REVIEW

# Considering ecological dynamics in resource selection functions

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## Summary

**1.** Describing distribution and abundance is requisite to exploring interactions between organisms and their environment. Recently, the resource selection function (RSF) has emerged to replace many of the statistical procedures used to quantify resource selection by animals.

**2.** A RSF is defined by characteristics measured on resource units such that its value for a unit is proportional to the probability of that unit being used by an organism. It is solved using a variety of techniques, particularly the binomial generalized linear model.

**3.** Observing dynamics in a RSF – obtaining substantially different functions at different times or places for the same species – alerts us to the varying ecological processes that underlie resource selection.

**4.** We believe that there is a need for us to reacquaint ourselves with ecological theory when interpreting RSF models. We outline a suite of factors likely to govern ecologically based variation in a RSF. In particular, we draw attention to competition and density-dependent habitat selection, the role of predation, longitudinal changes in resource availability and functional responses in resource use.

**5.** How best to incorporate governing factors in a RSF is currently in a state of development; however, we see promise in the inclusion of random as well as fixed effects in resource selection models, and matched case–control logistic regression.

**6.** Investigating the basis of ecological dynamics in a RSF will allow us to develop more robust models when applied to forecasting the spatial distribution of animals. It may also further our understanding of the relative importance of ecological interactions on the distribution and abundance of species.

**Key-words:** case–control, competition, density-dependent habitat selection, functional response, logistic regression, predation, random effects, resource selection function, RSF

## Introduction

Ecologists are united by an underlying motivation to understand those factors that govern the distribution and abundance of species. Describing distribution and abundance is requisite to exploring interactions between organisms and their environment, and so we have developed numerous methods to characterize and predict how species use space and resources. These include relatively simple comparisons between expectations of used and available resources [e.g. foraging or selection indices (Manly *et al.* 2002)], to more complicated techniques such as compositional analysis (Aebischer, Robertson & Kenward 1993), K-select analysis (Calenge, Dufour & Mallaird 2005), species distribution models (e.g. Phillips, Anderson & Schapire 2006), mechanistic home range models (Moorcroft & Barnett 2008), habitat suitability models (e.g. Hirzel *et al.* 2006; Hirzel & Le Lay 2008), and related resource selection and resource selection probability functions (Manly *et al.* 2002). Of the available procedures that quantify relative use of habitat resources, solving the resource selection function (RSF) is arguably the most popular.

The RSF is operationally defined by characteristics measured on resource units such that its value for a unit is proportional to the probability of that unit being used by an organism (Manly *et al.* 2002). Units being used are items,

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points or shapes in space (e.g. pixels, circles, cubes) and predictors associated with these units may be any number of variables or modifying covariates, both categorical (e.g. vegetation association, species of tree, type of food) and continuous (e.g. elevation, slope, distance to water, depth in a water column). A function can be estimated by sampling units for the presence or absence of organisms (used/unused design) or the use of available resource units by a sample of individuals in a population (use/availability design). A variety of statistical models are available to compute a RSF, the most common of which is the binomial generalized linear model (GLM). Scales of analysis (Johnson 1980) range from the selection of food items, feeding substrates and microhabitat (e.g. Jones & Tonn 2004; Lemaître & Villard 2005; Fore, Dauwalter & Fisher 2007) to the occurrence of species across a landscape (Nielsen *et al.* 2003; Johnson, Seip & Boyce 2004) or seascape (e.g. Goetz *et al.* 2007; Teo, Boustany & Block 2007). Applications of the RSF range from projecting single-species distributions (Boyce & McDonald 1999) to predicting species diversity (Nielsen *et al.* 2003), conservation planning (Johnson *et al.* 2004; Hebblewhite & Merrill 2008; Nielsen *et al.* 2008) and mapping higher trophic interactions (Hebblewhite, Merrill & McDonald 2005).

As the RSF increases in popularity, several issues have arisen concerning its use. These issues can roughly be divided into two categories: those that deal with sampling problems and methods of computing the most accurate RSF for a given circumstance; and those that deal with observed variation in a RSF that is not due to technique or sampling error, but rather ecological phenomena ('ecological dynamics'). The two issues are not mutually exclusive, as some of the refinements in statistical methodology will serve better to incorporate issues arising from ecology; however, it is fair to say that the latter has received much less attention than the former in driving development of the RSF. This is a problem because it is ecological dynamics in a RSF that, if not understood and explicitly modelled, may most compromise its intended purpose: predicting the proportional probability of use of resources by animals to forecast the future distributions of populations and species.

In this review, we are especially concerned about the need to make the RSF dynamic in space and time. Seasonal dynamics in the RSF are easily understood – the RSF changes due to phenology and fluctuations in food availability – and a general approach has been to develop separate models for species at different times of year (e.g. Nielsen *et al.* 2003). But what do we do when at the same time each year, or over different regions for the same species, the RSF is markedly different? For example, Boyce *et al.* (2002) presented a series of RSF models for five species of songbirds in the boreal forest for each of 7 years (1993–1999). Annual differences in the RSF for each species are striking and in many cases significantly different [table 2 of Boyce *et al.* (2002)]. Annual models also deviated significantly from their respective multi-annual mean (computed by pooling observations across years). Observing dynamics in a RSF – obtaining substantially different functions at different times and/or places for the same species – informs us that the underlying ecological processes of resource selection also vary.

Concern over lack of ecological theory behind operational application of the RSF is not new. Boyce & McDonald (1999), in promoting the link between habitat and populations via the RSF, noted that lack of theory in habitat ecology was an inherent result of the complexity of how animals use habitat, which is a: 'multi-faceted process requiring simultaneous consideration of several variables'. We argue that modelling the use of habitat by animals should carefully consider those variables important in defining the realized niche of a species. In this sense, we echo authors such as Hirzel & Le Lay (2008) who draw attention to the weak links we now have and must strengthen between niche theory and habitat models based on RSFs. What determines the realized niche for an organism is clearly more than its need for a multivariate suite of available resources modified by abiotic resource covariates. We know that the size and shape of the realized niche, and thus patterns of resource selection, depend on a multitude of factors other than resource availability, including critical processes, such as competition and predation, mutualism and parasitism (Hobbs & Hanley 1990; Garshelis 2000; Hirzel & Le Lay 2008). How processes such as these can be incorporated into existing methods used to estimate RSFs will go a long ways towards marrying what we know to be important to ecology into our assessment of how species use available resources.

Our goal is to draw attention to those factors underlying ecological dynamics in the RSF, and highlight avenues whereby factors might better be incorporated into models. We generally avoid revisiting problems discussed at length in previous reviews, including the importance of scale on the RSF (Boyce 2006) and most issues regarding the computation of a RSF (e.g. Boyce & McDonald 1999; Boyce *et al.* 2002; Manly *et al.* 2002; Keating & Cherry 2004; Johnson *et al.* 2006; Lele & Keim 2006; Aarts *et al.* 2008; Forester, Im & Rathouz 2009) and other related techniques for evaluating resource selection and species distribution. We do, however, draw attention to the often ignored but in our view critical role of competition on resource use – especially density-dependent habitat selection – and its implications for the RSF. Despite decades of work on density-dependent habitat selection (reviews in Rosenzweig 1981, 1991; Morris 2003), very rarely is this considered (in fact, mentioned) when we estimate functions and project population distributions on a landscape. We further discuss the importance of predation risk on the selection functions of prey (e.g. Mao *et al.* 2005), which can also be density dependent. Finally, we outline instances where selection patterns of a consumer are a function of spatial and temporal changes in resource availability [e.g. functional responses in habitat selection (Mysterud & Ims 1998)]. Understanding how these processes contribute to variation in a RSF is key to making our models of resource selection more robust. In the end, it may also help us to increase our understanding of the relative importance of different ecological interactions on the distribution and abundance of species.

## Definitions and primer on the RSF

Part of the lack of ecological theory in RSFs may be because of different terminology used by theorists interested in explaining ecological dynamics over time and space with respect to habitat, and empiricists trying to quantify habitat selection for populations or species. Empirical applications of the term generally refer to habitat as the suite of abiotic and biotic resources that permit occupancy and reproduction (Hall, Krausman & Morrison 1997). However, studies of the theoretical basis of habitat selection can be more strict in defining habitat. For example, most work involving ideal-free distribution (IFD) (Fretwell & Lucas 1969) or related models identify habitat following Morris (2003): 'a spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets'. Differences in how the term is applied thus appears to be largely a question of grain of study. A coarse-grained approach is usual for theory-based research on habitat selection (e.g. where individuals are free to occupy discrete habitats A, B or C), whereas a fine grained, multivariate approach is the norm for empiricists interested in quantifying habitat selection (e.g. where use or occupancy of a site is defined by a multivariate set of continuous and categorical resources or resource covariates). The latter applies to the RSF; however, as we point out here many of the processes identified by theorists using a coarse-grained definition of habitat also apply to resource selection measured using an RSF.

In this review, we use 'RSF' for convenience as a single term devoted to functions that may or may not also be able to provide true probabilities of use, as does the resource selection probability function, or 'RSPF' (e.g. in the case of used/unused designs and following advancements by authors such as Lele & Keim 2006). We present neither a defence nor attack of the methods used for estimation and inference of the RSF or RSPF; there are numerous papers on this topic (e.g. Boyce & McDonald 1999; Boyce *et al.* 2002; Manly *et al.* 2002; Boyce 2006; Johnson *et al.* 2006; Lele & Keim 2006; Aarts *et al.* 2008; Lele 2009). Recognizing this, but also hoping to assist readers that are as yet unfamiliar with the literature on RSF modelling, what follows is a brief summary of the most common methods and recent developments in computing a RSF.

There are two basic designs for developing a RSF: those based on the discrete classification of all resource units (i.e. presence/absence or used/unused design) and those based on sampling resource units that are used relative to a sample of those that are available (i.e. use/availability design). In the first, a GLM model may be employed to estimate model coefficients including the exponential, logit, probit and log–log link functions in logistic models (Manly *et al.* 2002). In the use/availability design, where not all resource units in the study area are sampled by researchers for occupancy or use, it is common to compute a RSF using logistic regression by assuming an exponential function:

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k) \qquad \text{eqn 1}$$

with resource (predictor) variables denoted $x_k$ and model coefficients $\beta_k$ (the intercept $\beta_0$ is often dropped; see Manly *et al.* 2002:100). In all cases, we are estimating a function that is predicted by a set of variables which may take on additive and higher-order terms; however, it is rare for all terms initially included in the computation of a RSF to be retained in the final model used for inference (i.e. we test multiple hypotheses as to the structure of a RSF).

Recent advancements in the RSF amenable to addressing factors underlying ecological dynamics acknowledge differences between individuals and/or groups. Two strategies currently stand out, although we acknowledge that this area of research is rapidly developing. The first, which relies on matched case–control designs for conditional logistic regression (Boyce *et al.* 2003; Craiu, Duchesne & Fortin 2008; Fortin *et al.* 2009), may prove useful for addressing situations where different components of a population are subjected to different environmental conditions while selecting resources. Here, each observed location of use (scored 1) is linked to a set of random locations (scored 0) where an individual or group could have been at that time, and the decision to use a given location becomes contingent on local alternatives which may differ from place to place. Habitat characteristics at observed locations are compared to the characteristics at random locations while accounting for non-independence between pairs of random and observed locations. This comparison can be achieved with conditional logistic regression (mixed or fixed effects models; Fortin *et al.* 2009).

The second strategy accommodates individual or group differences in sample size and behaviour by incorporating random effects into a RSF model. The Bayesian random-effects model of Thomas, Johnson & Griffith (2006) and random-effects designs for the logit-link GLM (Gillies *et al.* 2006; Hebblewhite & Merrill 2008; Koper & Manseau 2009) are examples. The random-effects GLM (generalized linear mixed model or GLMM) allows researchers to estimate conditional (individual or group) and marginal (population) responses to resource selection [see also Thomas *et al.* (2006), and for marginal estimates the generalized estimating equation framework of Craiu *et al.* (2008) and Koper & Manseau (2009)]. The RSF may be computed with random intercepts to account for unbalanced sampling among individuals and spatial autocorrelation, and random coefficients to account for unique differences in individual or group responses to resource use and availability (Gillies *et al.* 2006; Hebblewhite & Merrill 2008). A RSF with a random intercept and random coefficient extend eqn 1 to the form:

$$g(x) = \beta_0 + \beta_1 x_{1ij} + \cdots + \beta_k x_{kij} + \gamma_{kj} x_{kj} + \gamma_{0j} \qquad \text{eqn 2}$$

where $x_k$ are resource covariates with fixed regression coefficients $\beta_k$, $\beta_0$ is the mean intercept, $\gamma_{0j}$ is the random intercept, and $\gamma_{kj}$ is the random coefficient of covariate $x_k$ for group $j$. Hebblewhite & Merrill (2008) recently demonstrated significant advantages to modelling the RSF for wolves [*Canis lupus* (Linnaeus)] using a mixed model: models without a random

intercept were thousands of times less likely to be the best model. The incorporation of random effects into a RSF is an active area of research, and the best approach is still debated. For example, as Koper & Manseau (2009) point out GLMMs are analytically complex (Fitzmaurice, Laird & Ware 2004: 326) and this may inhibit convergence; further, hypothesis tests in GLMMs are highly sensitive to model and correlation structure misspecification (Overall & Tonidandel 2004), when model-based standard errors are used. Nonetheless, obtaining random coefficients, and other methods such as matched case–control regression models, may prove useful for addressing many of the ecological processes that might modify a RSF. We discuss these applications in more detail below, after first introducing those factors that are likely to underlie ecological dynamics in a RSF. We begin with density.

## Density-dependent habitat selection

Most studies do not directly account for the strong influence that density-dependent habitat selection can have on a RSF, nor the implications to forecasting distribution on a dynamic landscape. There are some exceptions, e.g. Boyce *et al.* (2002) invoke the potential for changes in abundance and shifts in distribution of territorial songbirds of the boreal forest to explain why their multiannual, mean RSF poorly predicted some annual functions. And recently, Mobæk *et al.* (2009) included density explicitly in their RSF models. However, acknowledging effects of competition on the RSF remains rare. This is likely because most studies are conducted at one density and/or during a single time step. This limits the development of a general theory of habitat selection for a species more than anything, not necessarily the lack of theory. Nonetheless, we contend that for almost all cases present in the literature, density-dependent habitat selection is not likely to be trivial to our overall understanding of how species use habitat. Our reasoning is best communicated by reacquainting readers with some theory on density-dependent habitat selection (Fretwell & Lucas 1969; reviews in Rosenzweig 1981, 1991; Morris 2003).

First, visualize a simplified landscape composed of three equal-sized areas of differing food productivity based on physical or floristic features. For this example, then, we are presenting a view of habitat in a relatively coarse grain, and greatly simplified from the multivariate nature of habitat that is more common in the RSF literature. The decomposition of nine vegetation types into three classes of productivity by Mobæk *et al.* (2009) for Dala sheep provides an analogy. We do not necessarily recommend this form of analysis, rather we use it to simplify our example. Assume that only two of these classes of productivity are occupied by the species of interest [the third is a black-hole sink with negative population growth at all densities (Holt & Gaines 1992)]. For example, we may have one class that is considered to be highly productive, the other of moderate productivity, and another that is always a sink. Now consider the case whereby an organism is selecting a site in a class of productivity that com-

pletely contains its movements during some period of time in which it is meaningful to measure fitness (e.g. a breeding site or range).

We also imagine that animals can occupy this landscape according to either an IFD or ideal-despotic (IDD) distribution (Fretwell & Lucas 1969). In the ideal-free case, individuals occupy productivity classes in a way that equalizes mean fitness between the classes. This strategy emerges when individuals can recognize that classes themselves are different, but nevertheless occupy acceptable sites within them at random. In our simple example, then, habitat choice and density-dependent selection thus occurs at the scale of the productivity class; we discuss incorporation of density dependence into finer-scale RSF models later in this section.

To build a simplistic but density-dependent RSF from this landscape we collect a large sample representative of all sites, and record whether or not each site is occupied (in this case we would in fact be computing a RSPF). Then, we repeat our assessment of presence and absence at different population sizes. We use logistic regression to calculate the probability that any given site is occupied depending on the two main effects [(i) productivity class; (ii) population density], and the interaction between them. What patterns will emerge under different scenarios of habitat selection and density dependence?

Consider the ideal-free case where fitness is identical at low density and declines linearly with increasing density (Fig. 1a, e.g. $[1/N][dN/dt]$ as in the assumptions of classic models of logistic population growth). Preference for a productivity class is revealed by plotting the system's habitat isodar, the set of joint densities in the two classes such that an individual's expected fitness is the same in each (Morris 1987, 1988). The ratio of densities at any point along the isodar corresponds to the relative abundance of individuals in the two productivity classes. In this example, the linear isodar passes through the origin and the proportional occupation of each class is constant at all population sizes (perfect habitat matching, Pulliam & Caraco 1984; Recer *et al.* 1987; Morris 2003). The distribution of randomly used sites by the ideal-free selector thus also will be constant at all population sizes. The RSPF will include only productivity class (PROD) and we would conclude, correctly, that density has no effect on resource selection.

$$w * (x) = \frac{\exp(\beta_0 + \beta_1 \text{PROD})}{1 + \exp(\beta_0 + \beta_1 \text{PROD})} \qquad \text{eqn 3}$$

Repeat this mental simulation by assuming that the fitness functions converge on one another as in Fig. 1b. The isodar informs us that resource selection depends on density. Sites in productivity class B only are occupied at low population size. As the population grows, individuals also occupy productivity class A, and do so with increased frequency as population size increases. The proportion of individuals in each is different at different population sizes, as is the number of occupied sites. The probability of occupying a site within a class will vary with density (the equation will include the main effect DENSITY):
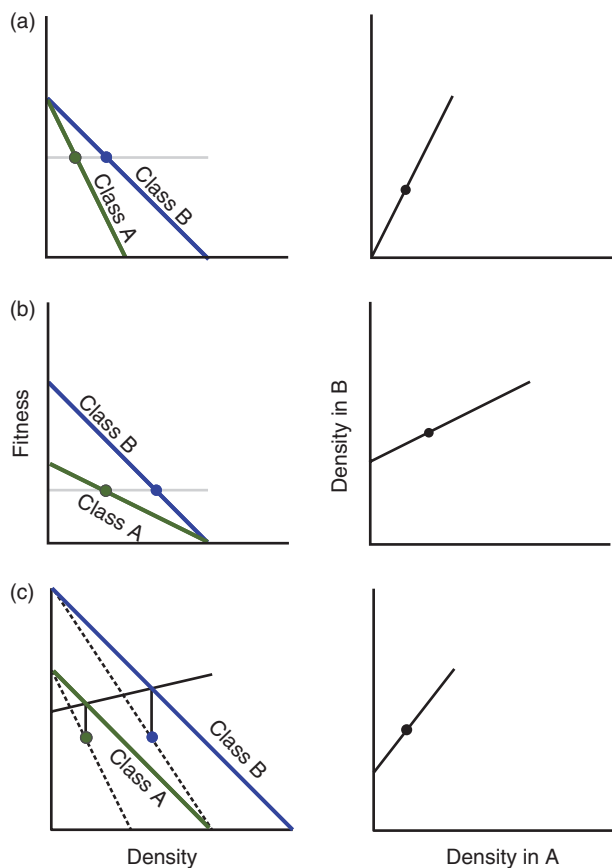
**Fig. 1.** Relationships between fitness and density for two regions of different productivity class under different scenarios of ideal habitat selection. Left-hand panels illustrate density dependence in fitness, right-hand panels illustrate the system's isodar. (a) Ideal-free habitat selection for diverging fitness functions. (b) Ideal-free habitat selection for converging fitness functions. (c) Ideal-despotic habitat selection where territorial individuals depress the expected fitness of individuals in each habitat. Dots correspond with examples of density expected under the different scenarios. Expected fitness (dotted lines) is equalized in panels a and b, but not in panel c (intersections with vertical lines yield higher mean fitness in productivity class B than in productivity class A).

$$w * (x) = \frac{\exp(\beta_0 + \beta_1 \text{PROD} + \beta_2 \text{DENSITY})}{1 + \exp(\beta_0 + \beta_1 \text{PROD} + \beta_2 \text{DENSITY})} \quad \text{eqn 4}$$

The main effects will be insufficient predictors of a RSPF under IDD, whereby individuals choose sites that yield maximum fitness within classes either by first selecting one over the other and then competing for the best site within it, or searching for the best available site in the landscape. Mean fitness is greater in one productivity class than in the other, and thus the quality of occupied sites will also vary with density [the interaction term will also contribute to the RSPF (additive effects are included but not shown); Fig. 1c]:

$$w * (x) = \frac{\exp(\beta_0 + \beta_1 \text{PROD} \times \beta_2 \text{DENSITY})}{1 + \exp(\beta_0 + \beta_1 \text{PROD} \times \beta_2 \text{DENSITY})} \quad \text{eqn 5}$$

Here, selectivity depends on the value of individual sites, the proportion of occupied sites varies with density, and that

proportion depends on the distribution of site qualities in each productivity class (also see Fortin, Morris & McLoughlin 2008). Both distributions can produce curved isodars described by higher-order (e.g. quadratic) effects (Morris 2003). So it will oftentimes be desirable to include higher-order density dependence and its interactions in the list of candidate variables.

The main points are these. First, any RSF that fails to include density represents a statistical snapshot of resource selection that may often be different at different population sizes. Second, different forms of habitat selection yield different density-dependent effects in a RSF, and thus provide a theoretical cornerstone on which to build our understanding of the interaction between resource selection and population dynamics.

The examples above serve to highlight the potential role for density effects on a RSF (or RSPF). Density-dependent habitat selection can be addressed in the context of a multi-variable RSF in different ways. One possibility may be to acknowledge density differences and build separate RSF models for each level of density encountered. Relating model coefficients ($\beta_i$) to levels of population density at the time of data collection may then provide us with some insight into which variables of a RSF are responding to density. A more direct inclusion of density effects on a RSF, however, would be to build the model using a GLMM (eqn 2) whereby observations are grouped according to density at the time of data collection (e.g. population size at one time vs. another). Here, we would be computing conditional estimates of the relative predicted probability of use of some resource variable as, e.g. a logit function, for sampled individuals that are grouped by a common exposure to population density. Interactions between the slope of conditional estimates and density would be revealed by a plot of log odds vs. a variable's gradient (Fig. 2). Those conditional estimates that are modified by density grouping would indicate a resource for which use is density dependent. Conditional, rather than marginal population estimates, could then be used to project distribution on a landscape (Boyce & McDonald 1999) under conditions of varying densities. Mobæk *et al.* (2009) presents an alternate but related approach to including density and density × habitat interactions in a RSF based on a GLMM.

The approaches above may be reasonable if we can assume that all sites in the landscape of interest are equally accessible to organisms. However, this is not always the case and indiscriminately incorporating densities into a RSF without attention to the scale of resource selection may easily mislead our interpretation of density-dependent resource use. Studies at finer scales that fail to incorporate density are bound to yield biased estimates of resource selection whenever density alters the proportional use of resources. Here, rather than quantifying mean population density we will need to collect detailed data on local density (e.g. proximity of individuals to one another; Coulson *et al.* 1997; McLoughlin *et al.* 2006; McLoughlin, Coulson & Clutton-Brock 2008) or group size. A matched case–control design then may be used to integrate local density of sampled animals or group size directly into a
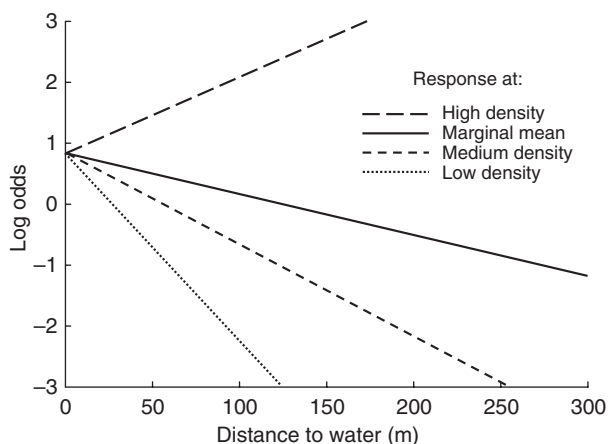
**Fig. 2.** Conditional estimates of the relative predicted probability of use for a hypothetical species and resource selection function (RSF) obtained from a random-effects generalized linear model using a logit link. Differences in random coefficients depend on the population density (or, if interested in predation risk, predator density) during which time samples were drawn to compute a RSF (each grouping is represented by a different line). In the case of density-dependent habitat selection, use of the resource 'distance to water' occurs in a despotic fashion. Coefficients increase (and become positive) as density increases (odds of occurrence on a landscape will be relatively high near water at low population sizes, but this changes as population size increases). The marginal estimate identifies the population mean predicted response. If we consider a species response to predator density, animals will be relatively avoiding areas close to water when predators are abundant, and vice versa. For simplicity, we assume a common *y*-intercept (i.e. there will always be a base number of consumers at the water source, although the relative distribution of consumers relative to the water source will change with density). Random intercepts and coefficients imply a functional change with respect to resource selection (Fig. 3). See Gillies *et al.* (2006) for another example of a plot of log odds vs. a resource variable for a conditional estimate of a random-effects RSF.

RSF (Fortin *et al.* 2009). Group size associated with focal individuals becomes an explanatory variable that takes a unique value for an observed location and its associated random locations. Group size thus remains constant within each choice set of the regression, but group size can change over time (between choice sets). Assuming that we are interested in the relative probability of use of *k* independent variables $(x_1,…,x_k)$, as well as in the potential influence of group size ($G$) on the selection for independent variable $x_1$, the group size-dependent RSF then takes the structure:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k + \beta_{k+1} x_1 G) \qquad \text{eqn 6}$$

where $\beta_{k+1}$ is the selection coefficient associated with the interaction term $x_1 G$. Because each observed location and its associated random locations are assigned the same group size, $G$ cannot appear in the model as a main effect, but rather as an interaction term whose interpretation is that the link between animal distribution and habitat attribute $x_1$ changes with group size.

The question of how best to incorporate density into a RSF will depend on the scale and intent of the research, as well as assumptions on resource use. Nonetheless, our main point is that density is likely to affect the RSF through space

and time, and that there are techniques available (including isodars) to model density effects in a RSF. Predicting occurrence on a landscape from a RSF without accommodating confounding effects of density, although perhaps presenting an accurate snapshot of probability of use during the time of data collection, may lead to errors in our interpretation of the importance of habitat resources at different population sizes.

## Predation

Predation risk, which may also depend on density, influences a wide range of behaviours related to the acquisition of resources including food, mates and shelter (review in Lima & Dill 1990); hence, we should expect that changes in predator abundances and behaviour will contribute to dynamics in any RSF model for prey. For example, Mao *et al.* (2005) compared seasonal functions of elk (*Cervus elaphus* [Linnaeus]) in Yellowstone National Park (USA) from 1985 to 1990 (without wolves) with those from 2000 to 2002 (after wolves were reintroduced). They demonstrated a shift in summer resource selection such that elk appeared to now select habitats that enabled them to avoid wolves, results supported by Creel *et al.* (2005), Fortin *et al.* (2005), and Kauffman *et al.* (2007). The behavioural basis for these shifts is likely due to initially naïve prey learning to associate what were once 'safe' habitat components with higher abundances of predators (Kauffman *et al.* 2007) and conflicts between vigilance and time spent foraging (Fortin *et al.* 2004). Assuming resource selection patterns will eventually reflect fitness, shifts in a RSF should occur whenever the costs and benefits of habitat selection are modified by predators. Significant impacts of predation on shaping long-term patterns in resource selection are further supported by results of McLoughlin, Dunford & Boutin (2005). McLoughlin *et al.* demonstrated clear consequences (higher risk of predation) for woodland caribou [*Rangifer tarandus caribou* (Banfield)] that deviated from the population mean response of selecting for peatlands in the boreal forest, where wolves exist at lower density compared to elsewhere on the landscape (i.e. in uplands where alternate prey occur at higher densities supporting higher numbers of wolves and hence greater predation risk).

Effects of competing species have been made explicit in isodar models of habitat selection (Morris *et al.* 2000); however, incorporating interactions like predation proves to be more challenging. Different approaches to modelling predation can lead to different effects on habitat isodars (Morris 2005), and correctly defining predation risk from a mechanistic basis may require more than simple measures of predator density (Hebblewhite *et al.* 2005). Techniques to acknowledge predation risk in a RSF could involve modelling resource use according to exposure or risk similar to what we suggest for effects of conspecific density (e.g. using a GLMM). There may be coefficient changes (Fig. 2) but also functional changes (Fig. 3) if predation limits the perceived availability of resources (e.g. if areas with high availability of some resource loses value because it proportionately attracts
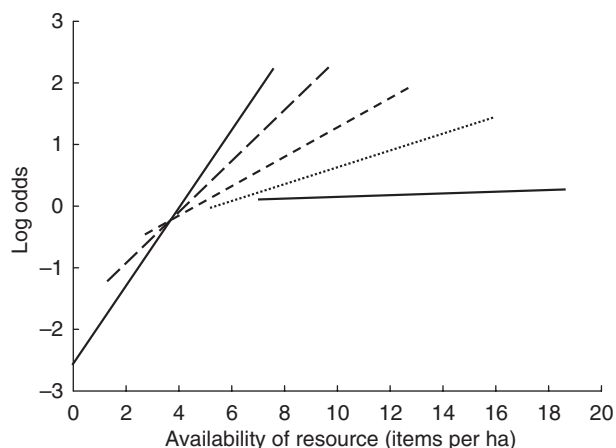
**Fig. 3.** Functional response in habitat selection for different individuals or groups subjected to varying amounts of resource availability (different lines, increases in availability occurs from left to right). For a given function (as might be obtained from a generalized linear mixed model logit-link RSF), the log odds predicting probability of use of the resource declines as availability increases. Resource availability may be a function of space or time, but also a perceived quantity if consumers avoid competitors or predators while selecting resources.

more predators (Hammond, Luttbeg & Sih 2007). Functional changes in predation due to habitat attributes, e.g. if landscape attributes render prey more or less susceptible to predation (Hebblewhite *et al*. 2005), may interact to modify functional responses to habitat in the presence of increasing predator density.

Including concurrent effects of competition and predation in predicting a RSF is interesting but complicated because of suspected interactions between density and predation risk and predation-sensitive foraging (Sinclair & Arcese 1995). One of the benefits of the GLMM for computing RSFs is that random effects can accommodate two or more levels, including, perhaps, samples divided according to level of conspecific density and level of predator density. The data required to develop such models will be beyond the sampling efforts of most research programmes; however, if it can be achieved, including competing factors in an analysis may tell us something about the relative importance of different ecological interactions. Further complications are bound to arise with inclusion of the effects of pathogens and parasites. For example, parasite-mediated changes in behaviour (Thomas, Adamo & Moore 2005) may also account for dynamics in a RSF.

## Dynamics in resource availability

That the RSF can fluctuate on a seasonal basis due to different requirements of species at different times of the year and phenology is long understood. To take this into account, we typically separate RSF models for different seasons or periods of annual food availability (e.g. Nielsen *et al*. 2003). What is perhaps less understood – and certainly less modelled – is the question of how RSF models might change with underlying shifts in habitat, e.g. due to climate change, ecological suc-

cession or anthropogenic disturbance. Shifts in the abundance or availability of resources may be directional, but may also entail increases in variability without changes in mean values; both are likely to affect the underlying basis of a RSF. If these changes occur in time steps during the course of data collection (e.g. if RSF models are built with data collected over several years), matched case–control RSF models are well suited for this type of analysis. Further, it should be possible to explicitly incorporate habitat change by adding a time or space effect to the RSF in a computation based on a GLMM or Bayesian discrete-choice model. Models may be arranged hierarchically, if we can also quantify group changes with respect to other potentially important and interacting factors like density and predation. If the source of change in habitat is known, we might then be able to improve on predicting effects of habitat dynamics on species occurrence.

Much of the work with RSF models is used to assist in the conservation and management of species (e.g. Johnson *et al*. 2004). Functions can include variables associated with threats, such as distance to edge or anthropogenic disturbance (e.g. Hebblewhite & Merrill 2008). Researchers often assume that if these variables are shown to be avoided in the RSF, they may be detrimental to the species or population. However, this finding may not lead to accurate projections of probability of occurrence if the variables themselves are progressively increasing or decreasing in availability on the landscape, or if animals can habituate to disturbances. For example, if populations are declining individuals may, on average, show increased use of more productive components of habitat (in response to reduced competition); individuals may learn to avoid disturbances or become habituated to them; and if resource availability changes through time, we may see modifications in how resources are used. What we are interested in here is the 'functional response' to resource selection (*sensu* Mysterud & Ims 1998; Fig. 3).

Theoretical work on functional responses in the context of predator–prey dynamics has matured in the literature (Neal 2004); however, only recently have we begun to contemplate how changes in availability of resources might affect preferences of consumers for habitat (Mysterud & Ims 1998; Mauritzen *et al*. 2003; Osko *et al*. 2004; Godvik *et al*. 2009). If animals require a particular resource, they may demonstrate a preference (relative use greater than expected from random) for it when it is rare on the landscape; however, when it is common, use of that resource may not increase proportionately with availability, and thus it would appear as though it is less preferred or avoided (Garshelis 2000). We can also envision functional responses to avoided habitat components (Hebblewhite & Merrill 2008). For example, if a disturbance on the landscape (e.g. a road or human settlement) is rare, it may be strongly avoided when first encountered; however, as that disturbance becomes more common, through habituation and potential rewards (e.g. refuge from predators, attraction to refuse) the variable may be proportionately less avoided or selected.

Explicitly incorporating the functional response into a RSF may be addressed in two ways. First, some authors have

included interaction terms of availability with resource covariates in the RSF (e.g. Craiu *et al.* 2008; Godvik *et al.* 2009). Here, the effect of selection for a resource is modified by its availability on the landscape. Second, controlling for functional responses may also be accomplished using a GLMM (Fig. 3), which appears amenable for the purpose (Gillies *et al.* 2006; Hebblewhite & Merrill 2008). Functional responses based on individual differences in spatial availability of resources can be accommodated, as well as responses based on higher-order groupings such as packs or herds, or even populations through time. We note, however, limitations to the GLMM approach in this context. These limitations include inability of the GLMM to currently include more than one or two random coefficients as functional responses because of computational limitations due to model complexity; and inability to model functional responses explicitly in one unified model, but instead in a two-step process where RSFs are modelled and then coefficients are regressed against the scale-specific measure of resource availability.

## Conclusions

The RSF is widely used to estimate the proportional probability of selection of resource units by populations and project their occurrence on a landscape. Processes that produce patterns, however, are seldom included in our descriptions. We believe that there is a need for us to reacquaint ourselves with ecological theory when interpreting RSF models; in particular, we need to realize that irrespective of resource availability, patterns may be a result of competition or predation (and other interactions not specifically addressed in this paper, including parasitism and mutualism), or may change with dynamics in resource availability in space and time. There is a call for long-term RSF studies linked to density and ecological dynamics, and how best to incorporate governing factors in a RSF is currently in a state of development. We see promise in the inclusion of random as well as fixed effects in resource selection models, and matched case–control logistic regression. Choice of technique and study design also will depend on the scale and intent of the research, and assumptions about resource selection. When the RSF changes with density, interacting species, and resource availability, its application for conservation and management (e.g. extrapolating distribution; Boyce & McDonald 1999) may be limited unless these factors are understood and accommodated. In building functions that explicitly incorporate ecological interactions likely to affect the RSF, we will further our understanding of the relative importance of ecological interactions on the distribution and abundance of species.

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