Research

Inferring behavioural mechanisms in habitat selection studies – getting the null-hypothesis right for functional and familiarity responses

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Recent studies of animal habitat selection are inferring more detail regarding the behavioural mechanisms involved, like functional responses and familiarity effects. Changes in animals' use or selection of a habitat type with changing availability are commonly interpreted as a functional response in habitat preference. Studies of familiarity inferred preference for familiar locations from selection for previously visited locations after accounting for habitat-related preference. We simulated movement paths on discrete landscapes using random walk models with known habitat selection behaviour to assess emergent properties related to habitat selection in the context of functional and familiarity responses. The behavioural interpretation of functional responses relies on the relationship between habitat use and preference. Unfortunately, this relationship is not unique and depends upon the habitat choice mechanism: habitat use can be proportional to preference or proportional to availability (called respectively, hierarchical and simultaneous choice). We found that when the analytical method did not match the choice mechanism, strong functional responses were observed in habitat selection, even though habitat preference was kept constant. Therefore, functional responses need to be discussed in the context of an animal's habitat choice mechanism. In the absence of familiarity-related preference, we found no familiarity effect while accounting for all habitat variables. However, when habitat models were incomplete (e.g. lack of information about resources and habitats in the landscape) – as in all field studies – spurious preference for familiar locations arose. Our study aids the interpretation of behavioural mechanisms in habitat selection studies, but also calls for a more thorough study of the approaches used to infer behavioural mechanisms in habitat selection studies.

Habitat selection is the process in which animals choose environmental characteristics from the available choice set (Johnson 1980). In recent years, several studies have gone beyond describing habitat selection patterns, and have focussed on behavioural processes involved in habitat selection, such as functional responses (Mysterud and Ims 1998, Gillies et al. 2006, Godvik et al. 2009, Gillies and St Clair 2010), the role of familiarity with a location (Dalziel et al. 2008, Wolf et al. 2009), and population density (Morris 1989). Even though habitat selection occurs in a context of interacting individuals (Fretwell and Lucas 1969), we limited our study to functional and familiarity responses of single individuals to simplify interactions among individuals of a population. Tests of functional and familiarity responses in habitat selection analyses rely on null-hypotheses stating that when preference remains constant we should 1) observe no change in selection with changing availability (i.e. no functional response), 2) nor a change in selection with changing prior exposure to a location (i.e. no familiarity effect). We used simulations to investigate the assumed relationship between habitat preference and selection, when availability or prior exposure changes.

Habitat selection can be distinguished from habitat preference, which is the likelihood that a habitat will be selected if equally available (Johnson 1980). However, no unique relationship exists between habitat selection and preference when availability is not equal. When selection occurs among more than two items, two alternative choice mechanisms exist: simultaneous versus hierarchical consideration of these items (Fotheringham 1988, Schuck-Paim and Kacelnik 2007). The items in the choice set of an animal moving on a landscape are the different spatial locations available to it. In the simultaneous approach (Fig. 1), all available locations x_n (with $n = 1 \ldots N$) are considered together (i.e. simultaneously) and each location is treated with preference $pref_y$ for habitat type y ($y = 0 \ldots Y$, we focus here on the simple case where $Y = 1$) that
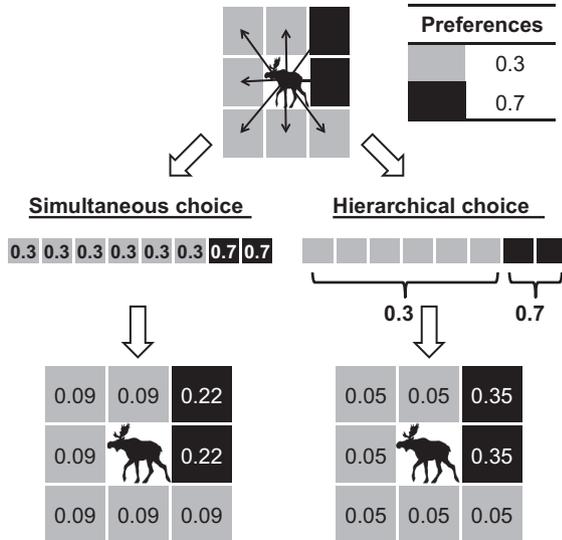
Figure 1. An example of an animal choosing among eight adjacent pixels with a simultaneous and hierarchical choice mechanism. The animal chooses between eight pixels, $x_{1...8}$, belonging to two habitat types, $y \in \{0, 1\}$. The preference for habitat type ($pref_y$) 0 and 1 is respectively 0.3 and 0.7. Using a simultaneous choice process (Eq. 1 in the text), the animal considers each pixel with the corresponding preference. With a hierarchical choice process (Eq. 2 in the text), all pixels of the same habitat type are merged and the habitat types are evaluated with their preference. Therefore, with a hierarchical choice process use is independent of availability, whereas use will increase with availability in a simultaneous choice process. See the main text for further discussion.

location x_n belongs to (and let the sum of preferences for all categories: $\sum_{y=n}^{Y} pref_y = 1$). Expected use of habitat type 1, $E(use)$, is then given as:

$$E(use) = \frac{\sum_{n=1}^{N} pref_y \times x_n}{\sum_{n=1}^{N} pref_y} \quad (1)$$

Division by $\sum_{n=1}^{N} pref_y$ keeps total expected use in one choice event limited to one. For example, consider an animal in a simple environment with two habitat types ($y = 0$ or 1, e.g. forested vs non-forested habitats), with preference $pref_0 = 0.3$ and $pref_1 = 0.7$. The expected use of habitat 1 by this animal, when it chooses among eight locations: $x_{1...6} \in \{y = 0\}$ and $x_{7...8} \in \{y = 1\}$, is 0.44. Thus, the simultaneous choice approach leads to the counter-intuitive consequence that a less preferred alternative will become more used with increasing availability (Supplementary material Appendix 1, Fig. A1). On the other hand, in the hierarchical approach (Fig. 1), all locations are first grouped by habitat type y and preference for habitat type y, $pref_y$, is then divided by the total number of locations M_y belonging to this habitat. Expected use of habitat 1, $E(use)$, is then given as:

$$E(use) = \sum_{y=0}^{Y} \sum_{m=1}^{M} \frac{pref_y}{M_y} \times x_{m_y} \quad (2)$$

with m the locations ($m = 1...M$) for a given habitat y. Thus, the probability of using one specific location from a habitat type will decrease with increasing availability. For example, in the same choice situation as before, the expected use of habitat 1 with hierarchical choice would be 0.7. Thus, the most preferred habitat is also used more. With the hierarchical choice approach the use of a habitat type will remain constant with changing availability. It is important to realize that neither the simultaneous nor the hierarchical approach conflicts with previous definitions of habitat use or preference. Merely, the definition of preference does not specify how selection occurs when multiple items belong to different categories in unequal proportions, such as the choice among spatial locations in natural habitats.

The type of multi-item choice mechanism is important for the definition of a functional response, because it affects how use changes with availability. Mysterud and Ims (1998) extended the functional response concept – originally describing kill-rates of predators as a function of prey density (Holling 1959) – to describe space use, and defined it as 'a change in relative use with changing availability of two habitat types' (Mysterud and Ims 1998, p. 1436). The underlying idea in most studies on functional responses is that they involve a change in the animal's preference, and this preference change is often interpreted as adaptive behaviour. However, in simultaneous multi-item choice, use is expected to change with availability even with constant preference.

Although, Mysterud and Ims' (1998) initial definition has been formulated for relative use, recent studies more often considered other habitat selection metrics to assess responses to availability (Hebblewhite and Merrill 2008, Herfindal et al. 2009, but see Pellerin et al. 2010). Habitat selection is distinguished from habitat use, as selection compares use to the available choice set (Manly et al. 2002). A change in habitat selection with changing availability is then often interpreted as a functional response in preference. When habitat use is constant, Beyer et al. (2010) showed that habitat selection will decrease with increasing availability. Such decreased selection is often considered indicative of a functional response – as a change in preference (however, Godvik et al. 2009). The constant use assumption in Beyer et al. (2010) implies they focussed on the hierarchical approach to multi-item choice. Little research has addressed the actual mechanisms animals use in multi-item choice. However, in their experiment with starlings *Sturnus vulgaris*, Schuck-Paim and Kacelnik (2007) found support for a simultaneous resource selection approach. It is therefore important to investigate change in habitat selection with availability for simultaneous choices.

Another factor shaping animal space use is previous experience or familiarity with the landscape. Several models of animal space use are built upon the principle that animals learn from their experience, which can lead to higher efficiency in space use (Stamps 1987, Van Moorter et al. 2009) or motor learning of escape routes (Stamps 1995). However, studies showing preference for familiar locations are few. Two pioneering studies have addressed familiarity and memory in free-ranging elk *Cervus elaphus canadensis* (Dalziel et al. 2008, Wolf et al. 2009),

and both studies reported selection for locations previously visited. In these studies, preference for familiar sites was inferred from returns to previously visited locations, after accounting for habitat-related variation in selection. The underlying idea is that familiarity-mediated preference can be inferred from differences in animal's selection among locations that contain the same habitat while having a different prior experience. However, when the habitat selection model is incomplete, then habitats that appear the same to us can be different from the animal's perspective. It is therefore important to assess whether the validity of these inferences is affected by incomplete habitat models, as in practice no habitat selection model will ever be complete.

In this paper, we addressed the null-hypotheses in both functional responses and familiarity effects in habitat selection using simulated data, in which the data-generating processes are completely known. We simulated data using a habitat selection process that chooses simultaneously versus hierarchically among available locations with constant preference for habitat types in the landscape. These data allowed us to investigate the baseline habitat use and selection in the absence of a functional response in preference. Similarly, the data were generated without any preference for previously visited locations, allowing us to assess the null-hypothesis that by accounting for habitat-related spatial variation in preference no familiarity effect is found. Moreover, such simulated data allowed us to compare a complete habitat model (i.e. a model that contains all habitat information affecting the habitat selection process) with an incomplete model (i.e. a model that does not contain all information, which is the more realistic situation).

Methods

We generated data from a random walk with habitat selection in random and clumped landscapes (see below, more details in Supplementary material Appendix 2). We then used conditional logistic regression (CLR, Hosmer and Lemeshow 2000) to search for functional responses and familiarity effects in habitat selection with simulated data, when both effects were absent in the habitat preference of the simulation process. For functional responses the temporal order of the locations is not of importance, therefore we complemented this CLR with ordinary logistic regression, which is commonly used in resource selection studies (Manly et al. 2002, Johnson et al. 2006), and the approach advocated by Mysterud and Ims (1998) using linear regression on a logit scale. We report the details of these additional analyses and their results in Supplementary material Appendix 3.

Habitat selection simulation

Landscapes
We simulated random and clumped landscapes (see Supplementary material Appendix 2 for a detailed description). For both landscape types we simulated sets of 3 habitat variables or layers on a 250×250 pixel landscape, each

layer consisted of the absence or presence of a habitat feature (i.e. binary variable: 0 or 1). We created several variables to be able to address the effect of incomplete knowledge of the environment on the familiarity analysis.

Habitat selection processes

To best reflect animal tracking data, we simulated habitat selection in a movement process (i.e. random walk [Kareiva and Shigesada 1983]) instead of a simple point process. At each time step the simulated animal moved from its current pixel towards one of all 8 neighbouring pixels (it did not remain in its current pixel). The probability to select each pixel (x_i) at time t among all pixels in the choice set (n = 8) depended upon the landscape variables ($LS1$, $LS2$, and $LS3$) of these pixels and followed a conditional logistic form:

$$p(x_{i,t}) = \frac{\exp\left(b_{LS1} \times LS1(x_{i,t}) - b_{LS2} \times LS2(x_{i,t}) + b_{LS3} \times LS3(x_{i,t})\right)}{\sum_{j=1}^{n} \exp\left(b \times LS1(x_{j,t}) + b \times LS2(x_{j,t}) + b_{LS3} \times LS3(x_{j,t})\right)} \quad (3)$$

with b the preference for each of these landscape characteristics. We use the following values for the different parameters in the habitat selection or movement process: $b_{LS1} = 0.50$, $b_{LS2} = 0.30$, $b_{LS3} = 0.20$. Our conclusions appeared robust for the particular values of b that were used (Supplementary material Appendix 3).

In the previous formulation (Eq. 3) each available location is considered simultaneously, without grouping locations into habitat categories. This shows that choice is assumed to be simultaneous and not hierarchical. Although never explicitly acknowledged, this assumption is the basis of resource selection functions currently used in habitat selection studies (Manly et al. 2002) and, to our knowledge, no study considered the alternative mechanism of hierarchical choice. Due to the importance of the choice mechanism for functional responses, we simulated both simultaneous and hierarchical choice processes on one habitat layer. Simultaneous choice considered as before all available locations simultaneous (as in Eq. 1):

$$p(x_{i,t}) = \frac{\exp\left(b_{LS1} \times LS1(x_{i,t})\right)}{\sum_{j=1}^{n} \exp\left(b_{LS1} \times LS1(x_{j,t})\right)} \quad (4)$$

For hierarchical choice we first grouped all locations together according to habitat type (as in Eq. 2), with the probability to choose habitat type y at time t, $p(H_{y,t})$, $y = 1$ or 2:

$$p(H_{y,t}) = \frac{\exp\left(b_{LS1} \times LS1(H_{y,t})\right)}{\sum_{j=1}^{2} \exp\left(b_{LS1} \times LS1(H_{j,t})\right)} \quad (5)$$

We then took one location randomly from the chosen habitat type. We explored parameter space by varying habitat preference b_{LS1} from 0.1, 0.3, 0.5, 0.7 to 0.9, and simultaneously varying the proportion available of habitat type 1 from 0.1, 0.3, 0.5, 0.7 and 0.9 on a random landscape, for both choice mechanisms.

Simulations

We simulated 1000 animals for each landscape type. Each animal was released within the landscape's geographical centre. For each animal 100 time steps were simulated, which is insufficient for an animal to move out the landscape during a simulation. To avoid effects specific to a given realization of the landscape, we produced a different set of simulated landscapes for each animal (i.e. 1000 different landscape sets for each of both landscape types). Hence, using Eq. 3 we simulated one animal with 100 steps on each of the 1000×2 landscape sets. With both Eq. 4 and 5 we simulated 5 animals with different habitat preference for 100 steps on 1000×5 random landscapes.

Habitat selection analysis

General

We analyzed the data generated by the habitat selection process described above with a conditional logistic regression (Hosmer and Lemeshow 2000). We limited our statistical model to a simple fixed-effects model, because no individual variation was present in the simulation process. For simultaneous choice, we investigated the selected pixel against all eight available pixels in the choice set at time t (also known as a step selection function; Fortin et al. 2005). The likelihood function that is maximized over all choices an animal made from time $t = 1$ to T in conditional logistic regression is:

$$L(\beta) = \prod_{t=1}^{T} \frac{\exp\left(\beta_{LS1} \times LS1(x_{i,t}) + \beta_{LS2} \times LS2(x_{i,t}) + \beta_{LS3} \times LS3(x_{i,t})\right)}{\sum_{j=1}^{n} \exp\left(\beta_{LS1} \times LS1(x_{j,t}) + \beta_{LS2} \times LS2(x_{j,t}) + \beta_{LS3} \times LS3(x_{j,t})\right)} \quad (6)$$

The correspondence between simulation process (Eq. 3) and statistical model (Eq. 6) guaranties the appropriateness of this model. Our full model contained all three landscape variables ($LS1$, $LS2$, and $LS3$).

For the comparison of functional responses in simultaneous and hierarchical choice on a two-habitat landscape, we analysed the data first using a classical simultaneous analysis similar to Eq. 6 using only one landscape layer:

$$L(\beta) = \prod_{t=1}^{T} \frac{\exp\left(\beta_{LS1} \times LS1(x_{i,t})\right)}{\sum_{j=1}^{n} \exp\left(\beta_{LS1} \times LS1(x_{j,t})\right)} \quad (7)$$

Second, we performed a hierarchical choice analysis, for which we considered the choice between habitat types the locations belong to instead of among locations:

$$L(\beta) = \prod_{t=1}^{T} \frac{\exp\left(\beta_{LS1} \times LS1(H_{y,t})\right)}{\sum_{j=1}^{2} \exp\left(\beta_{LS1} \times LS1(H_{j,t})\right)} \quad (8)$$

In this case all locations from a habitat type were merged together into a single choice option.

We used function 'coxph' from the package 'survival' (Therneau and Lumley 2010) for R (R Development Core Team) to estimate the parameters of this model.

Functional response

We assessed whether the estimated β_{LSc}'s (in Eq. 6, 7 and 8) for each landscape variable, c (with $c \in \{1, 2, 3\}$), changed with its proportion available, $prop(A_{LSc})$, using a linear regression:

$$\beta_{LSc} = \alpha_{LSc} + \varphi_{LSc} \times prop(A_{LSc}) + \varepsilon_{LSc} \quad (9)$$

We estimated the proportion available of a landscape characteristic c, $prop(A_{LSc})$, by averaging the characteristics of the pixels that appeared in the choice sets:

$$prop(A_{LSc}) = \frac{1}{100} \times \sum_{t=1}^{T=100} \frac{1}{8} \times \sum_{i=1}^{n=8} LSc(x_{i,t})$$

Thus, a pixel that appears several times in the animal's choice sets is considered more available to it. In the comparison of simultaneous and hierarchical choice we varied the preference in our simulations (from 0.1 to 0.9); we therefore added to Eq. 9 the preference as an explanatory variable ($\varphi_{pref1} \times pref(LS_1)$: note: we used only one habitat layer, thus $c = 1$ in Eq. 9). This allowed us to assess the relative importance of the variation in availability versus preference to the observed habitat selection. We expected slope $\varphi_{LSc} = 0$ in Eq. 9, because b_{LSc} in the process generating these data (Eq. 3, 4 and 5) did not change with the availability of the landscape characteristics. A functional response would be indicated by a slope φ_{LSc} in Eq. 9 different from zero.

Familiarity effects

A pixel was considered familiar when the animal had visited it at least once previously. Thus, at the beginning of the simulation each pixel was unfamiliar, but as the animal moved around it became familiar with the landscape (note: in our simulations, pixel choice was not affected by familiarity). We used conditional logistic regression, as described above, to account for the time-dependent nature of familiarity. To investigate familiarity effects we added the familiarity term to the conditional regression (Eq. 6) with the different landscape variables (Eq. 10a):

$$L(\beta) = \prod_{t=1}^{T} \frac{\exp\left(\beta_{LS1} \times LS1(x_{i,t}) + \beta_{LS2} \times LS2(x_{i,t}) + \beta_{LS3} \times LS3(x_{i,t}) + \beta_f \times familiarity(x_{i,t})\right)}{\sum_{j=1}^{n} \exp\left(\beta_{LS1} \times LS1(x_{j,t}) + \beta_{LS2} \times LS2(x_{j,t}) + \beta_{LS3} \times LS3(x_{j,t}) + \beta_f \times familiarity(x_{j,t})\right)} \quad (10a)$$

We then removed different landscape variables to study familiarity effects with decreasing knowledge of the animal's habitat (Eq. 10b–e):

$$L(\beta) = \prod_{t=1}^{T} \frac{\exp\left(\beta_{LS1} \times LS1(x_{i,t}) + \beta_{LS2} \times LS2(x_{i,t}) + \beta_f \times familiarity(x_{i,t})\right)}{\sum_{j=1}^{n} \exp\left(\beta_{LS1} \times LS1(x_{j,t}) + \beta_{LS2} \times LS2(x_{j,t}) + \beta_f \times familiarity(x_{j,t})\right)}$$

$$(10b)$$

$$L(\beta) = \prod_{t=1}^{T} \frac{\exp\!\big(\beta_{LS1} \times LS1(x_{i,t}) + \beta_{LS3} \times LS3(x_{i,t}) + \beta_f \times \mathit{familiarity}(x_{i,t})\big)}{\sum_{j=1}^{n} \exp\!\big(\beta_{LS1} \times LS1(x_{j,t}) + \beta_{LS3} \times LS3(x_{j,t}) + \beta_f \times \mathit{familiarity}(x_{j,t})\big)}$$

$$(10c)$$

$$L(\beta) = \prod_{t=1}^{T} \frac{\exp\!\big(\beta_{LS1} \times LS1(x_{i,t}) + \beta_f \times \mathit{familiarity}(x_{i,t})\big)}{\sum_{j=1}^{n} \exp\!\big(\beta_{LS1} \times LS1(x_{j,t}) + \beta_f \times \mathit{familiarity}(x_{j,t})\big)} \quad (10d)$$

$$L(\beta) = \prod_{t=1}^{T} \frac{\exp\!\big(\beta_f \times \mathit{familiarity}(x_{i,t})\big)}{\sum_{j=1}^{n} \exp\!\big(\beta_f \times \mathit{familiarity}(x_{j,t})\big)} \quad (10e)$$

We expected $\beta_f = 0$ in Eq. 10a–e, because familiarity did not play a role in the movement process underlying these data (Eq. 6).

Results

Functional response

The simulations with simultaneous choice in 3-layered random landscapes showed a small, but statistically significant, increase in beta-coefficients with availability ($\varphi_{LS1} \pm$ SE: 0.08 ± 0.04, p = 0.048; $\varphi_{LS2} \pm$ SE: 0.18 ± 0.04, p < 0.001; $\varphi_{LS3} \pm$ SE: 0.07 ± 0.04, p = 0.058; Fig. 2). Such increased selection for a landscape feature with availability became more pronounced in clumped landscapes ($\varphi_{LS1} \pm$ SE: 0.50 ± 0.06, p < 0.001; $\varphi_{LS2} \pm$ SE: 0.42 ± 0.06, p < 0.001; $\varphi_{LS3} \pm$ SE: 0.50 ± 0.06, p < 0.001; Fig. 2).

Comparing simultaneous and hierarchical choice showed that when the analysis matches the choice mechanism the beta-estimate remained relatively constant with changing availability (Fig. 3a, d; process simultaneous and analysis simultaneous: slope $\pm$ SE: 0.17 ± 0.03, p < 0.001; process hierarchical and analysis hierarchical: slope $\pm$ SE: -0.0006 ± 0.0045, p = 0.89). However, despite it only being a small effect, the increase in beta-estimate for simultaneous choice was statistically significant and remained so after excluding the strong increase at a proportion available of 0.9 (Fig. 3a; slope $\pm$ SE: 0.07 ± 0.006, p < 0.001). In contrast, when analysis and simulation process were misaligned, strong changes occur in beta-estimate with availability. A simultaneous choice process analysed with a hierarchical approach led to a strong increase in beta-coefficient with availability (Fig. 3c; slope $\pm$ SE: 4.04 ± 0.04, p < 0.001). Hierarchical choice processes that were analysed with a simultaneous analysis showed decreasing beta-coefficients with increasing availability (Fig. 3b; slope $\pm$ SE: 4.12 ± 0.02, p < 0.001). Under all four conditions, beta-coefficients were virtually isometric with preference (process simultaneous and analysis simultaneous: slope $\pm$ SE: 1.06 ± 0.03; process simultaneous and analysis hierarchical: slope $\pm$ SE: 1.11 ± 0.02; process hierarchical and analysis simultaneous: slope $\pm$ SE: 0.99 ± 0.04; process hierarchical and analysis hierarchical: slope $\pm$ SE: 1.03 ± 0.01).

Familiarity effects

Beta-coefficients from the familiarity analysis in random and clumped landscapes are reported in Table 1. Not surprisingly, using the same model to analyse the data (Eq. 6) as we used to generate them (Eq. 3), we found similar beta-coefficients. When adding a familiarity effect to this full model (i.e. Eq. 10a), we did not find a statistically significant familiarity effect in either landscape. After removal of the least important habitat variable (i.e. $LS3$) from the model (Eq. 10b), the familiarity effect increased, however deviance from zero remained statistically not significant. However, removal of more important habitat variables led to statistically significant familiarity effects, which increased with the removal of progressively more landscape variables (Eq. 10c–e, Table 1). Landscape structure (i.e. random or clumped) did not affect these results.

Discussion

Understanding the behavioural basis of habitat selection is crucial, but difficult, especially in secretive animals. Our simulations of animal movement paths showed that emergent properties in habitat selection at the home range scale, attributed earlier to familiarity effects or functional responses, could also occur as a consequence of data structure and analytical method. The null-hypothesis of no change in selection with availability in the absence of any such explicit behavioural responses in the animal appears to not be valid, and may lead to over-interpretation regarding behavioural mechanisms of observed selection patterns at the home range scale. Also, the null-hypothesis that no selection for familiar locations should occur when no such behaviour is present is invalid when the habitat model was incomplete with respect to landscape features explaining space use. Consequently, apparent selection for previously visited locations may be due to an unregistered resource in the location, rather than familiarity driving the habitat selection.

Clearly, our results do not imply the absence of real functional responses and familiarity responses in the wild, but highlight that caution is needed when interpreting results from habitat selection analyses. For instance, functional responses are expected to occur under density-dependent habitat selection. With increasing population density a decreasing preference for preferred habitat types is expected, if animals distribute themselves according to an ideal free distribution (IFD; Fretwell and Lucas 1969, Rosenzweig 1981, Mobæk et al. 2009). Under an IFD, habitat availability and animal density are correlated, as animals should occur at higher densities when high-quality habitats are more available (Fretwell and Lucas 1969). Thus, we expect a negative functional response in the preference of animals with increasing availability of good habitats. Our study did not focus on actual functional response in habitat preference. We merely addressed the issue of spurious functional responses; future research should further explore this important element in habitat selection (McLoughlin et al. 2010). Similarly, familiarity effects are expected to occur in wild animals, because the use of memory can substantially increase the efficiency of habitat use (Benhamou 1992, Van Moorter et al. 2009).

Several authors seem to implicitly assume that a functional response implies a change in preference depending on either availability per se or on temporal variations
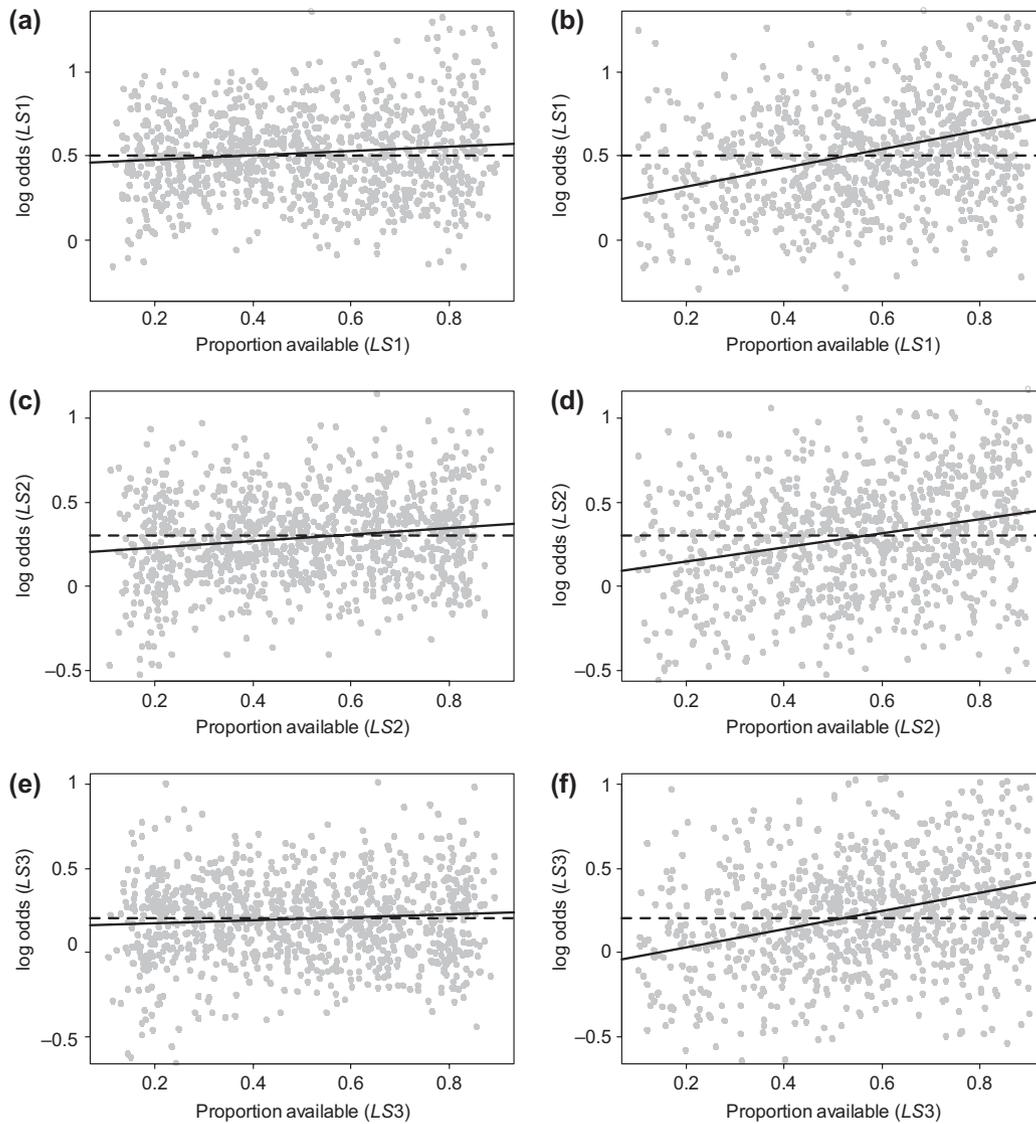
Figure 2. The estimated regression-coefficients from a conditional logistic regression as a function of availability for each habitat variable in both landscape types. Panels (a), (c) and (e) are the functional responses for the random landscape, respectively variable $LS1$, $LS2$ and $LS3$. Panels (b), (d) and (f) are the functional responses for the clumped landscape, respectively variable or layer $LS1$, $LS2$ and $LS3$. The full black line depicts the regression line between the beta-coefficients and proportion availability (Eq. 9 in main text), the dotted line is the expected beta-value used in the simulation (Eq. 3 in main text).

in preference (Mysterud and Ims 1998). Even though preference remained constant, we found strong changes in habitat selection with availability, when the statistical model did not match the habitat choice process. As with Beyer et al. (2010), we found a strong decrease in habitat selection with availability for a hierarchical choice process analysed with a simultaneous statistical model. We found the opposite effect for a simultaneous choice process analysed with a hierarchical statistical model. When process and statistical model matched each other, none or only minor changes in habitat selection were found with availability. Without an understanding of the animal's choice mechanisms it is difficult to attribute an empirically observed change in habitat selection with availability to a functional response in preference. The functional response in habitat selection can be indicative of a misspecified statistical model and may point to an alternative underlying choice

process. In our study we demonstrated analyses using choice sets for both simultaneous and hierarchical choice. For simultaneous choice processes the choice set is defined in geographical space (sensu Aarts et al. 2008) as the available spatial locations, whereas environmental space (sensu Aarts et al. 2008) is used to define the available environmental conditions in those locations for a hierarchical choice set. Matching the choice process and the statistical model allowed us to obtain the proper functional responses of preference.

The null-hypothesis that in the absence of familiarity an animal should not select for previously visited locations when accounting for habitat preferences is only correct from a theoretical point of view. Indeed, using an ideal mathematical representation of animal habitat use based on complete information on resource distribution we showed that this null-hypothesis is correct. However, a more
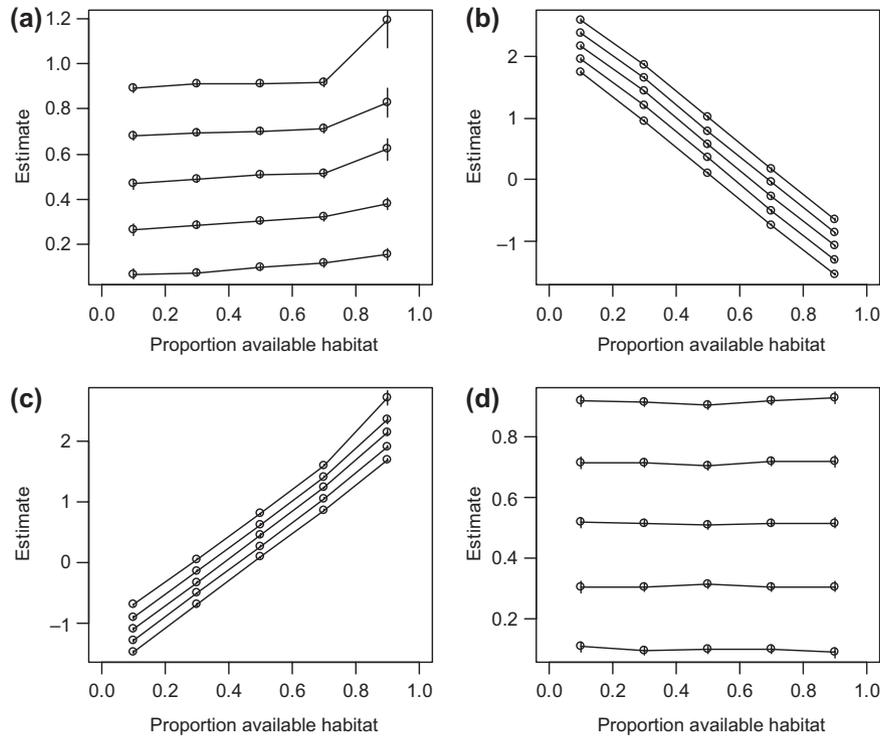
Figure 3. Estimated habitat preference as a function of availability and actual preference of the habitats. The data used in panel (a) and (c) were simulated with simultaneous choice, whereas panel (b) and (d) resulted from hierarchical choice. The data in panel (a) and (b) were analysed using simultaneous choice, whereas for panel (c) and (d) we used a hierarchical analysis. We connected in each panel results from the same preference: from bottom to top preference increased (from 0.1, 0.3, 0.5, 0.7, to 0.9).

realistic habitat selection model based on incomplete information on resource distribution that affects individual space use shows that in practice this null-hypothesis is a wrong baseline for inferences about the role of familiarity in habitat selection. This problem can be illustrated by imagining an animal confronted with a choice between location A and B, where location A is preferred over B based upon one or more unmeasured variables. At first, the animal likely chooses A. If nothing changes, the next time the animal will likely select again for A. The latter choice is between two sites similar in their measured habitat characteristics, but different in familiarity. Hence, the choice for A will be attributed to familiarity, whereas it is actually due to an incomplete habitat model. As no habitat selection model from field studies will ever be complete, we showed that it is problematic to discriminate between a real familiarity effects and an

incomplete habitat selection model. Even when including the most relevant habitat variables in a model, unmeasured variables of lesser importance will pool together and give rise to spurious familiarity effects.

The limitations to inferences about behavioural processes in habitat selection studies do not imply that current statistical approaches for habitat selection (e.g. resource selection functions [Manly et al. 2002]) are flawed. However, we warn researchers to carefully examine the properties of the statistical approaches adopted to test for familiarity or functional responses, as misspecified null-hypotheses can give rise to erroneous inferences when analyzing real data (see also Martin et al. 2008, Bastille-Rousseau et al. 2010 for other examples in habitat selection; for a more general discussion in biology see Houle et al. 2011). We cannot provide suggestions on how to discriminate

Table 1. Coefficients used in the simulation and obtained from the familiarity analysis in random (beta coefficient and SE on the left) and clumped (on the right) landscapes. Beta-coefficients are shown with their standard errors, and the statistical significance of the familiarity effect from a Wald-test (H_0: beta = 0): not significant (ns, $p > 0.10$), trend ($\cdot$, $0.10 > p > 0.05$) or significant (*, $p < 0.05$, and **, $p < 0.001$), and NA (i.e. not available) corresponds to variables not included in the model. The first line are parameter values for the simulated habitat selection process (Eq. 3 in main text), which did not contain a familiarity effect. The subsequent lines are the parameter estimates obtained from the conditional logistic regression (Eq. 6 and 10a–e).

	$LS1$	$LS2$	$LS3$	Familiarity
Eq. 3 (sim)	0.5	0.3	0.2	NA
Eq. 6	$0.51 \pm 0.01 \mid 0.51 \pm 0.01$	$0.29 \pm 0.01 \mid 0.29 \pm 0.01$	$0.20 \pm 0.01 \mid 0.21 \pm 0.01$	NA
Eq. 10a	$0.51 \pm 0.01 \mid 0.51 \pm 0.01$	$0.29 \pm 0.01 \mid 0.29 \pm 0.01$	$0.20 \pm 0.01 \mid 0.21 \pm 0.01$	$-0.005 \pm 0.008^{ns} \mid -0.0022 \pm 0.0075^{ns}$
Eq. 10b	$0.51 \pm 0.01 \mid 0.51 \pm 0.01$	$0.29 \pm 0.01 \mid 0.29 \pm 0.01$	NA	$0.0046 \pm 0.008^{ns} \mid 0.0043 \pm 0.0075^{ns}$
Eq. 10c	$0.51 \pm 0.01 \mid 0.51 \pm 0.01$	NA	$0.19 \pm 0.01 \mid 0.21 \pm 0.01$	$0.014 \pm 0.007^{\cdot} \mid 0.011 \pm 0.007^{\cdot}$
Eq. 10d	$0.50 \pm 0.01 \mid 0.51 \pm 0.01$	NA	NA	$0.023 \pm 0.007^{**} \mid 0.017 \pm 0.007^{*}$
Eq. 10e	NA	NA	NA	$0.081 \pm 0.007^{**} \mid 0.054 \pm 0.007^{**}$

between real and spurious familiarity effects or functional responses in field studies. Instead, we suggest focusing on the behavioural mechanisms of animal choices, i.e. simultaneous vs hierarchical multi-item choice mechanism (Schuck-Paim and Kacelnik 2007), because the relationship between habitat use and habitat availability depends upon the mechanism animals use to choose among habitats. In particular, if an animal chooses among different habitat simultaneously the correct null hypothesis to test for the existence of a functional response in habitat preference is that use of a habitat type increases with its availability (Supplementary material Appendix 1, Fig. A1 with mathematical proof in Appendix 4). On the contrary, in case of hierarchical multi-item choices the correct null hypothesis is that use would remain constant with habitat availability (Mysterud and Ims 1998, Beyer et al. 2010). Only when habitat selection process and statistical model matched, did we observe correspondence between selection and preference with changing availability. Our results call for the study of simultaneous and hierarchical habitat choice processes in field studies to allow inference on functional responses, and more generally they highlight the need for more attention to the null-hypotheses underlying current approaches for inferring behavioural responses from habitat selection studies.

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Supplementary material (Appendix E7291 at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.