

- 39 Wellnhofer, P. (1987) Die Flughaut von *Pterodactylus* (Reptilia, Pterosauria) am Beispiel des Wiener Exemplares von *Pterodactylus kochi* (Wagner), *Ann. Naturhist. Mus. Wien* 88A, 149–162
- 40 Unwin, D.M. and Lü, J. (1997) On *Zhejiangopterus* and the relationships of pterodactyloid pterosaurs, *Hist. Biol.* 12, 199–210
- 41 Lockley, M.G. *et al.* (1995) The fossil trackway *Pteraichnus* is pterosaurian, not crocodylian: implications for the global distribution of pterosaur tracks, *Ichnos* 4, 7–20
- 42 Bennett, S.C. (1997) Terrestrial locomotion of pterosaurs: a reconstruction based on *Pteraichnus* trackways, *J. Vertebr. Paleontol.* 17, 104–113
- 43 Mazin, J.M. *et al.* (1995) Des pistes de ptérosaures dans le Tithonien de Crayssac (Quercy, France), *C.R. Acad. Sci. Paris* 321, 417–424
- 44 Wright, J.L. *et al.* (1997) Pterosaur tracks from the Purbeck Formation of Dorset, England, *Proc. Geol. Ass.* 108, 39–48
- 45 Lockley, M.G. *et al.* (1997) First report of pterosaur tracks from Asia, Chullanam Province, Korea, *J. Paleontol. Soc. Korea, Spec. Publ.* 2, 17–32
- 46 Bennett, S.C. (1997) The arboreal leaping theory of the origin of pterosaur flight, *Hist. Biol.* 12, 265–290
- 47 Clark, J.M. *et al.* (1998) Foot posture in a primitive pterosaur, *Nature* 391, 886–889
- 48 Unwin, D.M. (1997) Locomotory roles of the hind limbs in pterosaurs, *J. Vertebr. Paleontol.* 17, 82A
- 49 Bennett, S.C. (1996) The phylogenetic position of the Pterosauria within the Archosauromorpha, *Zool. J. Linn. Soc.* 118, 261–308
- 50 Peters, D. (1997) A new phylogeny for the Pterosauria, *J. Vertebr. Paleontol.* 17, 69A

Relating populations to habitats using resource selection functions

Mark S. Boyce and Lyman L. McDonald

Ecology is the scientific study of the distribution and abundance of organisms.¹ If we know the distribution of resources on which the organisms depend, the distribution and abundance of organisms can often be characterized by resource selection functions (RSFs). As such, RSFs are fundamental tools for quantifying ecology. An RSF is any function that is proportional to the probability of use of a resource unit². The recent development of RSFs is a byproduct of research on quantitative models for characterizing natural selection³, which involve the same statistical approaches as quantifying resource selection by animals². The purpose of this review is to chronicle new advances in the use of RSFs for mapping the abundance of organisms using geographical information systems (GIS) and for estimating total population size in an area.

Habitat selection is usually a behavioural consequence of animals actively selecting where they live, or passively persisting in certain habitats. Ultimately, however, resource-use patterns are a consequence of the influence of selection on survival and reproduction, which determines fitness in various habitats⁴. Typically, the extent of habitat use suggests the quality and abundance of resources in those areas, which in turn reflects fitness in that habitat⁵, although there are exceptions⁶.

Recent developments in the use and analysis of GIS provide the opportunity to map habitats^{7,8}. We believe that RSFs are the most promising of procedures proposed for studying resource selection when combined with GIS because: (1) RSFs offer a quantitative characterization of resource use; (2) RSFs can accommodate virtually any type of resource being selected, including both categorical

Habitat use can be characterized by resource selection functions (RSFs) that are proportional to the probability of an area being used by an animal. We highlight two procedures that have recently been used to relate RSFs to population density, dependent upon which field procedures are practical for a species. These new developments allow RSF models to be interfaced with geographical information systems (GIS) to map the probability of use, and ultimately populations, across landscapes.

Mark Boyce is at the Dept of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9 (mark.boyce@ualberta.ca); Lyman McDonald is at WEST Inc., 2003 Central Avenue, Cheyenne, WY 82001, USA (lymanmcd@uswest.net).

and scalar variables²; and (3) RSF models easily accommodate spatial structure^{9,10} and can be interfaced with GIS to facilitate rapid analysis and use of remote sensing and other types of spatial data^{8,11}.

Because RSFs yield probabilities that are proportional to use, RSFs can also be used, with appropriate scaling, to tie populations to their habitats. If such a habitat or population link can be established, there are important applications for conservation and ecological management. For example, in the USA, the RSF approach has been used to model populations of spotted owls (*Strix occidentalis caurina*) in the Pacific northwest¹², to anticipate future timber wolf (*Canis lupus*) populations in the northern Great Lakes states¹³ and New England¹⁴, and to base a population viability analysis of California gnatcatchers (*Poliioptila c. californica*)¹⁵. This approach is also currently being used to anticipate the distribution and abundance of grizzly bears (*Ursus arctos horribilis*) in the proposed recovery zone in the Selway-Bitterroot wilderness of Idaho and Montana (M.S. Boyce *et al.*, unpublished).

Here, we outline two approaches for linking RSFs to population size, *N*. Using a reference area of known *N*, RSFs can be used to extrapolate *N* in a new area based on the area of resource units. RSFs are typically estimated using availability data versus use data. Alternatively, a resource selection probability function (RSPF) can be estimated over a finite collection of sample units, which can then simply be summed over an area to estimate population size. RSPFs can be obtained from samples of used versus unused resource units or by adjusting an RSF based on sampling intensity.

Using resource selection functions

The advantage of RSFs is that they are proportional to the probability of use of a resource unit² (Box 1). Therefore, if we know the distribution of a population among habitats by RSF values in a baseline area, we can then estimate the density of animals by habitat type (assuming that all units are equally available). If similar patterns of use can be assumed to occur in another area, we can predict the population size by estimating densities according to habitats and summing across habitat type (Box 2).

An example using this method for extrapolating the number of wolves in the northeastern United States is given in Box 3. In this case, suitable habitats are arbitrarily defined as those with a relative RSF > 0.5, but there is no reason to expect that poorer quality habitats would not be occupied as well. Consequently, the calculations yield underestimates of expected population size (also see Refs 15, 22). An extensive statistical treatment of RSFs and their estimation under various sampling protocols is provided by Manly *et al.*² and related sampling considerations are discussed by Aebischer *et al.*²³

Using resource selection probability functions

Whereas an RSF, w , is proportional to the probability of use for a resource unit, a resource selection probability function (RSPF) is scaled so that we can calculate w^* , which is the actual probability of use. Obtaining probabilities of use is useful because we can simply sum the probabilities of use over an area to estimate total population size. A study design suitable for estimating RSPFs is based on characterizing used and/or unused sample units (Box 4). However, a common problem with this sampling scheme is that, often, we cannot discern what constitutes an unused habitat unit^{24,25}. If we wait longer or collect data more intensively, we might discover that a habitat unit is used, making the distinction between used and unused less clear. A solution to this problem is to estimate an RSF using a generalized linear model assuming Poisson counts for the number of used units². A short-cut (Box 1) is to fit a logistic regression of used versus available sites, and then to adjust the RSF for different sampling intensities of randomly selected units (available) and used units².

Thus, for a finite number of possible habitat units, we first measure resources for a sample of used and available sites. Next, we use logistic regression to estimate an RSF to characterize the patterns of habitat use. The RSF equation is then modified to create an RSPF by altering the constant, β_0 , to adjust for differential sampling of random habitat units and used sites². The RSPF model can then be applied to a GIS map, predicting population size by summing the RSPF probabilities over an area of interest.

With this method, RSPFs are computed from samples of resource units that are finite in number. If the sampling unit is a point, such as a radiotelemetry location, scaling logistic regression for RSPF is not possible because there are an infinite number of possible sampling units. Estimating population size using RSPFs is most easily adapted to territorial species, where individuals (or families) occupy exclusive areas (Box 5). When territories overlap, however, an RSPF could still be used to estimate population size by adjusting for the extent of territory overlap.

Assumptions of RSF-based population estimation

We assume that the modeler knows the limiting factors that influence the distribution and abundance of the study organism and that data are available on key resource variables. When resource units are sampled, we also assume that

Box 1. Estimating resource selection functions (RSFs)

A variety of statistical approaches can be used to estimate an RSF, w_i , most simply as the proportion of used resource units of category i from those available. If a_{+} is the population of available resource units and a_i are those in category i , we can estimate a simple selection ratio:

$$w_i = a_i / \pi_i$$

where $\pi_i = a_i / a_{+}$, and similarly, o_i is the proportion of used resource units in category i . This 'foraging ratio' was first applied by R.E. Savage in 1931 to herring feeding on plankton off the coast of England¹⁶.

We can carry this idea a step further by modeling the use of habitats relative to their availability. For example, we might assume that our resource selection function, $w(\mathbf{x})$, can be characterized by a log-linear model:

$$w(\mathbf{x}) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)$$

where the x_i denote $i = 1, \dots, k$ independent habitat variables, and the β_i s are selection coefficients. This model can be fitted using a generalized linear model assuming Poisson counts for the number of used units², but a short-cut is to fit a logistic model, $\tau(\mathbf{x})$, to the independent variables where the dependent data are one for used units and zero for available units:

$$\tau(\mathbf{x}) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k) / [1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)]$$

The selection coefficients, β_i , in the log-linear model are estimated by the logistic regression coefficients. We simply use the numerator, $w(\mathbf{x})$, to distribute the use of resources across the landscape².

these are sampled randomly and independently. We further assume that organisms have free and ready access to available resource units. Although we assume that RSFs and resources do not change during the study, this assumption can be relaxed if sufficient data are available to estimate RSFs repeatedly. In some applications, habitats are dynamic and change rapidly, but RSFs can be estimated to document how resource selection changes through time. For example, Arthur *et al.*¹¹ studied variation in pack ice habitat for polar bears (*Ursus maritimus*) and measured habitat selection every three to six days. Similarly, seasonal changes in habitat use might require seasonal estimates of RSFs (Ref. 27).

In addition to the issue of temporal constancy in resource selection, there is also the problem of variation in the availability of resources and the effect of spatial variation on selection of a given unit. If not reconciled, an RSF or RSPF estimated in one area cannot be applied in another area except under some unusual circumstance in which

Box 2. Estimating population size using resource selection functions (RSFs)

For the i th habitat type with area $A(\mathbf{x}_i)$ and habitat vector \mathbf{x}_i the relative use is:

$$U(\mathbf{x}_i) = w(\mathbf{x}_i) A(\mathbf{x}_i) / \sum_j w(\mathbf{x}_j) A(\mathbf{x}_j)$$

where the summation is over the number of habitat types, $j = 1, 2, \dots, m$. If every habitat unit has a unique value of the variables \mathbf{x}_i then the sum is over the number of units in the study area. So, the number of animals expected in the i th habitat type is:

$$N_i = N \cdot U(\mathbf{x}_i)$$

and density of animals, $D(\mathbf{x}_i)$, in the i th habitat type is obtained by multiplying the total population size, N , by the relative use adjusted by area:

$$D(\mathbf{x}_i) = N \cdot U(\mathbf{x}_i) / A(\mathbf{x}_i)$$

When applied to a new area, to estimate the population size, simply sum over the product of density times area of the j th type of habitat in the new area, $A'(\mathbf{x}_j)$ for $j = 1, 2, \dots, m$:

$$\hat{N}' = \sum_j D(\mathbf{x}_j) A'(\mathbf{x}_j)$$

Standard errors for \hat{N}' and $D(\mathbf{x}_j)$ can be approximated by the delta method using the first few terms of a Taylor series expansion¹⁷.

Box 3. Wolves in northeastern USA

Mladenoff *et al.* projected timber wolf (*Canis lupus*) populations for the Great Lakes states⁹ and New England¹⁰ using resource selection functions (RSFs) with a variation on the procedure outlined in Box 2. They monitored wolf packs using radiotelemetry¹⁸ to secure a collection of 14 'used' pack areas containing at least 50 telemetry locations. Within the region of potential but unused habitat, they obtained habitat data from a collection of 14 random areas equal in area to the mean pack size. Each selected area was at least 10 km from the nearest known wolf pack. Therefore, the data were from used and unused sites, appropriate for a direct application of logistic regression analysis² (see Box 4). Habitat variables included road density, prey [white-tailed deer (*Odocoileus virginianus*)] density, land-cover type, human population density and land ownership. Road density (*R*) was the best predictor. The results of the logistic regression can be expressed as a logit function. The RSF is therefore:

$$\text{logit}(p) = 14.6R - 6.6$$

The resulting logistic-regression model was scaled from zero to one (i.e. a relative RSF). Suitable habitat was mapped using GIS based on areas with a relative RSF value of 0.5 or greater.

Using these suitable habitat areas, Mladenoff *et al.* employed two methods to extrapolate the eventual wolf population into Wisconsin and Michigan where wolf populations had recently become established. These methods were based on: (1) mean territory size, and (2) white-tailed deer (*Odocoileus virginianus*) density for prey. In the first case, the number of wolves was predicted using Fuller *et al.*'s¹⁹ model:

$$\hat{N} = \left[\frac{AW}{M(1+i)} \right] / (1-d)$$

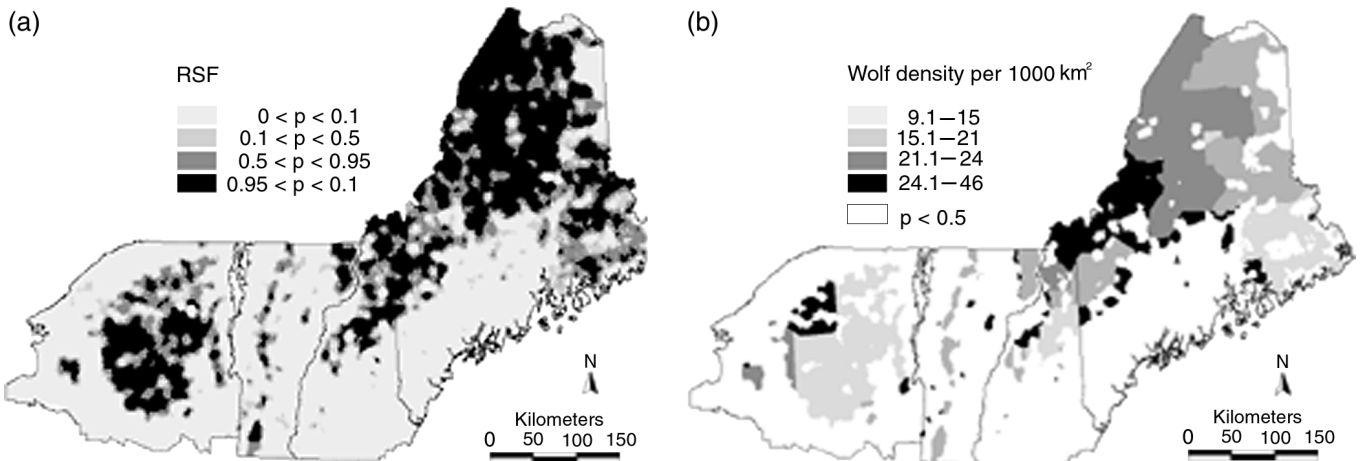
where \hat{N} is the number of wolves, *A* is the area of favorable habitat, *W* is the mean pack size (4.08), *M* is the mean pack territory size (179 km²), *i* is the proportion of saturated habitat in interstitial areas between packs (0.37), and *d* is an estimate of the proportion of nonpack wolves (0.15). Isolated habitat fragments less than 50 km² were not included. This method, therefore, offers an estimate of the saturated wolf density at equilibrium given pack characteristics such as those observed in Minnesota.

The second method extrapolates wolf population density, *D*, in numbers per 1000 km², based on a prey density estimate, specifically white-tailed deer density per km², *X*:

$$D = 3.4 + 3.7X$$

where deer density was estimated for each deer management unit by state wildlife officials^{20,21}. Again only 'suitable' habitat was used for the extrapolation and habitat fragments less than 50 km² were deleted. An illustration of anticipated wolf habitats in New England is presented in (a) where prey includes both deer and moose (*Alces alces*). Wolf population size (b) was obtained simply by summing over the areas of interest.

By monitoring the expanding wolf population in northern Wisconsin subsequent to publishing their model, Mladenoff *et al.* validated the model²¹ although finding that wolves will indeed occupy areas with RSF < 0.5. *Figure modified, with permission, from Ref. 14.*



(Online: Fig. 1)

the availability, including effects of spatial variation, is the same. Indeed, simply varying the size of the study area or excluding certain areas from the domain of the study can result in different models²³. This is not a fatal flaw, however, because sometimes we obtain robust models that are relatively insensitive to variation in availability, and in other cases we can model the relation between selection coefficients and availability explicitly, thereby taking availability into account.

When certain habitat attributes are key to the ecology of a species, the coefficients can be robust over a range of habitat types. This was the case for models of spotted owl, because old growth was such an overwhelmingly important variable in the estimation of RSFs – the amount of old-growth forest was a good predictor even in quite different landscapes²⁶. Specifically, the RSF estimated for habitats in southwestern Oregon accurately predicted the locations of spotted owl on the Olympic Peninsula and on the east slope of the Cascades of Washington – both of these areas

host very different vegetation. However, because the amount of old-growth forest was such an overwhelmingly important ecological variable, it was a strong predictor in each area and the models could be used interchangeably among areas with little loss of accuracy in predicting owl nest sites (Box 5).

In some circumstances, resource availability in a landscape varies considerably, as does the diet of animals in different habitats. Consider, for example, grizzly bears in the Yellowstone (USA) ecosystem. Some bears have seasonal access to cutthroat trout (*Oncorhynchus clarki*), whereas other bears might have no trout streams within their home range²⁸. Likewise, some bears feed extensively on army cutworm moths (*Euxoa auxiliaris*) in alpine talus, but, again, some bears have no access to this food resource²⁹. Availability of certain resources influences diet and habitat-use patterns. One solution to this problem is to sample home ranges over a range of habitats, and then to model the coefficients in the RSF as a function of the

availability of resources in each home range. Modeling the coefficients might be accomplished using linear regression analysis, for example. Then, when a new area is modeled, the β_i coefficients will be estimated based on the availability in this new area.

One of the potential applications of RSF models in a GIS context is to predict future habitat types using succession models, and then to anticipate future population sizes¹². Understanding how RSF coefficients might change as resource availability changes in the landscape is fundamental to the reliability of such population projections.

Autocorrelation of resource variables is an important consideration, especially for evaluating the statistical significance of alternative models. Autocorrelated data tend to yield estimates of variance that are too small and, consequently, we are likely to overestimate the differences of use among habitats². Radiotelemetry data, for example, might be abundant but not independent. By inspecting an autocorrelation function, one can identify the time interval over which observations become independent and use this interval for sampling observations.

Likewise, the distribution of organisms is seldom random in space – organisms are often clustered in good habitat or, possibly, aggregated as an antipredator strategy. But, the spatial autocorrelation structure of the distribution of the organism might be simply a function of the spatial pattern of its habitats, so RSF modeling might remove any such pattern. One approach is to examine the residuals from an RSF to see if spatial aggregations occur independently of habitat; for example, by using the Durbin-Watson statistic. If spatial autocorrelation occurs in the residuals, one might then develop autologistic models where the animals' use of resource units surrounding a used resource unit is a covariate in a logistic regression model⁹. Alternatively, one might use an interpolation method like kriging³⁰ or some other smoothing algorithm to create 'nicer' maps of distribution. For purposes of projecting population size, however, the β coefficients in a logistic regression model are not biased by spatial autocorrelation, so estimates of population size should not be affected. The primary advantage of modeling the spatial autocovariance is to create more realistic maps of distribution.

Implicit in attempts to model populations based on habitats is an assumption of equilibrium population dynamics. If populations are changing rapidly, we cannot expect RSF models to remain constant. There are two possible approaches to this problem. First, one might model RSFs at varying population densities to see how the coefficients vary in a density-dependent fashion³¹. Another approach is to model mean population densities assuming that population fluctuations are attributable to stochastic fluctuations around some long-term average¹². Otherwise, applications will be limited to species with equilibrium dynamics occurring at or near carrying capacity.

The value of habitats is not necessarily based upon their use⁶. For example, habitats used for sleeping might not be in short supply nor crucial for survival. Access to water, however, might be crucial but only a few minutes each day might be spent drinking. Other approaches can be taken to evaluate the importance of habitats. For example, one might multiply the RSF values by the caloric food value of each habitat to get an index of the value of a habitat (D.J. Mattson, unpublished). Another approach is to model the reproduction or survival of individuals as a function of habitat variables, thereby dissecting components of fitness. An understanding of the ecology of the species must be used in the interpretation of RSF models.

Box 4. Estimating resource selection probability functions (RSPFs)

There are several study designs that can yield an RSPF directly. Perhaps the easiest approach for estimating an RSPF, $w^*(\mathbf{x})$, is to use logistic regression on samples of used and unused units, where the selection function is modeled by a logistic function of k independent variables, x_i , hypothesized to influence resource selection, and β_i are coefficients to be determined when fitting the model to data^{2,24}:

$$w^*(\mathbf{x}) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)}{[1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)]}$$

Many statistical packages are available for logistic regression. Input data are the dependent variable (either zero for unused units or one for used units) and the corresponding values of the independent variables, x_i , measured on each unit. This approach yields outcomes directly interpretable as probabilities or alternatively as a ratio of odds.

Research opportunities

Summarizing his review of definitions of ecology, Krebs³² suggested that 'we are interested in *where* organisms are found, *how many* occur there, and *why*'. RSFs can do an excellent job of describing where, and under certain assumptions, how many. But RSFs are simply statistical descriptions of the distribution and use of landscapes, and as such, do not necessarily help us to understand why organisms are where they are. In contrast to individual-based models³³ that typically include many details, RSFs take a broad-scale or top-down perspective characterizing general patterns on the landscape. RSFs generally will be

Box 5. Northern spotted owls in the Pacific northwest

Declines in habitat for the northern spotted owl (*Strix occidentalis caurina*) in the Pacific northwest have been a major conservation concern during the past decade. We used RSF to evaluate the role of habitat variables in the distribution of spotted owl nest sites, including several measures of landscape pattern, such as patchiness, isolation, contagion and fractal dimension²⁶. Our sample unit was a 2 km² circle surrounding an owl site, approximately the area of an exclusively defended territory for a pair of owls. An intensive field survey effort by the USA Bureau of Land Management (BLM) and Forest Service personnel censused a total of 1780 owl pairs within the bounds of our study area in western Oregon. We measured details of habitat within 2 km² circles at 50 owl sites and 50 random forest-landscape locations.

We used logistic regression to estimate an RSF from a set of habitat variables that we hypothesized to be important to the owls, viz:

$$w^* = \exp[\beta_0 + \beta_1(\text{OldGrowth}) + \beta_2(\text{ElevRange}) + \beta_3(\text{Diversity})]$$

where w^* is the probability of use, 'OldGrowth' is the area within the 2 km² circle in old-growth forest, 'ElevRange' is the range in elevation at the site, and 'Diversity' is the Shannon Index of the diversity of forest types within the 2 km² circle.

Key to linking this relative RSF to population is the calculation of β_0 . Following Manly *et al.*² we estimated the β_0 from the logistic regression analysis by subtracting the ratio of sampling fractions, $P_u:P_a$. Here P_u is the proportion of used units sampled and P_a is the proportion of available units sampled. Assuming that the BLM-Forest Service census of 1780 spotted owl pairs up to 1993 was valid, $P_u = 50 \div 1780 = 0.028$ because we measured habitats for 50 out of 1780 possible pairs of owls. Likewise, we measured habitats at 50 nonoverlapping random landscape locations out of 18 079 possible 2 km² plots that would cover the entire study area yielding $P_a = 50 \div 18 079 = 0.0028$. Thus, a total of 1780 owls occupied a total available 18 079 sites or 9.8% of the sites were used¹².

We then estimated w^* for each of 50 landscape locations obtaining a mean w^* of 0.098 (± 0.031 ; 95% confidence interval), which is virtually identical with the proportion of available 2 km² plots used by spotted owls. The locations of these owls were accumulated over more than 10 years of sampling, and a substantial number of the sites had been monitored for several years. Our estimate of w^* is to characterize the location of owl sites, but these owl sites vary in how frequently they were occupied. We estimated the proportion of years that each site was occupied, and again modeled this as a function of habitat variables but using linear regression. Then this proportion was multiplied by w^* , which yielded the probability that a 2 km² area is an occupied owl site. By summing these over the study area, we estimated the total population size, thereby allowing our calculations to be cross checked¹².

preferable to individual-based models when data are scarce and the spatial scale is large. When applicable, RSFs offer a framework from which to explore the ecological processes that shape distribution and abundance.

Habitat ecology is a discipline depauperate of theory, even though habitats are fundamental to population biology, community ecology, behavioural ecology, landscape ecology, conservation biology and wildlife management. Indeed, given the definition of ecology at the beginning of this article, one might argue that habitat ecology rests at the very core of ecology.

There are several reasons for the lack of a theory of habitat ecology. By its very nature, habitat ecology is a multifaceted process requiring simultaneous consideration of several variables. However, RSFs based on multivariable models, such as multiple logistic regression, easily accommodate this problem. Interactions with other species, influences of a variety of physical and biotic factors, and the structure of the population all can be explicitly built into the model. Furthermore, habitat ecology is fundamentally spatial, which always has been difficult to model. Issues of scale are readily explored using RSFs constructed at alternative scales²⁷, or even multiple scales²⁶. Recent advances in GIS technology make spatial modeling much easier, especially when facilitated by RSFs.

RSFs can provide a framework for the development of a theory of habitat ecology. The simple methods that we have outlined in this paper forge a link between landscape ecology and population biology. More generally, however, ecological and behavioural processes shape the RSF coefficients. Foraging theory is behind the prediction of resource selection, providing the mechanisms that shape patterns of resource use. Likewise, physiological ecology is fundamental to predicting resource needs of organisms. If we can build models to predict the β_i s, we can generalize models that incorporate the processes.

Acknowledgements

We are grateful to Eric Anderson, Rick Mace, Bryan Manly, Evelyn Merrill, David Mladenoff, Neal Niemuth, Doug Ouren, Chris Servheen and John Waller for discussion and reviews of the manuscript. Thanks to Ted Sickley for preparing the figure. MSB was supported by the Boone and Crockett club and the Grizzly Bear Recovery Office, US Fish and Wildlife Service.

References

- 1 Andrewartha, H.G. (1961) *Introduction to the Study of Animal Populations*, University of Chicago Press
- 2 Manly, B.F.J., McDonald, L.L. and Thomas, D.L. (1993) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, Chapman & Hall
- 3 Manly, B.F.J. (1985) *The Statistics of Natural Selection*, Chapman & Hall
- 4 Southwood, T.R.E. (1977) **Habitat, the templet for ecological strategies?** *J. Anim. Ecol.* 46, 337–365
- 5 Fretwell, S.D. and Lucas, H.L. (1970) **On territorial behaviour and other factors influencing habitat distribution in birds**, *Acta Biotheor.* 19, 16–36
- 6 Van Horne, B. (1983) **Density as a misleading indicator of habitat quality**, *J. Wildl. Manage.* 47, 893–901
- 7 Alldredge, J.R., Thomas, D.L. and McDonald, L.L. (1998) **Survey and comparison of methods for study of resource selection**, *J. Agric. Biol. Environ. Stat.* 3, 237–253
- 8 Erickson, W.P., McDonald, T.L. and Skinner, R. (1998) **Habitat selection using GIS data: a case study**, *J. Agric. Biol. Environ. Stat.* 3, 296–310

- 9 Augustin, N.H., Muggleston, M.A. and Buckland, S.T. (1996) **An autologistic model for the spatial distribution of wildlife**, *J. Appl. Ecol.* 33, 339–347
- 10 Otis, D.L. (1998) **Analysis of the influence of spatial pattern in habitat selection studies**, *J. Agric. Biol. Environ. Stat.* 3, 254–267
- 11 Arthur, S.M. *et al.* (1996) **Assessing habitat selection when availability changes**, *Ecology* 77, 215–227
- 12 Boyce, M.S., Meyer, J.S. and Irwin, L.L. (1994) **Habitat-based PVA for the northern spotted owl**, in *Statistics in Ecology and Environmental Monitoring* (Otago Conference Series No. 2) (Fletcher, D.J. and Manly, B.F.J., eds), pp. 63–85, University of Otago Press
- 13 Mladenoff, D.J. *et al.* (1997) **Causes and implications of species restoration in altered ecosystems**, *BioScience* 47, 21–31
- 14 Mladenoff, D.J. and Sickley, T.A. (1998) **Assessing potential gray wolf restoration in the northeastern United States: A spatial prediction of favorable habitat and potential population levels**, *J. Wildl. Manage.* 62, 1–10
- 15 Akçakaya, H.R. and Atwood, J.L. (1997) **A habitat-based metapopulation model of the California gnatcatcher**, *Conserv. Biol.* 11, 422–434
- 16 Savage, R.E. (1931) **The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters**, *Fish. Invest.* 12, 1–88
- 17 Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*, Charles Griffin & Co.
- 18 Wydeven, A.P., Schultz, R.N. and Thiel, R.P. (1995) **Monitoring of a recovering gray wolf population in Wisconsin, 1979–1991**, in *Ecology and Conservation of Wolves in a Changing World* (Carbyn, L.N., Fritts, S.H. and Seip, D.R., eds), pp. 147–156, Canadian Circumpolar Institute (Occas. Publ. No. 35)
- 19 Fuller, T.K. *et al.* (1992) **A history and current estimate of wolf distribution and numbers in Minnesota**, *Wildl. Soc. Bull.* 20, 42–55
- 20 Fuller, T.K. (1989) **Population dynamics of wolves in north-central Minnesota**, *Wildl. Monogr.* 105, 1–41
- 21 Mladenoff, D.J. *et al.* (1995) **A regional landscape analysis and prediction of favorable gray wolf habitat in the Northern Great Lakes Region**, *Conserv. Biol.* 9, 279–294
- 22 Mladenoff, D.J., Sickley, T.A. and Wydeven, A.P. (1999) **Predicting gray wolf landscape recolonisation logistic regression models vs new field data**, *Ecol. Appl.* 9, 37–44
- 23 Aebischer, N.J., Robertson, P.A. and Kenward, R.E. (1993) **Compositional analysis of habitat use from animal radio-tracking data**, *Ecology* 74, 1313–1325
- 24 Buckland, S.T. and Elston, D.A. (1993) **Empirical models for the spatial distribution of wildlife**, *J. Appl. Ecol.* 30, 478–495
- 25 Osborne, P.E. and Tigar, B.J. (1992) **Interpreting bird atlas data using logistic models: an example from Lesotho, southern Africa**, *J. Appl. Ecol.* 29, 55–62
- 26 Meyer, J.S., Irwin, L.L. and Boyce, M.S. (1998) **Influence of habitat abundance and fragmentation on spotted owls in western Oregon**, *Wildl. Monogr.* 139, 1–51
- 27 Mace, R.D. *et al.* (1996) **Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana**, *J. Appl. Ecol.* 33, 1395–1404
- 28 Mattson, D.J. and Reinhart, D.P. (1995) **Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989**, *Can. J. Zool.* 73, 2072–2079
- 29 Mattson, D.J. *et al.* (1991) **Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem**, *Can. J. Zool.* 69, 2430–2435
- 30 Isaaks, E.H. and Srivastava, R.M. (1989) *An Introduction to Applied Geostatistics*, Oxford University Press
- 31 Hobbs, N.T. and Hanley, T.A. (1990) **Habitat evaluation: do use/availability data reflect carrying capacity?** *J. Wildl. Manage.* 54, 515–522
- 32 Krebs, C.J. (1978) *Ecology: the Experimental Analysis of Distribution and Abundance* (2nd edn), Harper & Row
- 33 DeAngelis, D.L. and Gross, L.J., eds (1992) *Individual-based Models and Approaches in Ecology*, Chapman & Hall