates relied on assumptions about their relationship to what they represented, and few ecologists would have difficulty imagining circumstances under which those assumptions could be violated. Nonetheless, as with any model, the relative merits of assumptions can only be evaluated if the assumptions are stated. Contrast how assumptions can be evaluated and tested in a model where fitness-based relationships are explicitly hypothesized with those implicit yet undefined in a model that defines habitat simply as, say, cover types. In the latter case, if a cover type is a perfectly predictive model for the behavior of interest, a researcher or a manager cannot know why it was.

In effect, any mapped habitat model is either implicitly or explicitly a fitness landscape representing a hypothesized or tested relationship between resources available to an animal and how it uses them, whether or not this is recognized. This fact should be dealt with explicitly and from the outset for any habitat model. What fitness relationship is the model intended to represent? Are those relationships operant at the scale of investigation (e.g. it may make no sense to include resources important to reproduction if observations used to build or test the model do not include the breeding season)? Should others have been included and how does their exclusion affect model performance? Under what circumstances could the assumptions of how the model captures fitness relationships be violated? A model that cannot stand up to such scrutiny invites questions about the biology underlying its predictions and, thus, about its usefulness for understanding or managing animals.

## 10.2 What is carnivore habitat?

Previous research on the habitat ecology of carnivores has focused too much on the environmental variables that predict carnivore presence or density, and not on variables with direct links to carnivore fitness. In the process, studies have often neglected biological first principles defining what it is to be a carnivore. Many carnivores are obligate predators; for these species, habitat definitions must include explicit measures of biotic interactions with prey. Such measures must include abundances and distributions of prey, and environmental characteristics that facilitate capture of prey. Instead, hosts of studies relate occurrence, use, or selection by carnivores to vegetation communities, digital elevation models, remote-sensing variables, and other kinds of spatial variables easily obtained in a geographical information system (GIS) framework. For example, Mace *et al.* (1996) and Boyce and Waller (2003) examined habitat selection by grizzly bears (*U. arctos*) in western Montana as a function of vegetation communities identified



**Fig. 10.6** Carnivore density ( $\#/100\text{km}^2$ ) as a function of prey biomass for tigers (solid circle and line); lion (gray), leopard (open/dashed), and Canadian lynx (\*/ $\text{---}$ ). Source: Carbone and Gittleman (2002).

from Landsat-TM imagery combined with topographic and some human features. Such an approach makes sense for omnivorous carnivores that rely heavily on vegetative resources, and may even be useful at prediction. However, the merits of these approaches are less certain for carnivores that are strongly reliant on mobile and unevenly available prey. For example, vegetation communities and glacial features explained little about use of space by wolves (*Canis lupus*) in the Canadian arctic (McLoughlin *et al.* 2004); or by wolves in the Canadian Rockies (Hebblewhite *et al.* 2005). The assumptions that such variables are surrogates for availability of plant forage for omnivores or of prey for carnivores are often unwarranted and infrequently tested. That these habitat models, convenient to mapping, do not explain carnivore behavior argues strongly for considering prey resources explicitly. Few studies of habitat for carnivores include availability of prey species, fundamental to the persistence of carnivores. The main factor driving densities of obligate carnivores is food, i.e. the density or availability of prey. (Miquelle *et al.* 1999; Fuller and Sievert 2001; Carbone and Gittleman 2002; Fuller *et al.* 2003). The ratio of carnivore to prey biomass scales to the reciprocal of carnivore mass (Figure 10.6, Carbone and Gittleman 2002). We do not argue that non-prey resources are irrelevant. Moorcroft *et al.* (2006), for example, showed that coyotes (*Canis latrans*) avoided scent marks from conspecifics in Yellowstone National Park; even in this case, however, prey density explained much of the variation in coyote movements. Thus, if we wish to define habitat in a manner that helps us understand why obligate carnivores do what they

**BOX 10.2** Empty forest syndrome: comparing predictions from Amur tiger habitat models with and without measures of ungulate prey availability

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The forests of Asia are “empty” of large ungulate prey for tigers, leading biologists to coin the term “empty forests” syndrome (Karanth *et al.* 2004a; Datta *et al.* 2008). This syndrome occurs when environmental, structural aspects of tiger habitat are present (forests, water, stalking cover) but the most critical factor, large ungulates, are not. The main cause for “empty forests” is overhunting and poaching, which leaves forests depopulated of sufficient ungulate prey for tigers (Miquelle *et al.* 1999; Karanth *et al.* 2004b). In this case-study, we illustrate the effects of empty forest syndrome on predictions from resource selection function (RSF) models developed for the Amur tiger in the Russian Far East. Basic study design is a used–unused design, whereby large units where tigers were detected during intensive winter snowtrack surveys during winter 2005 were compared to unused units using logistic regression. This used–unused design corresponds to a true probability. Miquelle *et al.* (2006) provided details of data collection.

The full analysis was conducted as part of predicting habitat for Amur tigers expanding their range from Russia into the Changbaishan region of NE China (Li *et al.* 2009). Russian biologists tracked Amur tigers in the snow during winter surveys and also collected data on the tigers’ main ungulate prey species: sika deer (*Cervus nippon*), roe deer (*Capreolus capreolus*), red deer (*C. elaphus*), wild boar (*Sus scrofa*), musk deer (*Moschus spp.*), and the rare moose (*Alces alces*). Data of similar resolution were not available in the Chinese portion of the study area. Hence, we were interested in quantifying the effect of not including prey availability in RSF models. We developed a two-staged approach to examine the effects of ungulate prey on habitat modeling by (1) developing an “environmental” RSF model, including surrogate environmental variables, such as land cover, elevation, net primary productivity, and snow cover from MODIS satellites (Huete *et al.* 2002), that would be expected to correlate with prey distribution; and (2) developing a “biotic” RSF model that also included track density of the main ungulate prey species. Modeling details were similar to Box 10.1.

The overall biotic RSF model was significant (Likelihood-ratio ratio  $\chi^2 = 125.5$ ,  $p < 0.00005$ ) and demonstrated good model fit (Hosmer and Lemeshow goodness of fit test, test,  $\chi^2 = 8.45$ ,  $p = 0.35$ ), and had better explanatory power, discriminatory power, predictive capacity than the environmental model (Table 10.2). Moreover, in a model selection sense, the biotic model was over 10,000 times more likely to be a better model compared to the environmental model (ratio of Akaike weights of the two models). Clearly, knowledge of ungulate distribution and relative abundance improved the ability of the model to predict tiger habitat. The biotic model had superior discriminatory ability at predicting tiger habitat as measured by an average ROC, pseudo- $R^2$ , and the  $k$ -folds cross-validation procedure

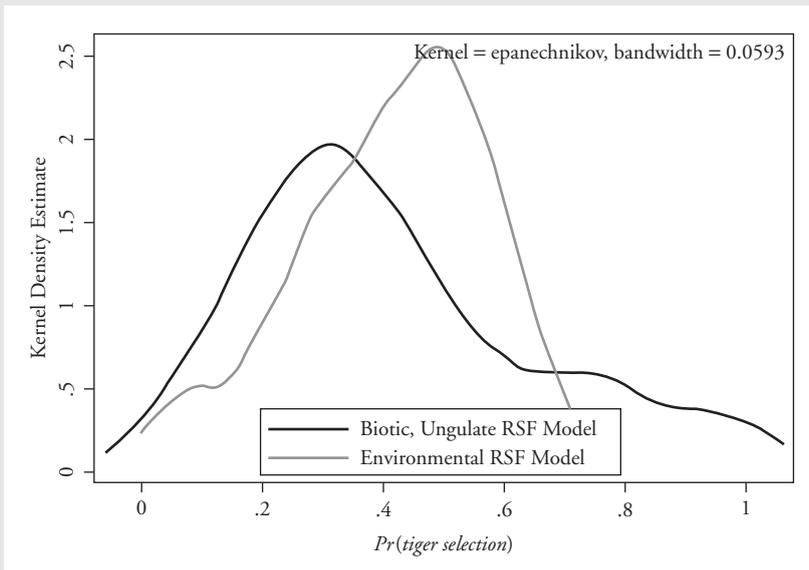
**BOX 10.2** *Continued*

**Table 10.2** Amur tiger resource selection function model diagnostics and covariate structure for the best environmental covariate RSF model and the best ungulate RSF model in the Russian Far East during winter 2004/2005. The top habitat and ungulate models are compared using AIC, ROC, pseudo- $R^2$ , and k-folds spearman rank correlations.

	AIC	ROC	Pseudo- $R^2$	k-folds
Environmental Covariate RSF Model	594.7	0.71	0.12	0.712
Ungulate RSF Model	531.8	0.89	0.25	0.881

(Table 10.2). ROC scores between 0.8 - 0.98 are indicative of excellent discriminatory ability, echoed with the very high  $k$ -folds spearman rank correlation of 0.881. The biotic model provided a higher overall classification success for survey units of 72%. Briefly, tiger's selected areas with high densities of sika deer, red deer, and wild boar in the ungulate model. Li *et al.* (2009) provided full details.

We compared the predicted distribution of tiger habitat probabilities between the two models (Figure 10.7). This comparison shows that without taking ungulate densities into account, the environmental model overpredicted the amount of



**Fig. 10.7** Relationships between the probability of tiger selection and ungulate track counts for red deer, sika deer, and wild boar from resource selection function modeling for tigers in the Russian Far East, winter 2005. Resource selection was assessed at the sample unit scale ( $135 \text{ km}^2$ ), and the best linear predictions from the logistic regression model from Equation 10.1 are shown against observed sample-unit scale predictions ( $Pr(\text{tiger selection})$ ).

**BOX 10.2** *Continued*

“high-quality” habitat available for tigers compared to the biotic model. The consequences of this overprediction was a poor Spearman rank correlation between the frequency of tigers and high-ranked categories of tiger habitat (environmental model Spearman rank correlation,  $r_s = 0.71$ , biotic model  $r_s = 0.88$ ). Therefore, even on the Russian side of the border, environmental covariates were not adequate spatial surrogates for ungulate data, and did not adequately capture the determinants of ungulate distribution and abundance, resulting in an optimistic prediction of the amount of high quality tiger habitat available. Results of our extrapolation of the environmental model to areas without similar prey density data should overestimate the availability of “high” quality tiger habitat in a similar fashion.

Unless we explicitly model the key resources for carnivore—namely, their prey—we risk creating habitat models for carnivores that are overly optimistic and leave out the key fitness-drivers of population dynamics. In the case of tigers, the recent criticisms of Project Tiger in India especially emphasize the critical conservation importance of these mistakes. Many of the tiger reserves created especially for tigers are devoid of the large prey that tigers need, driving tiger densities down to the point where many tiger reserves are devoid of tigers, too.

do, including prey availability should be the critical first step in addressing carnivore habitat ecology.

To be fair, quantifying the availability or abundance of prey across large spatial scales for most carnivore species is difficult. This is the main reason why surrogates, such as vegetation type or land-cover classifications from remote sensing, are often used, despite few tests of these surrogates. Numerous recent studies have attempted to integrate availability of prey resources into habitat-selection models for carnivores, however, and offer great promise for connecting habitat selection to population processes. Hierarchical analyses of habitat selection by Amur tigers (*Panthera altaica*) for the five main prey species available in the Russian Far East showed that it was the distribution of their main prey, not vegetation communities *per se*, that limited tiger “habitat” (Miquelle *et al.* 1996, 1999). Explicitly linking habitat selection by tigers to their ungulate prey (and hence to tiger fitness) made the case for controlling one of the main ecological reasons driving carnivore population decreases—poaching of ungulate prey (Miquelle *et al.* 1999; Chapron *et al.* 2008). Failure to include a biotic definition of habitat is the cause of the “empty forest syndrome” discussed in Box 10.2. This example illustrates the conservation costs of using poor, vegetation-only, definitions of habitat for obligate carnivores, and makes a convincing case for relating fitness directly to prey abundance.

Because many carnivores are threatened or limited by human activity, many studies include the biotic interaction with humans as an important influence on carnivore habitat. Thus, humans reduce habitat, changing the relationship between fundamental and realized niches of carnivores on a landscape. Conceptually, reducing conflict with humans would restore great amounts of “potential” habitat for many carnivore species. Researchers have investigated effects of humans and human developments on many carnivores, often focusing on roads. Gray wolves, cougars (*Puma concolor*), jaguars (*Panthera onca*), Amur tigers, Tasmanian devils (*Sarcophilus harrisii*), grizzly bears, and black bears all show that roads may be important limiting factors in the environments of these carnivores (Thurber *et al.* 1994; Mladenoff *et al.* 1995; Jones 2000; Gibeau *et al.* 2002; Dickson *et al.* 2005; Hebblewhite *et al.* 2005; Carroll and Miquelle 2006; De Azevedo and Murray 2007; Reynolds-Hogland and Mitchell 2007a; Cushman *et al.* 2009). Often, the effects of human persecution depend on context. In National Parks in Alaska and Alberta, for example, gray wolves do not avoid human activity inside protected areas, but show typical avoidance of human activity outside (Thurber *et al.* 1994; Hebblewhite and Merrill 2008). This context dependency explains recent debate about the mechanisms of road avoidance in the Great Lakes region of North America (Merrill 2000; Mech 2007). Thus, simply including human biotic interactions with surrogate variables, such as road density or distances to roads, may not capture the mechanisms of carnivore–human relationships.

### 10.3 Measuring habitat use and selection by carnivores

At least some of the confusion about habitat-selection studies can be attributed to the bewildering number of ways that carnivore ecologists can design habitat ecology studies: habitat suitability indices, resource-selection functions, resource-selection probability functions, resource-utilization functions, compositional analysis, environmental niche factor analysis, occupancy modeling, classification and regression trees (CART), genetic algorithm for rule-set prediction (GARP), maximum entropy, Mahalanobis distances, and the list goes on. Arguments and confusions within the literature (Boyce *et al.* 1999; Keating and Cherry 2004; Johnson *et al.* 2006) about the nature of statistical tests of habitat selection, while important from a statistical viewpoint, do nothing to remedy the confusion for the practitioner. Rigorous review of the statistical bases for all methods is outside the scope of this chapter. Instead, we review the importance of critical considerations often ignored: question-driven research, theoretical foundations for selectivity, scale-dependency of ecological processes, effects of density dependency, study design, and the relationships between different classes of habitat modeling approaches.

### 10.3.1 The over-riding importance of questions

Any habitat model is an answer to a specific question about causal relationships between an animal and its environment, whether the question is stated or not. Without well-stated questions about these causal relationships, however, analytical answers have limited or no meaning (much less usefulness). Yet the literature on habitat studies is replete with answers for apparently one unasked question: what is habitat for animal X? This approach presumes that understanding why the animal is where it is, is not important, and the approach does not reveal causation for observed effects. Such descriptive habitat models might pose credible explanations for why animals are found where they are, but until such models are tested, their credibility is unconfirmed and the cause and effect relationships implicit within them are hypothetical. Unfortunately, confirmed causes for why animals exist where they do are critical for conservation and recovery of a species, and underlie habitat-based conservation. The scientific method, fully employed, offers a comprehensive mechanism for understanding cause and effect habitat relationships. Nonetheless, surprisingly few habitat studies make complete use of the hypothetico-deductive logic it embodies. By far the most common approach to modeling habitat is to construct statistical models and to interpret their biological meaning a posteriori (i.e. the first two steps of the scientific method), resulting in the generation of untested hypotheses about causation. To conclude causation from an a posteriori hypothesis is to make the logical error of affirming the consequent (Williams 1997). Until an a posteriori hypothesis is tested using independent data (i.e. the remainder of the scientific method), its credibility and usefulness is no greater than the myriad other, equally credible, a posteriori hypotheses that could have been used to explain the same patterns.

Logically, causation can only be established by testing hypotheses, whereby predictions from hypotheses derived empirically (e.g. from previous observations or studies) or theoretically are compared to observations to determine their capacity to predict empirical patterns; doing so can provide evidence for causation in two ways that differ in their level of logical support. Hypotheses that are supported in classic experiments, where the magnitude of effects are evaluated both in the presence of hypothesized causes (e.g. environmental attributes in the case of habitat studies) and where the causes are known to be absent (i.e. the control), provide evidence of *sufficient causation*, wherein presence of the cause was alone sufficient to produce an observed effect (Williams 1997). A common, but misguided, justification for a posteriori analyses in habitat studies is that causation cannot be established in ecological research because classic experiments are difficult to conduct. Controlled experiments, however, are not the only means to establish

causation. *Necessary causation* can be established using observational studies, where the magnitude of effects are evaluated only where hypothesized causes are present and not where they are absent (generally the case for ecological studies); in these cases, a supported hypothesis indicates that the proposed cause produced the observed effect, at least in part, but other possible causes that were not evaluated cannot be excluded (Williams 1997). Whereas establishing necessary causation lacks the inferential strength of finding sufficient causation, it far exceeds the logical rigor of generating an untested hypothesis that establishes no causation at all. Testing meaningful, a priori hypotheses always provides stronger inferences on the cause and effect relationships that underlie habitat selection, than failing to do so.

Few circumstances exist where a researcher should choose to generate hypotheses rather than test them. For the vast majority of habitat studies, the empirical and theoretical fodder for constructing excellent hypotheses is vast, though often neglected in favor of sophisticated statistical approaches to generating a posteriori models. However sophisticated the means for generating an a posteriori habitat model might be, though, what can be learned from such an untested hypothesis is logically limited, compared to what can be learned through the test of any carefully considered a priori habitat model, however simple. We argue that the best approach to developing a robust understanding of carnivore habitat is to do a lot of thinking in advance of collecting a single data point, figuring out what the relevant questions motivating the study really are, and developing hypothesized answers to those questions that can be tested using field observations. Doing this thinking will increase inferential strength for the study; it will also allow effective planning for the data needed, the necessary sample sizes, the hardware required, the analytical framework, etc., needed to maximize study success and effectiveness of conservation applications based on the research.

### 10.3.2 Why should carnivores be selective?

A fundamental but rarely considered question for those who embark on habitat study is “why do we expect that habitat should predict animal behavior or population dynamics?” The clear answer is that natural selection has shaped behavior of animals to be selective, and that they will generally choose to exploit those places providing the resources that most contribute to their fitness. Without this assumption, no reason exists for quantifying relationships between behavior and habitat. Nonetheless, the theoretical foundations underlying the assumption are often completely ignored or even denied. The discipline of optimal foraging (Pyke *et al.* 1977; Pyke 1984; Stephens and Krebs 1987) is devoted to exploring precisely the fitness-based behaviors assumed in habitat analyses. Habitat research,

in fact, is no more than a subdiscipline within optimal foraging, yet habitat studies rarely take advantage of the rich theoretical and empirical background available to them from this field of inquiry.

When applied to habitat selection, the optimal-foraging approach explains both the central tendencies we expect to see (optimizing phenotypes), and the variation around those central tendencies (e.g. error associated with learning through iterated experiences, extrinsic influences of competition, variation in resource productivity, etc.). The challenge common to studies of both foraging decisions and habitat selection is discerning the expression of the optimizing phenotypes amidst the processes that shape and influence them. Generally, habitat studies pursue a straightforward, if simplistic, approach to this question, using proportional use as an indicator of habitat value. This is directly analogous to Charnov's (1976a) model of optimal choice of prey, whereby proportions of different prey types in a predator's diet result from an iterated decision-making process that maximizes profitability of the diet by weighing the benefits of consuming an encountered prey against the costs of capturing it. Note, however, that whereas the prey model is explicit about the economic mechanism determining the proportional representation of prey types in a diet, habitat analyses assume such mechanisms result in disproportionate use of habitat features without specifying what they are; disproportionate habitat-use is thus taken as *prima facie* evidence of selection. This is a safe assumption when proportional use of habitat characteristics differs from that available and extrinsic factors, such as predation, competition, and population density, have little effect on habitat use. The absence of mechanistic explanations is problematic for forecasting or extrapolating, however, where such factors play important roles.

Using a fitness-based definition of habitat based on resource distribution and productivity promotes quantifying the benefits of selecting habitat characteristics (for a rare example, see Andruskiw *et al.* 2008), but costs and constraints that also influence selection can be more difficult to quantify. Finding the means to identify and to measure these costs and constraints on optimal use of resources is one of the defining challenges for the future of habitat studies. Inevitably, costs and constraints of habitat use will be measured as imperfectly and indirectly as the benefits. Nonetheless, even simplistic measures of costs and constraints offer strong explanatory improvement to habitat models. For example, relatively coarse measures of resource depression, travel costs, and conspecific avoidance have strong explanatory power in predicting how animals balance costs and benefits of habitat use in their selection of home ranges (Mitchell and Powell 2004, 2007; Moorcroft and Lewis 2006; Moorcroft *et al.* 2006; Moorcroft and Barnett 2008; van Beest *et al.* 2010).

### 10.3.3 The importance of scale

Habitat is inherently scale-dependent (Figure 10.1). When considering scale, most habitat researchers immediately think of Johnson's (1980) nested scales of habitat selection, including 1st order (geographic range of the species), 2nd order (placement of home ranges within the range of the species), 3rd order (use of habitat patches by an individual within its home range), and 4th order selection (foraging within patches). These scales outline a continuum of behaviors producing ecological patterns that depend on the geographical and temporal scales of observation. Johnson's scale, however, is categorical, whereas space and time are continuous. Thus, even within Johnson's scales of habitat selection, observations and therefore inferences can vary strongly depending on the spatial and temporal scales of observation (Figure 10.1). The important context of spatial and temporal windows of observation is often misunderstood or ignored when modeling habitat (Boyce 2006). Because this context drives the robustness and usefulness of habitat models, a researcher needs a strong understanding of the variation in the ecological processes driving habitat selection during observations. Thus, space and time define a window of observation within which ecological processes are often uniquely expressed. Conceptually, this is intuitive: observing an animal during a single day precludes extrapolation of its behavior over a year. Intuitiveness can break down, however, when explanatory patterns at one spatio-temporal scale are absent, completely different, or even reversed at another scale.

Knowing a priori how a spatio-temporal window of observation or application frames what can be learned about ecological processes is challenging. Hierarchy theory (Allen and Starr 1982; O'Neill *et al.* 1986; King 1997) offers a conceptual framework for inferring a priori mechanisms, whereby ecological processes are understood in terms of both lower level mechanisms and higher level constraints. A researcher can begin designing a study by placing his or her question on the spatio-temporal continuum of ecological processes (Figure 10.1) and asking whether the spatial and temporal extents required to answer the question are feasible for study. If not, how could the question be changed so that its answer can be found within an ecological process observable within realistic constraints on time and space? Perhaps this seems obvious, but it can be argued that the spotty predictive record for habitat models (Garshelis 2000) can at least in part be attributed to failure to acknowledge hierarchical structure of ecological systems, whereby decisions by animals influencing their use of habitat at broad temporal or spatial scales were naively modeled using data collected over short time periods and within small spatial extents. Additionally, studying a phenomenon at one scale, and assuming that it scales up or down linearly to another, presumes a perfectly nested hierarchy

with no emergent properties across spatial and temporal scales. This presumption is highly questionable in ecological systems (Allen and Starr 1982; O'Neill *et al.* 1986; King 1997). To avoid such outcomes, Reynolds-Hogland and Mitchell (2007b) suggested that habitat studies could be conceptually organized according to hierarchy theory using three intersecting and interdependent axes: time, space, and ecological process of interest. The ecological axis is, by definition, hierarchically organized, such that any point selected along that axis has a correspondingly appropriate intersection point on the time and space axes. A shift in any one of the axes (e.g. a smaller temporal window of observation, or a different resolution for the ecological process) requires concomitant shifts in the other axes.

Results of habitat studies are extremely scale-dependent. Failure to acknowledge and plan for such dependency can result in misleading inferences (Boyce 2006). Understanding the hierarchical organization within an ecological system before attempting to tease out its processes in space and time is essential for successful, applicable habitat research.

#### 10.3.4 Density dependence and habitat selection

The effects of population density on habitat selection are important yet underappreciated (Fretwell 1972; Rosenzweig 1981; Haugen *et al.* 2006; McLoughlin *et al.* 2010). Extending optimal foraging-type models, Fretwell (1972) showed that, for animals foraging to increase fitness, habitat (patch) selection would be affected by the density of conspecifics in a density-dependent fashion. Given the two basic assumptions, that individuals have “ideal” knowledge about the distribution of resources and that they are “free” to move between patches to maximize fitness, as density increases, animals will select patches in a frequency dependent fashion that equalizes realized fitness among individuals. This scenario results in an evolutionary stable strategy, where individuals make the best of a bad situation as density increases and no individual can achieve higher fitness. The density ratio between two patches at ideal free distribution is the habitat “isodar,” which reflects differences in demographic quality between habitat patches (Morris 2003a, 2003b). The “ideal free distribution” predicts habitat selection for a wide variety of species (Oksanen *et al.* 1995; Beckmann and Berger 2003; Haugen *et al.* 2006; Griffen 2009). Unfortunately, the ideal free distribution has been tested only once for carnivores (black bears; Beckmann and Berger 2003), yet many studies assume density equates to fitness, clearly not the case under this form of habitat selection. Testing predictions of ideal free distribution theory should help carnivore ecologists understand the mechanisms governing habitat selection, even when animals clearly are neither ideal nor free.

As an extension of the ideal free model, consider territorial animals that are not “free” to move. Here, animals are divided into territory holders and non-territorial animals. Territory holders take the best real estate for themselves and achieve high fitness payoffs, making an “ideal despotic distribution” (Fretwell and Lucas 1970) in which density and fitness are not necessarily equal. The ideal despotic model has predicted spacing of Serengeti lions (Mosser *et al.* 2009), male black bears in California (Beckmann and Berger 2003), wolves in Yellowstone National Park (Kauffman *et al.* 2007), and other carnivores. Unfortunately, few studies, and almost none with carnivores, have examined (or acknowledged) the potential role of density in shaping habitat selection. Habitat selection by carnivores should change in density dependent fashions.

### 10.3.5 Understanding habitat selection: study design

Selection implies a behavior shaped by natural selection, whereas use is the observed outcome of that behavior. Some research questions lend themselves to understanding patterns of use, such as utilization distributions (Millsbaugh *et al.* 2006), analyses of the amount of use (North and Reynolds 1996), and hazard models of resource use rates (Freitas *et al.* 2008). Understanding the process of selection, however, provides the only opportunity to address why or how a particular pattern of habitat use is achieved, particularly given the multiscale nature of habitat. For this reason, we focus on selection, studying the use of resources by an animal and also what resources *could* have been used but were not. Two main different sampling protocols underlie almost all habitat-selection studies: comparing (1) used resources with unused resources, or (2) used resources with available resources. A third design compares unused resources with available resources (Manly *et al.* 2002) but we know of no example of this design.

Used–unused (presence–absence) designs are perhaps the more powerful and straightforward for habitat-selection studies because we can use any number of statistical frameworks to compare attributes of used versus unused units and we can make inferences about utility of habitats from the resultant statistical functions. A common statistical framework for comparison is logistic regression, which uses a binary response variable for used and unused (Hosmer and Lemeshow 2000). When density or counts are modeled, generalized linear modeling (GLM) frameworks, such as Poisson, probit, zero-inflated Poisson, or zero-inflated negative binomial models are used (Guisan *et al.* 2002; Manly *et al.* 2002; Nielsen *et al.* 2005). Common used–unused data include remote-camera trapping (animals are either photographed or not-photographed); vegetation plots where plants are either present or absent, eaten or not eaten; mark–recapture trapping, photographing, and DNA sampling; and aerial surveys where animals are seen or not seen. The key

here is that a survey unit was sampled and had a probability of either containing the animal (i.e.  $p$ ) or not containing the animal ( $1 - p$ ), and that sampling had no bias.

When animals occupying a unit may not be observed, resulting in a false absence, then detection probability  $< 1$  (MacKenzie *et al.* 2005; see Chapter 4). Occupancy models that explicitly incorporate detection probability into the habitat model are beneficial, especially when detection probability itself is a function of habitat (MacKenzie *et al.* 2005; Hines *et al.* 2010). To estimate probability of detection, repeated sampling of units is required. For example, when a carnivore that is detected in 3 out of 5 surveys of a sample unit, detection probability is  $3/5$ , or 0.6, and the probability is 0.4 that the carnivore occupies units where it was not observed (under a set of assumptions, MacKenzie *et al.* 2005). Marucco and McIntire (2010) used this approach with wolves. If detection probability is constant, or if multiple sampling is not conducted, then the used–unused design reduces to the use–availability design. In this case, relative probability of detection is estimated, which is still extremely useful for conservation and management.

Use–available (presence-only) design only has information about where animals used habitats (Pearce and Boyce 2006). Radio-telemetry studies are perhaps the most common method used to collect such data, and use–available designs are among the most common for analysis of habitat selection. Other studies with the use–available design include studies of animal distributions from museum collections (Pearce and Boyce 2006), aerial surveys where detection probability  $< 1$ , scat analyses, and track count surveys. Resource selection functions (RSFs) and environmental niche factor analysis (ENFA or niche-factor analysis, Hirzel *et al.* 2002) are used commonly to compare used and available locations. Niche models are identical to RSFs from a study design perspective because used locations are compared to what is available within some defined study area. Thus, distinctions between different use–available designs are often false.

The distinction between a use–available design and used–unused design, however, can sometimes be tricky and often researchers can adopt both designs with the same data. For example, researchers conducted surveys over 10-km<sup>2</sup> grid cells in northern Ontario for wolverines (*Gulo gulo*), recording the presence or absence of wolverine tracks (Krebs *et al.* 2004). Their goal was first to describe the distribution and occurrence (use) of wolverines, yet this rich dataset clearly could be used with habitat-selection models. Both a used–unused design (units with and without wolverine tracks) or a use–available design (units with wolverine tracks versus the entire study area) could be adopted. Moreover, in this case, a used–unused design could be extended to a true occupancy model because sites were surveyed multiple times and detection probability could be estimated. Which study design is the “best” to use in this case? The answer depends on the research question. If knowing

a relative probability is sufficient for conservation, then a used–available design is fine. If the true detection probability is needed, then the additional costs of collecting multiple sampling rounds was worth doing.

Within these two broad categories of study designs in habitat-selection studies, data can be collected and inferences applied among populations and individuals levels on at least three levels. Often, researchers collect data on wildlife only at the population level with no information about individual patterns of use, non-use, and availability. Manly *et al.* (2002) called this Design I (see Chapter 11). Common examples include aerial surveys, track or scat transects, distance sampling, diet selection based on scats, 2nd order scale (Johnson 1980) comparisons of resources used within animal home-ranges compared to what they could have used across the whole study area. In this design, animal observations occur at the population level and data include what animals did not use or was available to them. In Design II, inferentially between the population and individual level, resource use by individual animals is recorded but not where individual animals did not occur, or what was available to individual animals. Availability is measured at the population-level. An example includes observing individual bighorn sheep on aerial surveys or distance sampling and comparing their individual use of resources to that which was available to the entire population (Manly *et al.* 2002). For Design III, use and availability or lack of use is known at the individual level. Radio-telemetry is the most common tool for this design. An example is habitat selection by individually snowtracked wolves, compared to availability sampled along individual movement paths (Whittington *et al.* 2005). Costs and benefits of the different study designs depend on the research question and cost. Design I studies are often relatively inexpensive but lack mechanistic insights into why carnivores select habitat.

### 10.3.6 Using resource-selection functions and other approaches

In the North American literature, resource selection functions (RSFs) have gained prominence in habitat-selection studies (Boyce and McDonald 1999; Manly *et al.* 2002), although they are conceptually identical to niche-factor analyses that compare presence-only data to availability within a fixed study area. Other modeling approaches include maximum entropy models (MAXENT, Peterson and Robins 2003; Phillips and Dudik 2008), habitat suitability index models (Brooks 1997), and occupancy models (MacKenzie *et al.* 2005). Manly *et al.* (2002) defined RSFs as any function that is proportional to the probability of use, so this broad definition encompasses almost all other types of habitat models that could be conceived.

For the most common used–unused study designs, the used and unused sample units are commonly contrasted with logistic regression using the following equation (used–unused):

$$\hat{w}(x) = \exp(\beta_0 + \beta X) / (1 + \exp(\beta_0 + \beta X)),$$

where  $\hat{w}(x)$  is the probability of selection as a function of variables  $x_n$ ,  $\beta_0$  is the intercept, and  $\beta X$  is the vector of the coefficients  $\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \dots + \hat{\beta}_n x_n$  estimated from fixed-effects logistic regression (Manly *et al.* 2002).

In applying the used–unused design,  $\hat{w}(x)$  is a true probability and is referred to as the resource selection probability function (RSPF).

For the use–available design, the resultant function is a relative probability, and is estimated using:

$$\hat{w} * (x) = \exp(\beta X),$$

where  $\hat{w} * (x)$  is the probability of selection as a function of variables  $x_n$ , and  $\beta X$  is the vector of the coefficients  $\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \dots + \hat{\beta}_n x_n$  estimated from fixed-effects logistic regression (Manly *et al.* 2002).

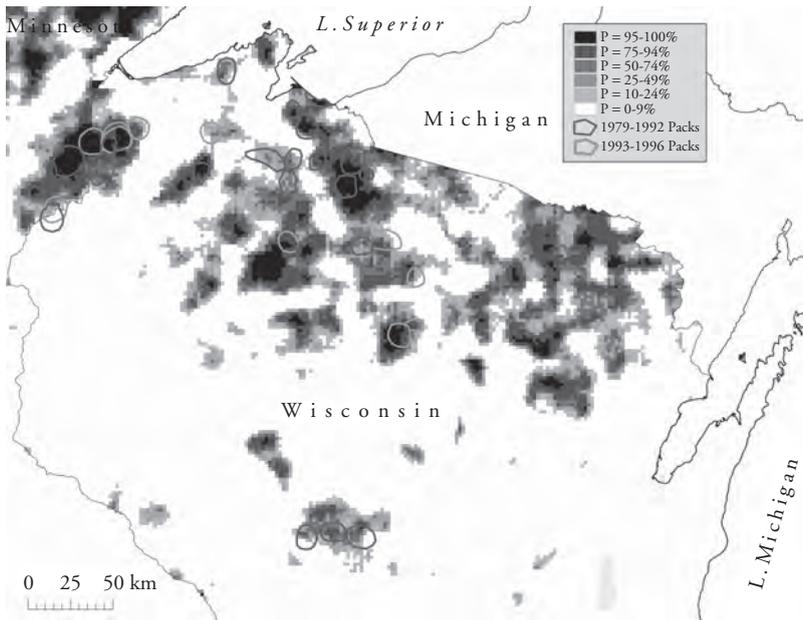
In the use–available design, because the true sampling fraction is unknown, the prevalence of use, or the absolute amount of use, cannot be estimated and, hence, the intercept is meaningless.

RSFs have been commonly used to develop a posteriori statistical models to describe habitat (i.e. to generate hypotheses) but they also lend themselves readily to hypothesis testing, as do other modeling approaches. The selection of environmental variables,  $x_n$ , for inclusion in RSF analyses implicitly reflects hypothesized contributions of habitat characteristics to selection. Stating these hypotheses explicitly makes clear their biological justification for inclusion in a habitat model; the proximity of coefficients,  $\hat{\beta}_n$  to 0 (i.e. whether 0 is included in the confidence intervals for  $\hat{\beta}_n$ ) and their relative magnitude estimated by logistic regression, thus, represent tests of the hypothesized contribution of each variable to habitat selection. Hypotheses about the relative importance of specific habitat features to specific carnivores, and about the importance of combinations of those features, can be tested by evaluating competing multivariate RSF models (using Akaike's Information Criterion, AIC; Burnham and Anderson 2002). Ciarniello *et al.* (2007) demonstrated a novel way of testing hypotheses through cross-validation of RSFs generated for the same species at different study sites. Testing the ability of an RSF generated on one dataset to predict observations for an independent dataset remains the most robust means of using RSFs to test the hypothesized causes and effects of habitat relationships.

Considerable debate about RSFs has centered on the statistical mechanics and the interpretation of functions estimated from use–available designs. The problems are that contamination arises because some available points may actually contain used points and that the overall prevalence in a logistic model with a use–available design is unknown (Keating and Cherry 2004). These problems exist, but so long as the output from a logistic regression based on use–available design is treated as relative, resources or habitat quality can be interpreted validly (Johnson *et al.* 2006; Lele and Keim 2006). The debates, unfortunately, have taken focus away from the ecology of habitat selection (McLoughlin *et al.* 2010). Readers can read the relevant literature (Boyce and McDonald 1999; Manly *et al.* 2002; Johnson *et al.* 2006; Lele and Keim 2006).

Researchers should adopt a particular modeling approach only if it is useful. A researcher must know how a model will be used and have some way of measuring the predictive accuracy, precision, or generality of the model. To measure the latter for used–unused models, typical logistic regression diagnostics apply; for use–available designs, the problems of defining availability renders these approaches suspect (Boyce *et al.* 2002). Regardless, cross-validation, both with internal and external data, is necessary to test the predictive accuracy and utility of a habitat model (Roloff *et al.* 2001; Boyce *et al.* 2002; Johnson and Gillingham 2005; Johnson *et al.* 2006). Cross-validation also provides insight into how robust a habitat models is to aspects of study design, such as autocorrelation, non-independence, multicollinearity, and sample size (Manly *et al.* 2002; Johnson and Gillingham 2005; Gillies *et al.* 2006). Typically, in a k-fold procedure, a researcher divides data into k-partitions and cross-validates the predictive capacity between observed frequency of use and predicted frequency of use across the partitions of the data. This is internal cross-validation because the data used to generate the model is used to test different “versions” of the model. Conceptually, this is similar to evaluating model fit with the coefficient of determination, and gives a measure of how well the data are explained by the model. Boyce *et al.* (2002), however, showed substantial annual variation in predictive ability of RSF models for boreal songbirds, throwing caution on the utility of the “average” year model in predicting distribution over time. In addition, biased datasets may show good internal validation despite being ecologically wrong.

Obviously, a far better way to test generality, accuracy, and precision of a model is to compare model predictions to independent data, i.e. external validation. Independent data can be collected in different years, different study areas, and with different technology (e.g. GPS vs. VHF data). Ultimately, only the test of time reveals how “useful” a particular habitat model is. In perhaps the best example of model validation, Mladenoff’s *et al.* (1999) tested a previously developed RSF



**Fig. 10.8** Spatial predictions of gray wolf habitat in the American Midwest by Mladenoff *et al.* (1999) made using data from 1979–92 (wolf pack polygons in white) tested against observed distribution of new packs (black boundaries) observed during 1993–98. Model fit was remarkably high, and the model was able to predict colonization of new smaller patches previously unused by wolves. Source: Mladenoff *et al.* (1999).

for the expanding gray wolf population in the Great Lakes states of the US against new data collected later. The initial RSF model predicted accurately the wolf distribution 5 years later (Figure 10.8). More often, model validation reveals systemic problems with the model, such as poor prediction across individuals, or spatial differences in habitat selection that suggest selection may vary systematically as a function of some biological gradient (called functional responses in resource selection, Mysterud and Ims 1998).

### 10.3.7 Functional responses in resource selection

One extremely important ecological mechanism is the variation in the strength of selection as a function of availability. Such functional responses in resource selection for *spatial* variables (habitat) may be extremely common in carnivores, and parallel the concept of frequency dependence in *non-spatial* selection of prey, which has been recognized for a long time (Greenwood and Elton 1987). Functional responses address how selection for a spatial resource should change as that

resource changes in availability (Mysterud and Ims 1999). For example, selection for oak forests (and, presumably, the productivity of acorns) by gray squirrels (*Sciurus carolinensis*) declines with increasing availability of oak forests on the landscape (Mysterud and Ims 1999). Functional responses should be common whenever animals make a tradeoff between two resources, or when thresholds exist for resources. Understanding functional responses in resource selection, therefore, allow researchers to develop habitat models that are general, flexible, and able to predict resource selection in novel settings (Matthiopoulos *et al.* 2011). Application of mixed-effects models to the study of resource selection enables researchers to investigate functional responses across individuals (Gillies *et al.* 2006).

Two important studies of carnivores relate show how functional responses in resource selection relate to frequency-dependence. As the availability of land increases in polar bears' (*Ursus maritimus*) home-ranges, bears select for ice closer to land, which affords greater hunting opportunities, (Mauritzen *et al.* 2003a), typical of a tradeoff between areas good for hunting and areas good for resting. An analysis of functional responses of wolves to human activity helped Hebblewhite and Merrill (2008) to synthesize conflicting results of wolf–human interaction studies. Previous studies of wolves' responses to roads showed attraction, ambivalence, and avoidance. Such results caused Mech *et al.* (1988) to conclude that wolves showed no consistent responses to human activity. What previous studies had not done, however, was address how selection changed as a function of the availability of human activity. Hebblewhite and Merrill (2008) found that avoidance of human activity by five wolf packs living in different human activity levels, depended on the overall amount of human activity in their pack territories. Packs with little human activity in their territories showed weak or no responses, whereas packs with high human activity showed strong avoidance, especially outside of protected areas. This and other recent examples of wolf–human functional responses (Houle *et al.* 2010) illustrates the power of understanding functional responses to produce syntheses of previous studies and to produce a solid framework for understanding carnivore–human relationships. We expect that carnivores commonly exhibit functional responses in resource selection. The most powerful approach to understanding functional responses is to combine an understanding of frequency dependence in prey selection (Greenwood and Elton 1979) with functional response analysis of spatial selection for these same prey species by a predator.

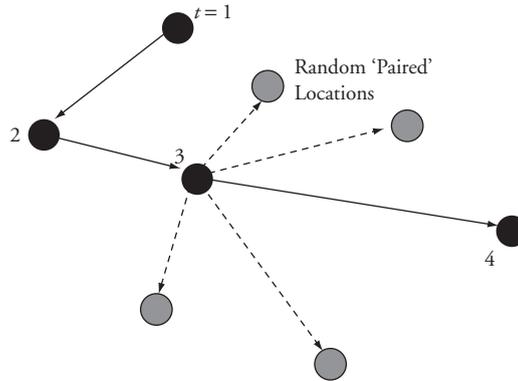
### 10.3.8 The importance of defining availability: recent advances from the field of movement modeling

Inferences from habitat-selection modeling with the use–availability design are highly contingent on how availability is defined (Beyer *et al.* 2010). Unfortunately,

no biologically objective means of calculating availability exist; researchers can only infer indirectly what resources an animal considers to be available from what it did, compared to what we imagine it could have done. Further, the concept of availability is inherently scale-dependent and depends on the spatial scale at which resource selection is investigated. In other words, no “correct” way exists to sample availability. Many studies have compared telemetry locations for an animal to a set of random locations within its entire home-range (i.e. 3rd order selection; Johnson 1980), making the implicit assumption that animals can move anywhere within their home ranges at any time between successive locations. While this assumption could biologically be true for some highly mobile carnivores (e.g. wolves), it is clearly unrealistic for many others. And, with the growing use of global positioning system telemetry collars (GPS) in carnivore research, assuming that a carnivore can go anywhere within its home range between locations that are mere minutes apart, is unrealistic. Moreover, the debate over the use–available design has confirmed that the way this design had been applied in previous studies has problems. Improved understanding of availability is needed.

Fortunately, GPS technology has helped ecologists define availability somewhat more from an animal’s behavioral perspective, and these definitions help circumvent some of the other problems with the use–available design. A study on turtles started it all. Comparing locations of slow-moving wood box tortoises (*Clemmys insculpta*) to random locations across their home ranges made no sense to Compton *et al.* (2002). Consequently, the authors borrowed a statistical method from the biomedical literature, matched-case control logistic regression, and defined availability as the area each tortoise could have reached from each location, based on its history of movements (Figure 10.9). The used and available locations are then compared using a conditional logistic regression model (also known as case-control, paired logistic and conditional logistic regression; Hosmer and Lemeshow 2000). The key here is that each used location is paired against  $n$  number of cases that represent where the animal could have actually moved (availability). The conditional likelihood of the logistic model takes into account what was available at each step and, consequently, the inferences from the overall model are conditional on the availability at each time step (Aarts *et al.* 2008; Moorcroft and Barnett 2008). This is now the recommended approach for determining availability in the use–available design at the individual level, especially including weights of “available” locations at different distances. Whittington *et al.* (2005) adopted this design to demonstrate that wolves avoid human activity in Jasper National Park, Alberta.

A caveat to this approach, however, is that restricting available points based on movement rates defines the scale of selection under evaluation (Forester *et al.* 2009). On a continuum of infrequent to frequent locations, the decisions being



**Fig. 10.9** Matched-case control sampling design for use-available study designs with animal-tracking data. Sampled locations (black circles) are paired with biologically realistic samples of “availability” given where the animal could have gone at time  $t = 3$  in this example. Random paired available points can be generated from the observed step length from  $t = 3$  to  $t = 4$ , or the empirical step length and turning angle distribution for the vector of animal relocations along the entire path  $t = 1$  to  $t = 4$ , in this case.

modeled by this approach transition from Johnson’s (1980) 3rd order selection to something on a finer scale, perhaps to Johnson’s 4th order. Alternatively, the resources selected by an animal while it moves are environmental characteristics that facilitate safe and efficient travel. This begs an interesting question about how decisions made during movement represent selection in their own right vs. the extent that these decisions are structured and constrained by selection at higher orders. In the first case, decisions made during movement may very well represent an order of selection new to the nested orders traditionally considered, requiring further theoretical development before empirical results are fully understood. In the second case, selection of a travel route may be nothing more than the most convenient way to move between two selected habitats, rendering the notion of habitat selection during movement moot.

### 10.3.9 Quantifying resources

Two approaches, which can be combined in some cases, exist for examining resource availability at used and unused or available locations. The first is a “macro” approach to measure resource availability at broad landscape scales using spatial GIS models (Franklin *et al.* 2001; McDermid *et al.* 2005, 2009). This approach has been used most successfully for abiotic or loosely biotic variables, such as vegetation cover, topographic variables (digital elevation models), and human-related variables, such as distance to roads or road density.

The second is a more “micro” approach, whereby small-scale habitat covariates are measured at sites used and unused or available by using standard field-based monitoring approaches. For example, Kunkel *et al.* (2004) measured the availability of vegetative cover, tree species, and snow depth along travel routes of wolves, compared to areas where wolves killed ungulate prey, and compared to “random” areas not along travel routes. Values for such micro-variables are expensive and time-consuming to collect but often provide richer mechanistic insights into the factors influencing different stages of carnivore habitat selection, such as hunting, resting, or attacking.

Both approaches usually rely on availability of static or abiotic surrogates that do not reflect what was truly available to an animal, leading to two problems. First, maps of “static” vegetation types do not really reflect availability of resources for most animals, including carnivores. While a static land-cover model using different forest cover types (such as spruce, open conifer, shrubs, grasslands) has some explanatory power as a habitat model, it does not capture what might be important to a carnivore in a dynamic sense. For example, if we accept that prey are a critical biotic resource for many carnivores, grassland land-cover types could have dramatically different “value” to an ungulate over the course of a year, and hence, to a carnivore (Hebblewhite *et al.* 2008). Moreover, many spatial covariates (such as vegetation and snow cover) are temporally dynamic, yet habitat-selection models

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**BOX 10.3** A prey-based habitat model for gray wolves in Banff National Park

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Gray wolves are the most widely distributed terrestrial, mammalian carnivore in the world (Mech and Boitani 2003). They require only the availability of large ungulate prey. As such, wolves are habitat generalists and densities are driven solely by ungulate biomass (Fuller and Sievert 2001), except when limited by human-caused mortality.

In this example, we illustrate including prey availability directly into habitat-selection models. Our goals here are to compare habitat-selection models based on just environmental covariates, to those based on prey availability, to illustrate the insights gained by explicitly considering prey availability, and also the drawbacks of such an approach.

We developed use-available resource selection functions (RSF, Boyce and McDonald 1999) for VHF telemetry locations for 14 wolves during winters 2001–05 in Banff National Park (Hebblewhite *et al.* 2002; Hebblewhite 2005). We estimated 99% kernel home ranges with a 6-km band width. We accounted for correlation within packs using a random effect for each wolf pack. Attributes of

**BOX 10.3** *Continued*

used locations were compared to those of available locations using a mixed-effects logistic regression model (Gillies *et al.* 2006) that yielded a relative probability of wolf use of a resource type. We considered two broad types of models: (1) “typical” RSF models as a function of spatial covariates, including topographical variables (elevation, slope) and land cover type derived from LANDSAT imagery (McDermid *et al.* 2009); (2) “biotic” RSF models that explicitly modeled prey availability and distance to high human activity (Hebblewhite and Merrill 2008). We used a previously developed habitat suitability index for prey (Holroyd and Van Tighem 1983). Moose, deer (white-tailed, *Odocoileus virginiana*, and mule deer *O. hemionus*), elk, bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*) models were considered. Wolf diet was ~50% elk, 30% deer, 10% moose, and 10% other species, such as bighorn sheep and mountain goats (based on biomass, Hebblewhite *et al.* 2004). Thus, we predicted that 3rd order habitat selection within the home ranges of wolf packs would correspond to previous results of diet selection. Despite the importance of this hypothesis, which would allow us to scale up to spatial distributions from simple and easy to collect diet studies, few ecologists have tested the generality of correspondence between scales in carnivore habitat studies.

Covariates were screened for colinearity using a liberal correlation cutoff of  $r > 0.7$  (Menard 2002). We used stepwise-AIC model selection to select the top typical and biotic RSF model, and compared the two models using AIC, and predictive capacity using k-folds cross-validation (Boyce *et al.* 2002). Because this model was use-available, using normal logistic regression diagnostics was invalid (Boyce *et al.* 2002).

Comparing the top typical and biotic models illustrates the tradeoffs carnivore ecologists will often face between predictive capacity and ecological understanding with habitat-selection models. The typical covariate model was by far the best model from an AIC perspective, with the biotic model over 66 AIC units “worse” than the typical model. Nonetheless, examination of the models’ abilities to predict within-sample wolf telemetry data revealed that the biotic model fared better, explaining 10% better than the typical model. Coefficients for all models were as expected from previous studies on wolves in mountainous terrain (Oakleaf *et al.* 2006; Hebblewhite and Merrill 2008) and the rank order of predictions from the diet of wolves in Banff matched the rank-order of selectivity coefficients from the RSF model (Table 10.3, Figure 10.10). The relative probability of the five ungulate prey species changed as a function of habitat quality, confirming that as diet suggests, wolves avoid goat and sheep habitat, and select for moose, and deer, and elk approximately equally (Figure 10.10).

**BOX 10.3** *Continued*

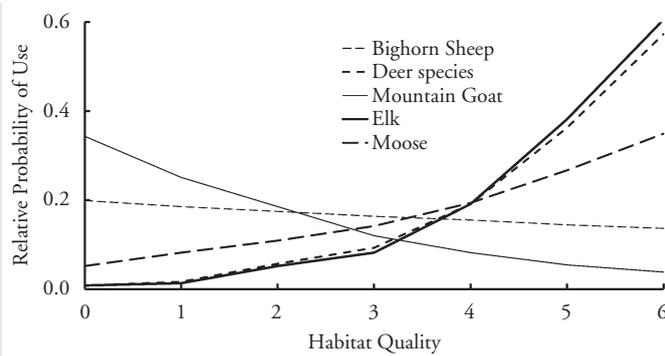
Insights from this biotic-RSF model are limited by the usual restrictions of regression-based studies. These regression models do not demonstrate whether wolves are really selecting elk or deer because these prey species were highly correlated in space; likewise for avoiding goats and bighorn sheep. Wolves could

**Table 10.3** *Resource selection function (RSF) model structure and diagnostics for the top competing environmental covariate and biotic covariate models for wolves in winters 2001–05 in Banff National Park, Alberta, in two wolf packs.*

Model	Logistic Model Structure and Coefficients (K = number of parameters)	AIC	k-folds Spearman rank correlation
Environmental covariate model	K = 10, Pr(Use) = -0.005*Elevation + 1.67*Burn + 0.67*Water + 1.4*Shrub + 0.28*OpenConifer + 0.28*ModerateConifer + 1.44*MixedForest + 1.14*Herbaceous - 2.9*Alpine	1587	0.83
Biotic covariate model	K = 7 Pr(Use) = -0.439*DistHuman - 0.23*Sheep - 0.48*Goat + 0.72*Elk + 0.30*Moose + 0.66*Deer	1653	0.92

Notes: elevation is in meters; see Hebblewhite & Merrill (2008) for explanations of the landcover covariates; DistHuman is the distance, in kilometers, to high human access, defined by Hebblewhite and Merrill (2008).

\* = ×



**Fig. 10.10** Relative probabilities of use of five ungulate prey species by wolves as a function of relative habitat quality for five ungulate prey species in the Canadian Rockies from Resource Selection Functions.

**BOX 10.3** *Continued*

be selecting elk but, because they encounter deer between predictable elk patches, deer could, actually, not be actively selected by wolves (*sensu* Huggard 1993). To tease this apart requires comparisons among wolf packs with different availabilities of prey (e.g. a functional response). Regardless, this example illustrates the exciting biological hypotheses that can be generated if we move from merely trying to predict habitat selection by carnivores to understanding the mechanisms of how prey availability drives carnivores.

have done little to link the spatially dynamic resource selection process to similarly dynamic measures of resource availability (Hebblewhite 2009). The growing access to remote-sensing products that measure the dynamic availability of forage, through indices like the normalized difference vegetation index (NDVI) and snow cover through MODIS satellites, means that future carnivore habitat models should be dynamic measures of resource availability (Hebblewhite 2009).

The second more critical problem is capturing the availability of dynamic, biotic resources, such as prey availability. A growing number of studies do include biotic covariates in habitat models (Miquelle *et al.* 1999; Hebblewhite *et al.* 2005; Heikkinen *et al.* 2007; Webb *et al.* 2008; Basille *et al.* 2009; see Box 10.2). While collecting sufficient data on availability of prey across large areas for many carnivores is difficult, carnivore habitat studies will increasingly include mechanistically measures of prey availability (Box 10.2, Box 10.3). Recent advances in non-invasive monitoring will certainly help. Camera-trapping and snowtracking can collect data on prey and predator simultaneously (Stephens *et al.* 2006).

## 10.4 Linking habitat selection to population consequences

Numerous authors have addressed the difficult conceptual and empirical challenge of linking habitat selection by individuals to population consequences (reviewed by Fryxell and Lundberg 1997). Here we focus on three empirical approaches with a demonstrable record for carnivore studies and that are perhaps the best scientifically defensible approaches: (1) population extrapolation based on habitat models, (2) combining habitat models with spatial models of mortality risks to develop core and sink habitat maps, and (3) spatially explicit models of population viability. No particular method is necessarily superior but note that data requirements, complexity, and assumptions increase from method 1 to 3.

### 10.4.1 Habitat-based population estimates

This approach combines habitat modeling with information about population densities to predict the number of animals in a given area, and has strong potential for answering questions about mechanistic links between habitat and population sizes and distributions. The principles behind this approach are first to model habitat selection, relate this habitat model to known abundance in the same area, and then to extrapolate the potential population size and distribution by applying the spatial habitat-selection model and habitat-abundance ratio to a new area (Boyce and McDonald 1999; Johnson and Seip 2008). It was this approach that Mladenoff and coworkers used successfully to predict the distribution and abundance of the recovering wolf populations in the Great Lakes region of the United States (Mladenoff *et al.* 1995, 1999; Mladenoff and Sickley 1998). It was also used to predict the numbers and distribution of grizzly bears in the Selway–Bitterroot ecosystem following potential reintroduction (Boyce and Waller 2003); the grizzly bear distribution and abundance in the Parsnip river area of Northern British Columbia (Ciarniello *et al.* 2007); recolonization habitats and population sizes of recolonizing Amur tigers expanding into NE China from the Russian Far East (Li *et al.* 2009; Box 10.2); and potential habitat and population size for critically endangered Far Eastern leopards (*P. pardus occidentalis*, Hebblewhite *et al.* 2011).

The first step involves developing a habitat-selection model for a particular carnivore species using (ideally) empirical data on the spatial locations of animals. The model should, ideally, have high predictive capacity, good model fit, and be hypothesis driven. One might use an RSF model to obtain the spatial prediction of the relative or absolute probability of use ( $\hat{w}(x)_i$  from Equation 10.1) for a particular study area with a known or estimated population size of the focal species ( $\hat{N}$ ). Next, the total predicted “habitat” required for each animal is estimated by dividing the total amount of habitat across the study area by the population size  $\sum \hat{w}(x)_i / \hat{N}$ . This ratio then provides the habitat/population ratio that can be used to extrapolate population size in adjacent areas, over time, and in different study areas. The assumptions of this approach, which include (1) the right biotic variables driving fitness have been measured, (2) similar selection patterns will exist for spatial variables in both areas, (3) similar landscape configurations exist for available spatial variables in both areas, (4) similar relationships between population parameters and available habitat in both areas, and (5) resource selection results in higher densities in those habitat types (or resource units) that are selected by a species. These are valid assumptions for many theoretical patterns of habitat selection (such as ideal free distribution, Fretwell and Lucas 1970). For an endangered species caught in an ecological trap, where animals select habitats

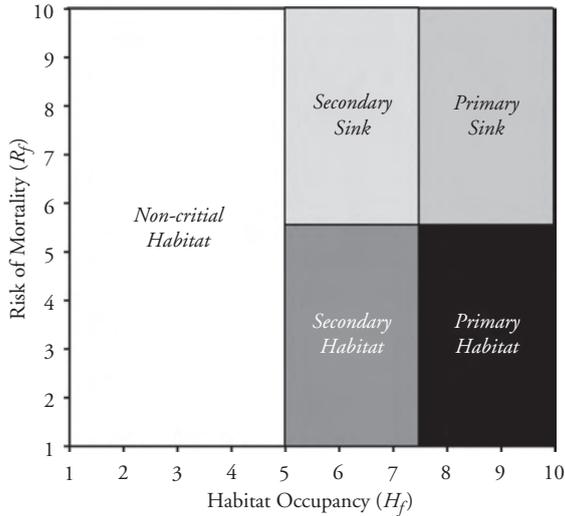
that lead to reduced fitness (Robertson and Hutto 2006), the positive correlation between habitat selection density may break down. This potential problem leads us to the second potential approach to link populations and habitats.

#### 10.4.2 Combining habitat and spatial models of mortality risk

A second approach to link habitats to population sizes is to combine a habitat model, such as the RSF designed above, with a complementary spatial mortality model that allows biologists to relax the assumption that selection = density. This approach entails identifying areas that are selected for high use by a species and identifying areas that cause high mortality and then dividing the area into habitat that can be classified as a sink (selected, high mortality) or source habitat (selected, low mortality), and non-habitats.

In the first example of this approach, Nielsen *et al.* (2004) developed spatial habitat models using resource selection functions for threatened grizzly bears in Alberta, and combined this habitat model with a spatial model of mortality risk for bears developed using spatial locations of mortalities, mostly human-caused (Nielsen *et al.* 2004). They then combined the two spatial models to identify primary sink and source habitats, secondary sink and source habitats, and non-critical habitat for grizzly bears. This model was then spatially mapped for grizzly bears on the landscape, identifying important sink areas for grizzly bears (Figure 10.11). Sink habitats were closely associated with roads and timber harvest. Therefore, Nielsen *et al.* (2006) recommended adopting access management of industrial roads to increase security and habitat quality for grizzly bears (Figure 10.11).

While Nielsen *et al.* (2004) used a large sample size of over 279 spatial mortalities of grizzly bears over 25 years, other recent studies have developed spatial models mortality risk for endangered species using fewer data and complementary approaches. For example, Falcucci *et al.* (2009) developed an integrated occurrence–mortality model for the small brown bear (*U. a. marsicanus*) population in central Italy to identify the “attractive sink” and source habitats. They contrasted bear presence (2544 locations) and mortality data (37 locations) used as proxies for demographic performance. Both Johnson *et al.* (2004) and Schwartz *et al.* (2010) used a landscape-linked Cox-proportional hazards survival model with telemetry locations of grizzly bears over 22 years in the Greater Yellowstone Ecosystem and with 63 grizzly bear mortalities to develop spatial mortality risk models. More carnivore ecologists should use these methods to combine risk and habitat models to define source-sink habitats.



**Fig. 10.11** Predicted habitat states for west-central Alberta based on combining habitat quality from an RSF model and spatial mortality risk predictions. Source: Nielsen *et al.* (2006).

### 10.4.3 Spatially explicit population models

A sophisticated approach to linking critical habitat to population size is to develop spatially explicit, individually-based, population models (Morris and Doak 2002; Carroll and Miquelle 2006; Linkie *et al.* 2006). Population viability analyses (PVA) predict the probability of persistence of a population (Boyce *et al.* 2001; Morris and Doak 2002). Although PVA models have faults (Caughley 1994), they are useful for making relative comparisons between different management or recovery scenarios for endangered species, and often help identify critical knowledge gaps (Brook *et al.* 2000; Holmes *et al.* 2007). Making PVA spatially explicit requires a link between populations and habitats. This link is most often made using simulation models of realistic movements and survival of individual animals on a specific landscape. Spatial PVA accommodate the landscape context, habitat fragmentation, and meta-population structure (Carroll *et al.* 2003b; Linkie *et al.* 2006). The cost of these models, of course, is the requirement of large datasets and the difficulty of parameterizing all required inputs with empirical data. The models present a tradeoff of parsimony versus complexity. Spatially explicit population viability models have been used for tigers (Carroll *et al.* 2003a; Linkie *et al.* 2006), wolves (Carroll *et al.* 2003b), and have even included the effects of climate change for Canada lynxes (*Lynx canadensis*) and American martens (*Martes americana*) in the eastern US (Carroll 2007).

Alternatively, spatially explicit, individual-based models of space use can be used to model population dynamics based directly on landscape characteristics and estimates of basic behavioral parameters. Mitchell and Powell (2004) presented optimality models for home ranges that maximized the benefits of spatially distributed resources over costs of repeatedly visiting resource-bearing patches. These models predicted home ranges and their distribution on a landscape under resource-maximizing and area and minimizing strategies. The resulting spatial distribution of home ranges depended on spatial characteristics of resources and the extent to which animals reduced the value of resources (i.e. resource depression) to conspecifics through consumption or protection. Simulating home ranges on a landscape using these models produced predicted distributions of animals that ranged from ideal free to ideal despotic (Fretwell and Lucas 1970; Fretwell 1972), depending on the degree of resource depression.

Using these spatially explicit, individual-based, home-range models, Mitchell and Powell (2007) showed that black bears living in the southern Appalachian Mountains generally pursued an area-minimizing strategy for selecting their home ranges, with slight levels of resource depression (e.g. Box 10.1, Figure 10.5). This



**Fig. 10.12** Change in area of simulated, area-minimizing home-ranges for female black bears in the Pisgah Bear Sanctuary, North Carolina, as a 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 the Pisgah Bear Sanctuary. Source: Mitchell and Powell (2011).

finding has very strong ecological implications because resource depression sets a maximum number of home ranges a landscape can support. Thus, home-range models such as these can be used to estimate both the distribution of animals and the carrying capacity ( $K$ ) of a landscape for those animals, without knowing their abundance. Accordingly, Mitchell and Powell (2011) estimated carrying capacity for adult female bears,  $K_{AF}$ , in their study site by sequentially adding simulated, area-minimizing home-ranges to a resource landscape comprising the food component of a habitat suitability index (HSI, Zimmerman 1992; Mitchell *et al.* 2002; Box 10.1) and using behavioral parameters found best to predict home ranges for adult females (Mitchell and Powell 2007). Simulated home-ranges increased in area as the simulated population grew; the point at which no new home-ranges could be added predicted that  $K_{AF}$  was approximately 52 (Figure 10.12). Mitchell and Powell (2011) then estimated carrying capacity for all bears (all age and sex classes except cubs),  $K$ , by adjusting  $K_{AF}$  for the proportion of adult females in the population, yielding  $K = 126$  bears. For the 235-km<sup>2</sup> study site, density at carrying capacity was 0.54 bears/km<sup>2</sup>, which is only slightly higher than the upper limit of density estimated for black bears living in the nearby and fully protected Great Smoky Mountains National Park (0.35 bears/km<sup>2</sup>; McLean and Pelton 1994).

## 10.5 Conclusions

Research that provides the most rigorous understanding of carnivore habitat scientifically possible is based on asking good questions first and foremost, hypothesizing good answers to these questions based on both theory and empirical evidence, testing the hypotheses by comparing their predictions to empirical data using the best analytical approaches available, and linking selection behavior directly to population consequences. This is a demanding process at all levels: asking good questions is difficult, developing good hypotheses is difficult, mastering rapidly evolving, highly complex analytical techniques is difficult, bridging from behavior to demography is difficult. Pressing management and conservation needs facing carnivores rarely allow the luxury of easier approaches that provide weak to poor inferences, limited scope and generality, and ultimately uncertain applicability (at best).