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*Review*

# The interpretation of habitat preference metrics under use–availability designs

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Models of habitat preference are widely used to quantify animal–habitat relationships, to describe and predict differential space use by animals, and to identify habitat that is important to an animal (i.e. that is assumed to influence fitness). Quantifying habitat preference involves the statistical comparison of samples of habitat use and availability. Preference is therefore contingent upon both of these samples. The inferences that can be made from use versus availability designs are influenced by subjectivity in defining what is available to the animal, the problem of quantifying the accessibility of available resources and the framework in which preference is modelled. Here, we describe these issues, document the conditional nature of preference and establish the limits of inferences that can be drawn from these analyses. We argue that preference is not interpretable as reflecting the intrinsic behavioural motivations of the animal, that estimates of preference are not directly comparable among different samples of availability and that preference is not necessarily correlated with the value of habitat to the animal. We also suggest that preference is context-dependent and that functional responses in preference resulting from changing availability are expected. We conclude by describing advances in analytical methods that begin to resolve these issues.

**Keywords:** habitat preference; resource selection; movement; telemetry; functional response

## 1. INTRODUCTION

Animals are subject to competing demands and motivations, such as the needs to acquire food, find mates, rear offspring, defend limited resources and avoid predators. Most of the habitat (defined below) that influences these objectives is distributed heterogeneously in space. Thus, the process of balancing these trade-offs is often mediated by animals adjusting their location in space (Hebblewhite & Merrill 2009). By examining the dynamics of how animals use heterogeneously distributed habitat, we can begin to untangle the complex, often competing demands that influence animal behaviour and, ultimately, fitness (Rosenzweig 1991; Morris 2003; Gaillard *et al.* 2010).

While descriptive models of space use based solely on spatial coordinates (e.g. home ranges) can be useful in conservation and management applications (Kie *et al.* 2010), our ultimate goal as ecologists is to understand the processes that give rise to these patterns. Difficult ecological problems, such as understanding how animals manage trade-offs and predicting how animals might respond to habitat loss and climate change, require an understanding of the processes that govern movement and distribution. If habitat characteristics at animal locations are also described, we can model distribution and abundance based on a statistical comparison of samples of used and available habitat (Boyce & McDonald 1999; Manly *et al.* 2002; Calenge *et al.* 2005; Lele & Keim 2006; Johnson & Seip 2008). This comparison is considered important because it allows us to identify habitat that is used disproportionately to its availability (i.e. in a non-random manner; Johnson 1980). In quantifying habitat preference (defined below),

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we might hope to identify habitat that is particularly important to an animal, or is avoided by an animal, and hence infer something about the way that animal perceives and uses its environment. More fundamentally, we might use preference as a tool to understand how environment, behaviour and fitness are linked (e.g. McLoughlin *et al.* 2006, 2007, 2008; Gaillard *et al.* 2010).

Preference has been applied to a broad range of ecological questions and applications, including: drivers of species geographical range (Aldridge *et al.* 2008); home-range placement (Mladenoff *et al.* 1995; Boyce *et al.* 2003; Nielsen *et al.* 2006; Aldridge & Boyce 2007) and within-home-range space use (Roever *et al.* 2008); mechanistic movement models (Fortin *et al.* 2005) and improved corridor design (Chetkiewicz *et al.* 2006); population size (Allen *et al.* 2008) and viability (Aldridge & Boyce 2007; Nielsen *et al.* 2008); and spatially mediated intra- and inter-specific interactions (Hebblewhite *et al.* 2005; Fortin *et al.* 2009). Quantifying and interpreting preference, however, is not straightforward. The estimate of preference is contingent upon the samples of both used and available habitat, and is therefore sensitive to factors that affect either of these samples. Some of these factors are the biological processes that interest us (e.g. animal behaviour that drives habitat use), but some are methodological issues relating to sampling design and efficacy, such as subjectivity in defining availability, bias and error in animal location data (Frair *et al.* 2010), and correlated and autocorrelated data (Fieberg *et al.* 2010). These methodological issues can confound our biological inferences and reduce the predictive value of habitat preference models. As noted by Johnson (1980) and Aarts *et al.* (2008), the importance of these issues is not widely appreciated.

Here, we review the concepts associated with use versus availability analyses, discuss the impact of factors that influence the samples of use and availability, and discuss the appropriate scope of inferences that can be drawn from these study designs. We provide an empirical and analytical demonstration of how the estimate of preference is contingent upon the sample of availability, and discuss progress in evaluating preference in terms of functional responses (i.e. how preference changes as a function of availability). Although these comments apply generally to use versus availability designs regardless of the technology used to collect location data, we end by discussing the potential for modern technology, such as global positioning system (GPS) telemetry devices, to resolve the issues we present. This technology improves our ability to collect frequent location data, which may allow us to detect weaker effects and facilitate the development of more mechanistic models of movement and habitat use. However, we show that simply acquiring more data, or more accurate data, does not fundamentally alter many of the difficulties in understanding animal–habitat relationships (Cagnacci *et al.* 2010; Hebblewhite & Haydon 2010). In particular, we argue that to begin to address the fundamental question of why animals use habitat, it is essential to quantify how habitat is used and what life-history requirements are met by the use of habitat.

## 2. DEFINITIONS: USE, SELECTION, AVAILABILITY AND PREFERENCE

*Habitats* can be defined as regions in environmental space (Aarts *et al.* 2008; Hirzel & Lay 2008) that are composed of multiple dimensions, each representing a biotic or abiotic environmental variable; that is, any component or characteristic of the environment related directly (e.g. forage biomass and quality) or indirectly (e.g. elevation) to the use of a location by the animal. Environmental variables can be dynamic or static (e.g. predator density and slope, respectively) and may be positively or negatively associated with use. The distribution of habitats in geographical space can be complex: regions of environmental space may have a patchy distribution over landscapes (Hirzel & Lay 2008). Whereas all points in geographical space can be characterized in environmental space, the opposite is not true as some combinations of environmental variables will not exist in nature (Aarts *et al.* 2008). Habitat *use* is the proportion of their time that animals spend in a particular habitat. *Selection* of habitat is the process by which an animal actually chooses habitat (Johnson 1980). Use is considered selective if habitat is used disproportionately compared with its *availability*, the latter being the amount of that habitat accessible to the animal. In controlled environments, *preference* is the likelihood of an animal selecting a given item when offered alternative choices on an equal basis (Johnson 1980). In field studies, however, where the availability of habitat is variable, habitat preference is the use of habitat relative to its availability in the environment and is conditional on the availability of all habitat to the animal (Aarts *et al.* 2008). Although selection and preference are sometimes used synonymously, in this paper selection refers to the behavioural process of choosing habitat, whereas preference reflects an attempt to quantify selection given a particular sample of availability. Preference is a statistical description of habitat use relative to a particular sample of availability, but it may not necessarily reflect the underlying selection process.

## 3. ISSUES PERTAINING TO THE SAMPLE OF USE

If we hypothesize that patterns of space use result from behavioural decisions animals make to meet life-history requirements and trade-offs, then behaviour is the mechanism by which they manage their fitness in a dynamic and heterogeneous environment. Although spatial location is one of the properties resulting from this behavioural process, sampling space use independently of the behavioural process limits our ability to make inferences about that process, and therefore to develop a mechanistic understanding of animal movement and distribution.

A common assumption is that the presence of an animal at a location implies its selection by the animal. However, this interpretation of occupancy as selection fails to differentiate between locations that

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are actively selected by the animal and contribute to the fulfilment of a life-history requirement (e.g. foraging patches) versus locations that are used incidentally, for instance occupied in transit between selected patches or during exploration. While interpreting occupancy as selection might facilitate a model describing differential space use by an animal, if we are interested in selection as a behavioural process, then sampling space use without a behavioural context may be of limited value. Different habitat may be required in order to fulfil different life-history objectives; therefore, preference is likely to be behaviour-specific. Similarly, activity patterns and habitat use can vary widely diurnally and seasonally (Schooley 1994; Ager *et al.* 2003; Jonsen *et al.* 2006; Godvik *et al.* 2009; Owen-Smith *et al.* 2010). Preference is, therefore, likely to be highly dynamic, so quantifying average preference among all behaviours may result in a more phenomenological, less insightful model.

Knowledge of the behaviour of an animal is also essential when quantifying the value of habitat to that animal and, therefore, the contribution of habitat to fitness. The proportion of time an animal spends in a habitat, which can be estimated from location data, is not necessarily an indication of the value of that habitat to an organism. Thus, the usually false assumptions that occupancy indicates selection and that intensity of use is proportional to habitat value have important consequences for how we interpret habitat preference models and what they describe (preference versus occupancy), and these assumptions should be explicitly discussed. Frair *et al.* (2010) also review several methodological issues that can result in bias in the sample of use and analytical approaches to resolving these issues.

## 4. ISSUES PERTAINING TO THE SAMPLE OF AVAILABILITY

Availability can be quantified at a wide range of spatial and temporal scales, and different scales are hypothesized to imply different selection processes. Johnson (1980) suggests that four scales broadly capture the range of behavioural processes that occur: the geographical range of the species, the placement of an individual home range (or the range of a social group in the case of gregarious species) at a landscape scale, habitat use within the home range and fine-scale decisions that occur over short periods of time (such as consumption of individual food items within a foraging patch). The questions being investigated, therefore, determine the spatio-temporal scale at which availability is quantified.

Accessibility, however, is also an important aspect of defining what habitat is available to an animal. Accessibility—the ease with which an individual can reach a point in space—is a complex function of many social, inter-specific and environmental factors that might limit access to habitat in geographical space (Garshelis 2000; Matthiopoulos 2003*b*; Aarts *et al.* 2008). Generally, we are not able to quantify these factors, so the assessment of accessibility is necessarily subjective. While this subjectivity does not prevent us from quantifying preference, the preferences we estimate may not reflect the intrinsic, behavioural selection process of the animal. The assumption that all habitat within a given domain of availability is equally accessible is an important implicit assumption of many habitat preference studies (Aarts *et al.* 2008; Moorcroft & Barnett 2008). The degree to which equal accessibility is a valid assumption will depend on the biology of the animal and the spatial extent over which availability is sampled. One approach to quantifying availability is to use a movement model, which can include many of the factors that may influence accessibility, to weight the availability samples by an estimate of their accessibility by the animal (Hjermann 2000; Matthiopoulos 2003*b*; Aarts *et al.* 2008; Fieberg *et al.* 2010). Remember, however, that different models of accessibility may alter the estimates of preference profoundly.

## 5. THE CONDITIONAL NATURE OF PREFERENCE

We illustrate the conditional nature of preference with a simple example, the purpose of which is to demonstrate how preference can be sensitive to subjective decisions about how available habitat is sampled. We generated 50 hypothetical animal locations in two landscapes that are characterized as either meadow or forest (figure 1*a*,*b*). In each landscape, the relative frequency of use of the two vegetation types is identical: 14 locations occur in forest, and 36 occur in meadow. Although the relative use of forest and meadow might vary in each of the two landscapes for a real animal, we use a constant ratio here because our purpose is to evaluate the effect of different samples of availability on the estimate of preference, given a specific sample of use. Equally, this example could represent use of a resource up to a minimum threshold, which is consistent with a constant ratio of use in the two landscapes.

We sample availability by generating 500 random points at a range of scales, with each scale defined as the area within a specified distance (200 m to 5 km, in 200 m intervals) of any of the use points (figure 1*a*,*b*). Preference was calculated at each scale and at each site independently using logistic regression. The regression coefficients, which are our measures of preference, clearly vary among the sampling scales (figure 1*c*). Note that even though use never changes (the observed sample is constant), the coefficient can vary widely, even changing sign. Preference changes with scale only because the relative availability of the two vegetation types changes across these scales. If we plot the coefficient as a function of the proportion of meadow available at each scale (figure 1*d*) we observe that as availability increases, the coefficient decreases for a given sample of use. This problem applies to a broad range of study designs and modelling frameworks, and limits the inferences that can be made regarding habitat preference.

A variety of models can be applied to habitat preference problems (Manly *et al.* 2002; Keating & Cherry 2004; Lele & Keim 2006). The appropriate model depends primarily on the question being addressed and the sampling design (Manly *et al.* 2002; Keating & Cherry 2004). When the comparison is between used

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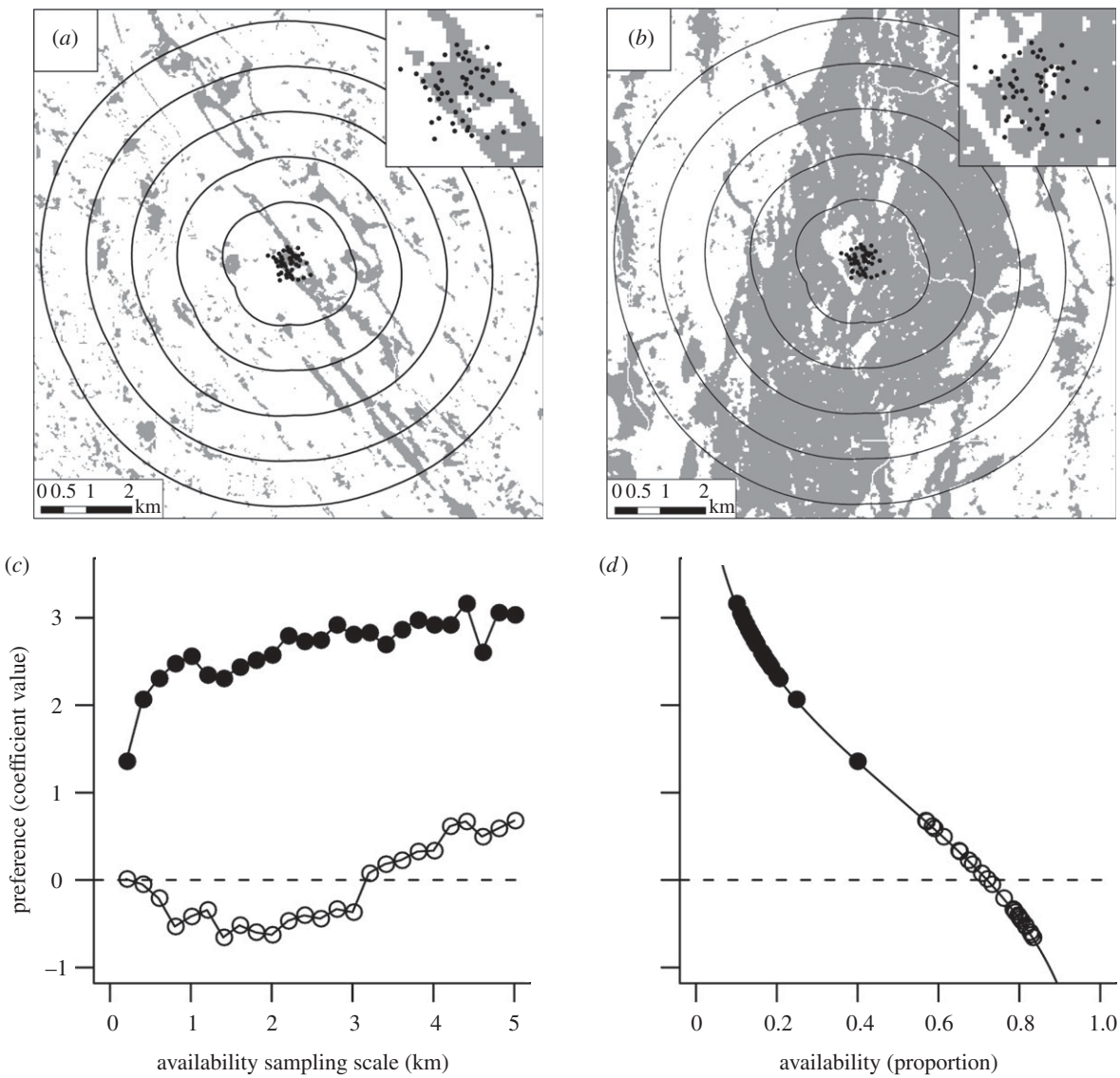


Figure 1. This simulated example illustrates how preference is conditional upon the sample of available habitat. Fifty hypothetical use locations (black dots) were generated in each of two landscapes (*a*,*b*; see insets for magnified view of use locations). The background depicts the distribution of forest (white) and meadow (grey) vegetation types. The scale at which availability was sampled ranged from 200 m to 5 km in 200 m intervals (black lines). For clarity, only every fifth contour is shown, representing scales of 1, 2, 3, 4 and 5 km. Preference for meadow was estimated using logistic regression at each sampling scale. (*c*) The relationship between the regression coefficient for meadow and sampling scale in each landscape (black and white circles correspond to landscapes *a* and *b*, respectively). (*d*) The same coefficients plotted against the proportion of meadow available at each sampling scale. The inverse logit-shaped line is the prediction based on an analytical solution of this problem (see text).

and unused samples, the logistic model can be used to estimate the probability of use, described by Manly *et al.* (2002) as the 'resource selection probability function' (RSPF):

$$h(x) = \frac{\exp(\beta_0 + \beta_1 X_1 + \cdots + \beta_p X_p)}{1 + \exp(\beta_0 + \beta_1 X_1 + \cdots + \beta_p X_p)}, \tag{5.1}$$

where $\beta_0, \ldots, \beta_p$ are constants estimated from the data, and $X_1, \ldots, X_p$ are independent variables that are descriptors of the probability of use of a location (e.g. variables describing habitat). This can also be expressed as

$$\log\left(\frac{h(x)}{1 - h(x)}\right) = \beta_0 + \beta_1 X_1 + \cdots + \beta_p X_p. \tag{5.2}$$

When comparing samples of use to availability (as is often the case with sampling designs based on telemetry data), the sample of availability may contain both used and unused locations, the relative proportions of which are not known (Manly *et al.* 2002). This may have ramifications on the application and interpretation of the logistic model (Keating & Cherry 2004; Johnson *et al.* 2006). In use–availability designs, the exponential model, $w(x) = \exp(\beta_1 X_1 + \cdots + \beta_p X_p)$, is therefore often used to evaluate the relative probability of use (Johnson *et al.* 2006), and is fitted using logistic regression to find the maximum-likelihood values of the model coefficients (Manly *et al.* 2002). Recent analytical advances based on the theory of weighted distributions (Johnson *et al.* 2006; Lele & Keim 2006; Lele 2009) provide a powerful alternative approach to

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fitting RSPFs, not restricted to the logistic and exponential functional forms. We therefore do not advocate the use of the logistic model in general but, because of its simplicity, use it here to demonstrate how model coefficients are sensitive to the sample of availability. The form of the relationship between model coefficients and availability will be different for other modelling frameworks.

In this simple example, we imagine a single categorical covariate ($p = 1$), $X$, with one of two values: zero or one. It is therefore an indicator variable and might represent a distinction between vegetation types, such as forest (/) versus meadow (1). The sample of use in this hypothetical example consists of $N^u$ locations, $n_0^u$ of which are located in vegetation type 0, and $n_1^u$ of which are located in vegetation type 1. The sample of availability consists of $N^a$ locations, $n_0^a$ of which are located in vegetation type 0, and $n_1^a$ of which are located in vegetation type 1. In this simple model, the preference for vegetation types 0 and 1 is the proportion of locations in each of those vegetation types divided by the total number of (used and available) locations in that vegetation type ($n_0^u/(n_0^u + n_0^a)$ and $n_1^u/(n_1^u + n_1^a)$, respectively). Thus, when $X = 0$,

$$\log\left(\frac{n_0^u/(n_0^u + n_0^a)}{1 - n_0^u/(n_0^u + n_0^a)}\right) = \beta_0. \tag{5.3}$$

When $X = 1$,

$$\log\left(\frac{n_1^u/(n_1^u + n_1^a)}{1 - n_1^u/(n_1^u + n_1^a)}\right) = \beta_0 + \beta_1. \tag{5.4}$$

Thus,

$$\beta_1 = \log\left(\frac{n_1^u/(n_1^u + n_1^a)}{1 - n_1^u/(n_1^u + n_1^a)}\right) - \log\left(\frac{n_0^u/(n_0^u + n_0^a)}{1 - n_0^u/(n_0^u + n_0^a)}\right), \tag{5.5}$$

which simplifies to

$$\beta_1 = \log\left(\frac{n_1^u}{n_1^a} \cdot \frac{n_0^a}{n_0^u}\right). \tag{5.6}$$

The availability of vegetation type 1, $\rho_1$, is the number of locations from the availability sample in vegetation type 1 divided by the total number of locations in the availability sample (i.e. $\rho_1 = n_1^a/(n_0^a + n_1^a)$). Therefore,

$$\frac{1 - \rho_1}{\rho_1} = \frac{n_0^a}{n_1^a}. \tag{5.7}$$

The expression that describes how the coefficient representing preference for vegetation type 1, $\beta_1$, changes as a function of availability of vegetation type 1 ($\rho_1$) is therefore

$$\beta_1 = \log\left(\frac{1 - \rho_1}{\rho_1} \cdot \frac{n_1^u}{n_0^u}\right). \tag{5.8}$$

The fraction $n_1^u/n_0^u$ is constant (our sample of use does not change). The relationship between preference and availability is therefore an inverse logit function (figure 1*d*). Note that at the extremes of availability (the covariate is not present at all, or is the only condition available) preference is undefined (plus or minus infinity). Also, for preference to remain constant across all availabilities, the fraction $n_1^u/n_0^u$ must change as a function of availability in inverse proportion to the ratio $(1 - \rho_1)/\rho_1$; that is, relative use must follow a logit-shaped curve for $\beta_1$ to remain constant.

Thus, *for a given sample of use*, we have quantified how the coefficients in the logistic regression model change as a function of availability of habitat, and have shown that the coefficient always decreases as availability increases and that the coefficient can change sign.

## 6. INFERENCE FROM USE VERSUS AVAILABILITY DESIGNS

The aforementioned issues have three important consequences for the inferences that can be made from use versus availability designs. First, the estimates of preference are not directly interpretable as reflecting the intrinsic behavioural motivations of the animal. Positive (or negative) preference for a given habitat implies only that the habitat is used more (or less) frequently than expected by chance, *conditional upon the defined sample of availability*. Even high levels of use of a habitat can be associated with negative coefficients if that habitat is common, and, conversely, low levels of use can be associated with positive coefficients if the habitat is rare. The sign and magnitude of the coefficient cannot be interpreted with respect to the behavioural decision the animal is making. Furthermore, the interpretation of preferences of categorically modelled habitat is even less straightforward. In generalized linear models, for instance, categorical variables are modelled with respect to a reference category. Thus, estimates of preference associated with a categorical variable are conditional upon both the sample of availability and the reference category. Interpretation of these coefficients (preferences) therefore requires care (Osko *et al.* 2004).

The second consequence is that estimates of preference based on different samples of availability (e.g. Design III in Manly *et al.* 2002) are not directly comparable. The sign and magnitude of the estimate of preference is a function of both the sample of use and the sample of availability. This creates an identifiability problem because preference can change as a function of changing use and/or changing availability. If the sample of availability differs between two estimates of preference, it is meaningless to draw inferences based on the difference in preference. Different preferences can arise from the same selection process, and similar preferences can arise from different selection processes.

This consequence has implications for the application of generalized linear mixed-effects models to habitat preference, a modelling framework that can accommodate potential bias arising from unequal sample sizes among individuals, lack of independence in temporally correlated location data, variation in preference among individuals and ecological dynamics (Gillies *et al.* 2006; Hebblewhite & Merrill 2008; Fieberg *et al.* 2009, 2010; McLoughlin *et al.* 2009). While this is an innovative approach, the sampling

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design of available habitat has important ramifications for the interpretation of these models. If the sample of availability is constant among all individuals, then the population-level inferences (e.g. the population mean and variance of a coefficient) and conditional inferences (e.g. the individual-level estimates of preference) can be interpreted as an average measure of preference for the population and individual, respectively, conditional on that sample of availability (but see Fieberg *et al.* 2009). If, however, the sample of availability is different among individuals (e.g. samples drawn from within home ranges), then the population-level inferences are more difficult to interpret because of the aforementioned identifiability problem.

Models of habitat preference that are parameterized in one area may not be transferable to other areas in which availability and landscape configuration is different. Given that preference is conditional on availability, that availability is likely to vary in space and that preference is likely to change as a function of availability, there is little theoretical basis for believing that preferences estimated in one area will be good predictors of preference in others. Suitable model and prediction validation can, however, justify such an extrapolation (Boyce *et al.* 2002; Wiens *et al.* 2008).

The third consequence is that preference is not necessarily correlated with the value of habitat to an animal, and therefore cannot be used to gauge the relative importance of different habitats. A related problem is the interpretation that no preference (indicated by a model coefficient for which the confidence intervals include zero) implies that the animal is not responding to the habitat, or that the habitat is unimportant. This inference is likely to be incorrect. At some range of availabilities, preference is expected to be zero regardless of the importance of the habitat to the animal (figure 1*d*). A coefficient of zero may indicate habitat for which selection was made at other levels of availability, rather than habitat that the animal does not respond to at all.

However, despite these issues, with suitable model validation, habitat preference models can provide insight into space use (Mladenoff *et al.* 1999; Boyce *et al.* 2003; Aarts *et al.* 2008; Hebblewhite & Merrill 2008), and inform resource management and conservation planning (Chetkiewicz *et al.* 2006; Nielsen *et al.* 2006, 2008; Aldridge & Boyce 2007). Models based on use–availability designs can be useful and have predictive power, but caution is always required to ensure that inferences based on these models are reasonable.

## 7. FUNCTIONAL RESPONSES

We have discussed how sampling issues affect preference, but differences in habitat availability in landscapes may also result in behaviourally driven changes in preference. Smooth, but non-linear, changes in preference as a function of availability were named 'functional responses' by Mysterud & Ims (1998). More broadly, preference for a particular habitat is conditional on the availability of all habitats to the animal (Aarts *et al.* 2008). Even if the availability of a particular habitat is fixed and known, the estimated preference will vary as a non-trivial function of the availabilities of all other habitats.

There may be numerous physiological, behavioural or social processes that result in functional responses in habitat preference, for which evidence has been found in several systems (Mysterud & Ims 1998; Boyce *et al.* 2003; Mauritzen *et al.* 2003; Osko *et al.* 2004). Several studies suggest that functional responses may result from trade-offs between habitat that fulfils different life-history requirements, such as a trade-off between forage and safety (Mauritzen *et al.* 2003; Godvik *et al.* 2009), forage quantity and quality (Hansen *et al.* 2009) or prey density and human disturbance (Hebblewhite & Merrill 2008).

Disagreement exists, however, on how best to model a functional response in preference. Mysterud & Ims (1998, p. 1436) defined it as 'a change in relative use with changing availability of two habitat types'. Their example, like ours, uses a simple dichotomous vegetation-type covariate to demonstrate the functional response concept. For categorical variables, a simple measure of availability is the proportion of a given category relative to the other categories. Using this metric, quantifying a functional response in preference is straightforward by modelling how preference changes as a function of availability. But availability of continuous covariates or of categorical covariates that are weighted to reflect accessibility are more difficult to characterize. The frequency distribution of continuous values provides one simple description of availability, but then quantifying how preference changes as a function of a changing frequency distribution is difficult. Some authors have quantified how preference changes as a function of the average magnitude of the continuous variable (Gillies *et al.* 2006; Hebblewhite & Merrill 2008). While this may be useful biological information, it may not describe a functional response if the average magnitude is not a sufficient description of availability. A measure of availability must reflect the frequency with which habitat is encountered in the landscape. The problem of how to characterize the availability of a continuously described habitat in a manner that facilitates quantifying a functional response in preference has not yet been adequately resolved.

## 8. THE EMERGING FRONTIER OF ANIMAL–HABITAT MODELS

Models of habitat preference provide a phenomenological description of habitat use, conditional on the sample of availability. Although some of the simplifying assumptions upon which these models are often based may be biologically unrealistic, they can still have predictive power (Boyce *et al.* 2002; Wiens *et al.* 2008). The degree, however, to which simple models of habitat preference help us to develop a mechanistic understanding of animal movement and distribution is limited. Mechanistic models are required to advance our biological understanding of the behavioural processes that result in animal movement, distribution and habitat use.

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One essential issue that more mechanistic models must resolve is that animal movement and habitat preference are not independent processes. Movement characteristics and constraints influence the availability and accessibility of habitat to the animal, and the distribution and abundance of habitat influences the movement of the animal. Estimating preference independently of the movement characteristics of the animal can therefore result in bias in the estimates of preference (Johnson *et al.* 2008; Forester *et al.* 2009). Early efforts to bring together movement modelling and habitat preference typically either used a predetermined model of movement to quantify availability and accessibility in habitat preference models (e.g. Hjermann 2000; Matthiopoulos 2003*b*; Fortin *et al.* 2005), or used predetermined habitat preference to fit a movement model (e.g. Matthiopoulos 2003*a*). More recently, several methods have been developed that estimate the movement and habitat preference models simultaneously (Rhodes *et al.* 2005; Christ *et al.* 2008; Horne *et al.* 2008; Johnson *et al.* 2008; Fieberg *et al.* 2010; Smouse *et al.* 2010). For instance, Moorcroft *et al.* (2006) compared competing mechanistic models of coyote space use based on an underlying diffusion model (random movement) that incorporated the effects of den-site fidelity, conspecific avoidance and either scent-mark avoidance or prey availability. The benefit of this approach is that habitat availability and accessibility are defined using a movement model, it can predict actual patterns of space use rather than relative probability of use and it incorporates multiple factors that affect space use (e.g. social factors, habitat preference and constraints to movement such as den sites) in a single analytical framework (Moorcroft *et al.* 2006). Furthermore, these models are fitted using maximum likelihood, which facilitates model comparison and the testing of hypotheses (e.g. using AIC) based on different theoretical models of movement and space use.

An alternative and equally promising approach to modelling animal–habitat interactions is a state–space movement model (Morales *et al.* 2004; Jonsen *et al.* 2005; Forester *et al.* 2007; Eckert *et al.* 2008), which has two components. First, an observation model relates the observed dependent variables (typically Cartesian or polar coordinates that describe the movement path) to an unobserved 'state variable' that we hypothesize plays an important role in the biological processes that generate the movement path. Second, a process model predicts the state variable at time $t$ as a function of the state variable at time $t-1$ and any other independent variables that we hypothesize are important (e.g. habitat-related variables). This is a flexible framework and there are several approaches to designing both the observation and process models (reviewed in Patterson *et al.* 2008).

In the context of using modern technology (e.g. GPS) to quantify animal–habitat relationships, state–space models offer four important advantages. First, they can estimate the values of missing data, such as missed telemetry fixes. This provides a method of addressing bias resulting from habitat-dependent measurement error associated with spatial locations (e.g. the probability of acquiring a GPS telemetry fix is not equal in all habitats; Frair *et al.* 2004, 2010; Nielson *et al.* 2009). Second, the observation model can be used to explicitly model the measurement error, and estimate the value of a variable we are truly interested in (the state variable) based on the proximate variable that is actually measured. For instance, Morales *et al.* (2004) and Eckert *et al.* (2008) used state–space models to estimate behavioural movement states from satellite telemetry data and simple movement models. This development is important because it establishes a method by which behaviour can be linked with habitat use in studies where behaviour is not monitored directly. Third, state–space models account for temporal dependencies in the data (Fieberg *et al.* 2010). Finally, they can also accommodate complex, hierarchical model structures that allow us to incorporate effects such as circadian patterns in movement (Forester *et al.* 2007) and behavioural transition models (Morales *et al.* 2004), and to estimate both population and individual-level effects (Clark *et al.* 2004). This framework also has the flexibility to incorporate non-spatial data to inform the movement or state transition models, and higher-order behavioural processes, such as memory, that may drive movement and distribution.

The disadvantage of these mechanistic modelling techniques is that they are computationally intensive, currently difficult or impractical to apply to large telemetry datasets and require considerable statistical expertise to implement and interpret.

## 9. DOES MODERN TELEMETRY TECHNOLOGY HELP IMPROVE OUR UNDERSTANDING OF ANIMAL–HABITAT RELATIONSHIPS?

In comparison to previous technologies such as VHF radiotelemetry, satellite-based technology (e.g. GPS and Argos systems) has drastically improved our ability to collect more and better positional data (Tomkiewicz *et al.* 2010). This has provided statistical power to parameterize complex models and, importantly, to detect subtle effects. This allows us to characterize selection at finer spatial and temporal scales, improving our understanding of animal–habitat relationships, and, therefore, in principle, facilitating better management of environments. Cautionary lessons regarding the interpretation of analyses based on telemetry data have therefore never been more pertinent.

Quantifying how preference changes as a function of habitat availability is an important focus for future work that will provide insight into the behavioural mechanisms by which animals manage life-history trade-offs. Establishing the value of habitat to an animal, however—and, therefore, the consequences of habitat preference—requires that fitness is also measured (McLoughlin *et al.* 2006, 2007, 2008; Gaillard *et al.* 2010). Monitoring the survival and reproductive success of the animals we track is therefore also important. Furthermore, quantifying functional responses in preference requires sampling designs that monitor animals occurring across a wide range of habitat availabilities. Sampling individuals in

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similar landscapes provides limited scope for investigating functional responses in preference.

We argue that analysing location data outside its behavioural context limits our ability to establish the link between habitat use, preference, selection and, ultimately, fitness. Behavioural data are what allow us to establish what life-history requirements are met by the use of habitat, and thus to begin to address the fundamental question of why animals use habitat. Improvements in telemetry data have driven recent analytical advances in mechanistic models, which provide promising approaches to linking behaviour, movement modelling and habitat preference within a single framework. Collecting behavioural data to complement fine-scale location data is prerequisite to developing a better mechanistic understanding of habitat use. Thus, although advances in telemetry technology have proved advantageous, there is still a need to collect behavioural and condition data, and to quantify survival and reproductive success, which are key to understanding animal habitat use in the context of fitness and natural selection.

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