Holling meets habitat selection - functional response of large herbivores revisited

Claudia Dupke¹*, Anne Peters²,³, Nicolas Morrellet⁴ and Marco Heurich²,³

Abstract

Background: Holling (1959) was the first to describe a functional response between a predator's consumption-rate and the density of its prey. The same concept may be applied to the habitat selection of herbivores, by considering the change in relative habitat use with the change in habitat availability. Functional responses in habitat selection at a home-range scale has been reported for several large herbivores. However, a link to Holling's original functional response types has never been drawn despite its potential to understand availability dependence in habitat selection more profoundly.

Methods: Discrete choice models were implemented as mixed-effects baseline-category logit models to analyze the variation in habitat selection of a large herbivore over seasonal and diurnal scales. Specifically, changes in habitat use with respect to habitat availability were investigated by monitoring 11 habitat types commonly used by roe deer (Capreolus capreolus) in the Bavarian Forest National Park, Germany. Functional response curves were then fitted using Holling’s formulas.

Results: Strong evidence of non-linear functional responses was obtained for almost all of the examined habitat types. The shape of the functional response curves varied depending on the season, time of day and in some cases between sexes. These responses could be referenced to Holling’s types, with a predominance of type II.

Conclusions: Our results indicate that Holling’s types could be applied to describe general patterns in habitat selection behaviour of herbivores. Functional response in habitat selection may occur in situations of trade-off in the selection of habitats offering different resources, due to temporally varying physiological needs of herbivores. Moreover, the two associated parameters defining the curves helps to identify the temporal variations and clarify how strongly the cost-to-benefit ratio is pronounced for a specific habitat. The presented novel approach of using Holling’s equations to describe functional response in habitat selection of herbivores could be used for assigning general habitat attraction values, independent of habitat availability, which might facilitate the identification of suitable habitats.

Keywords: discrete choice; herbivore; landscape complementation; landscape of fear; mixed effects; multinomial; ungulate
Introduction

Habitat selection studies have shed light on the mechanisms and driving forces underlying the spatial behaviours of animals (1). Variations in habitat selection behaviour of animals were linked to differences in environments individuals were occupying, usually characterized by available resources (2). Despite the continuously increasing effort in characterizing landscape by modern high-precision remote sensing of climatic and environmental variables (e.g. 3), many studies still stick to the obsolete assumption of constant habitat selection over the spectrum of available habitats (or resources) in an area (4, 5). However, an availability dependence in habitat selection has been confirmed in several empirical studies of different large herbivores at the home-range scale (e.g. 6–10). Already in 1998, Mysterud and Ims published a seminal paper showing that the use of a habitat varies non-linearly with its availability and merging the concept of functional response with the concept of habitat selection of animals at the home-range scale (second-order selection, 11).

The patterns of functional response on the population level show that habitat selection behaviour is altered on the individual-level with respect to the availability of habitats since habitats are used for available resources such as food or cover that are related to the fitness of an individual (12, 13). Habitats differ in the structure of their vegetation and from the animals’ perspective in their cost-to-benefit ratio of selecting it meaning that an animal has to trade-off between often opposing needs like protection against predators and food intake (14). The strength of this trade-off is affected by the resources a habitat offers and affects habitat selection with respect to availability (15). For example, for moose (Alces alces) the strength of a food/cover trade-off was linked to the strength of functional response whereby patterns of functional response were particularly pronounced during the most constraining periods such as when exposed to high predation risk or when lactation increases energetic requirements (16). Consequently, functional response in habitat selection reflects the seasonal variation of the landscape of fear and the necessity for roe deer to manage the risk-resource trade-off over time (14, 17) and should therefore vary over time.

Although a variety of methods to quantify the variation of habitat selection with respect to environmental covariates have become available (1, 18, 19), the most widely employed is the analysis of resource selection functions (RSFs, 20), a technique that relates spatial use of animals to landscape characteristics based on a combination of case-control sampling and logistic regression (6, 21). RSFs have been applied to identify functional responses in habitat selection using different approaches. For example, habitat selection coefficients can be estimated separately for individuals or groups with different habitat availabilities with or without including random effects (22, 23), however, the integration is strongly recommended (24). Alternatively, habitat availability can be included as a fixed effect to model the functional response explicitly (10, 15, 25). Functional response is usually presented as the effect of availability on odds ratios (13, 15) or on the selection coefficients (10, 23, 25). Although the relationships revealed by RSFs may indicate the presence of a functional response, they are difficult to interpret and to quantify (4, 26, 27) as they represent selection for or against a certain habitat but do not directly depict the relation between the availability and the actual use of a habitat (e.g. 15, 28). Specifically, use cannot be inferred from a resource selection analysis because habitat selection depends on availability as it is a function of availability (5). Following Johnson (1980), use and selection would only be identical in the theoretical case of equal availabilities of resource types.

Here, we demonstrate that Holling’s types can be used to model functional response in habitat selection based on real data (see an theoretical approach in 27). Holling (29) first described the behavioural
adjustments of carnivores, specifically those of small insectivorous mammals, according to the level of prey availability. Depending on the time required for searching, handling and consuming individual prey, three types of functional responses curves describe the relationship between carnivores consumption and prey availability: linear (type I), concave (type II) and convex (type III). Specialist carnivores were presumed to have a type II functional response, i.e. the number of killed prey increases rapidly with prey density and levels off when the search time and prey manipulation constrain the predators’ ability to consume more prey (30). For a generalist predator by contrast, e.g. wolves (Canis lupus, 31) and lynx (Lynx lynx, 32), the slower increase in the number of killed prey results in a sigmoid curve indicating a type III response, which reflects changes in the search target and foraging habitat as well as prey switching (33).

Here, we propose multinomial logit discrete-choice models (34) as an alternative method of assessing functional responses in habitat selection. An advantage of this approach is the simple inference of functional response because proportional use is directly related to proportional availability as originally described by Mysterud and Ims (1998). Moreover, functional response curves can be directly related to Holling’s types (29), thereby potentially allowing new interpretations of the habitat use behaviour of herbivores.

We used GPS locations of 36 free-ranging roe deer in the Bavarian Forest National Park, Germany, to analyse the habitat selection of roe deer in 11 habitat types located within the home ranges of individuals. Specifically, we investigated how the proportional use of a particular habitat varied depending on its relative availability within the home range (35), taking temporal variations in selection patterns at daily and monthly scales (15, 36) as well as differences between sexes into account (37–39).

The goal of this study was to relate the functional response curves of roe deer for each habitat type for summer (June) and winter (December) seasons and during day (noon) and night (midnight) to Holling’s types. Based on previous studies of prey consumption by large mammalian carnivores (31, 40), we predicted (H1) that a non-linear relationship between the proportional use for a given habitat and the availability of that habitat (Holling’s type II or III) would prevail over habitat use proportional to habitat availability (Holling’s type I). Specifically, we expected (H2) type II responses in more frequently selected habitats providing a specific resource, such as forage on meadows and (H3) type III responses in the use of difficult to access habitats, e.g. dead wood areas. That is because the use of habitat which requires overcoming or adjusting to movement barriers, e.g. dead wood, would be required only if the availability of that habitat within the home range exceeds a certain threshold and therefore could not be avoided or if specialization takes place (25). Given the seasonal changes in the cost-to-benefit ratio of habitats and their use intensity as well as the variations in risk perceived by roe deer over time, e.g. due to human disturbances during daytime, (H4) the functional response was expected to differ both seasonally and over the course of the day due to seasonal variation of the landscape of fear and the necessity for roe deer to manage the risk-resource trade-off over time (14, 15, 41, 42). Moreover, we predict that functional response curves will differ (H5) between sexes (38).

Material and Methods

Study area and data
The study area was located in the Bavarian Forest National Park (BFNP), which lies in south-eastern Germany along the border with the Czech Republic (centre coordinates 49°3′19″N, 13°12′9″E). The BFNP has three major forest types structured along the altitudinal gradient. Sub-alpine spruce forests of
Norway spruce (*Picea abies*) and to a lesser extent mountain ash (*Sorbus aucuparia*) prevail above 1,100 m (16% of the area) whereas mixed montane forests containing Norway spruce, white fir (*Abies alba*), European beech (*Fagus sylvatica*) and sycamore maple (*Acer pseudoplatanus*) predominate on slopes between 600 m and 1,100 m (68 % of the area, 43). Since the mid-1990s, massive bark beetle (*Ips typographus*) proliferations have occurred in the BFNP’s forests, resulting in a dieback of old spruce trees over an area of ~7000 ha (44). Multispectral aerial images of the study area from 2008 (45) were used to classify forest areas according to the land cover (46), which was grouped into 11 classes (see Table 1). Images with a resolution of 0.4 m were used to isolate vegetation against the background of other underlying surfaces, different kinds of vegetation and different stages of vegetation of the same species (47).

The estimated roe deer population density was low, ranging between 1-3 animals/km² (48). Hence, density was not expected to affect habitat selection behaviour (25, 27). Between 2005 and 2012, 168 roe deer individuals were monitored (see Details on roe deer capture and data processing in Appendix S1a). The final analysis consisted of 15,267 locations of 17 females and 19 males.

**Statistical methods**

The methods described here are implemented and available in the R-Package FunResp (49).

**Habitat availability**

Availability was assessed for each individual per month and was calculated as 95% minimum convex polygons around an individual’s locations on a monthly basis using the R-package adehabitatHR (50). Data from individuals with a biologically unrealistic home range size, due, for example, to dispersal behaviour, were discarded, using the 90th percentile as a cut-off value (for females: 182 ha, for males: 459 ha). A rasterised landscape with a grid cell size of 10 × 10m² was used to obtain the relative availability for each habitat type within the monthly home ranges.

**Multicategorical logit model**

Discrete choice models were found to provide the most accurate and precise estimate of coefficients in a simulation study about habitat selection (51). If an animal is assumed to choose from a discrete set of options, e.g. habitat types or specific patches, its choice can be modelled using discrete-choice models (52–54). Data with a multicategory response can be fitted using baseline-category logit models (52). Following Agresti (52), in our study the habitat type with the highest prevalence was chosen as the baseline, which in the BFNP was the old mixed stand, used in 27% of all recorded locations.

The probability of choosing the baseline category $K$ was calculated as: $\pi_K(x_t) = 1 - \pi_1(x_t) - \ldots - \pi_{K-1}(x_t)$, where $x_t$ is a vector of the covariates describing the habitat and/or the individual (e.g. sex) at time $t$. Probabilities $\pi_i(x_t)$, $i = 1, \ldots, K - 1$ were derived by first fitting $K - 1$ binary logit models separately to the data (for all habitats except the baseline category) with $log\frac{\pi_i}{1-\pi_i} = f_i(x)$. The $i^{th}$ model included observations from habitat $i$ and the baseline category $K$ only, where $Y = 1$ if an individual was observed in habitat $i$ and $Y = 0$ if it was observed in the reference habitat $K$. Hence, no pseudo-absence points needed to be generated. From the logistic regression models, odds ratios $f_i(x)$ were obtained to
model the choice between habitat \( i \) and the reference type \( K \). Given the odds ratios \( f_i(x) \) for all habitats the probability of use (or the proportion of use) was estimated using the multinomial logit link:

\[
\pi_i(x) = \frac{\exp(f_i(x))}{1 + \sum_{s=1}^{K-1} \exp(f_s(x))}
\]  

with \( f_i \) being a general functional form of the explanatory variables. It can be regarded as a form of resource selection function. Both, smooth effects of the variables and random effects can be included to account for flexible forms and multiple sources of variations in habitat selection, as well as the characteristics of the animal (e.g. age or sex, 52). \( f_K \) is 0 for identifiability reasons. The denominator of Eq. 1 was the same for each habitat \( i \) at a specific time.

**Model components**

The models for the odds \( f_i(x) \), \( i = 1, \ldots, K - 1 \) included the effects of time and the relative availability of the habitat on habitat choice. Potential differences in the choice behaviours of males vs. females were also considered. Variations in selection behaviour across individuals and years were accounted for by including random effects on the intercept which allows the prevalence to vary between individuals and year (7).

The availability \( x_i \) of habitat type \( i \), i.e. the fraction of the area covered by habitat type \( i \), varied across the home ranges of different animals \( j \) and depending on time of year (month). This variation was accounted for by including the logarithm of the availability \( x_{jm}^{(i)} \) of a land-cover type within the corresponding monthly home range of the animal \( j \) as an offset term (called “base rate” in chapter 7 in 1). The offset assumes a linear increase of selection with increasing availability. Any deviation from such a direct proportionality with factor 1 (functional response, 35) was detected by including either a parametric or non-parametric (i.e. smoothing spline) effect of availability. We then investigated whether the type of functional response varied depending on the time of year (on a monthly basis) and with respect to the individual’s sex. The smoothness of the spline functions over the range of availability was controlled by setting the smoothing parameter to \( \lambda = 2 \) (55, p.128). Temporal variation in choice behaviour was accounted for by including a term for time, modelled by a cyclic (tensor product) smooth function, with or without distinguishing between the sexes (56). For the sake of simplicity, we did not include further covariates such as continuous variables, e.g. distance to roads, or random slopes in the model formula, however, extensions are technically feasible (52).

**Model selection & model fit**

Thirty-nine different models \( f_i(x) \) that estimated the effects of the above mentioned variables on the odds that roe deer select habitat type \( i \) over \( K \), were estimated for each habitat type \( i = 1, \ldots, K \). To take into account the problem of overfitting, the prediction performance of all models was measured by applying cross-validation (for Details see Appendix 1b). The predictions of models \( f_i(x) \), \( i = 1, \ldots, K \), with the highest predictive power were inserted in equation 1, obtaining real probability values for each habitat type at all times. These probability (or proportion of use) values were then related to the associated availability values resulting in functional response curves sensu (35).
Model prediction

Since the model is multinomial, proper selection probabilities can be obtained. In a first step odds ratios were calculated which are the relative selection strength with respect to the reference type, which is in our case the old mixed stands. By applying Eq. 1 probabilities were derived. Here, we had to make sure that the inserted values for all model variables were reasonable, namely that odds ratios are calculated with respect to the same reference, e.g. the same time of day and time of year and the sum of availabilities of all habitat is supposed to equal 1. When testing for the effect of a varying variable, all other values were held constant. In the case of varying relative availability, the availabilities of the other habitat types were equally proportionally adapted to ensure that the sum of availabilities of all habitat equals 1.

Referencing Holling’s types in the context of habitat use

To link functional response curves of roe deer to Holling’s equations (29). Theoretically, this could have been done for all times of year and day for each habitat type. However, we focused only on specific times, namely summer (June) and winter (December) for day (noon) and night (midnight). For type I: \( h_I(x) = ax \), where \( x \) is the relative availability of a habitat, a value between 0 and 1, and \( a \) the proportionality factor; for type II: \( h_{II}(x) = \frac{ax}{b+x} \) and for type III: \( h_{III}(x) = \frac{ax^2}{b+x^2} \). The optimisation routine minimised the residual sum of squares between the values of \( h_I(x) \), \( h_{II}(x) \) and \( h_{III}(x) \) and the values of \( \pi_i(x) \) (Eq. 1) estimated from the multicategory logit models by finding optimal values for \( a \) and \( b \). The R function optim of the package stats (57) was used for this purpose, with the values of \( a \) and \( b \) limited to 0 and 1 for \( h_{II} \) and \( h_{III} \). The Holling type with the smallest residual sum of squares was considered to best explain the shape of the functional response curve.

Results

A general behavioural pattern of roe deer in the BFNP was to change its proportion of use of a habitat based on habitat availability (Fig. 1). Notable functional responses were observed for almost all habitat types, as the estimated proportions of use differed strongly from straight lines (Fig. 1). The exception was the use of old mixed stands, especially during winter, as the proportion of use equals availability (Fig. 1). When calculating the proportion of use as a function of availability, given the selected models, three main patterns emerged (Fig. 1): an approximately linear pattern (relatable to Holling’s type I), a concave curve (type II) and a sigmoid curve (type III).

A type II response indicates an increasing use with increasing availability, but a decrease in the selection strength with increasing availability. The parameter \( a \) and \( b \) can assist in determining whether a habitat type is selected for or avoided and to what degree. The parameter \( a \) is the asymptote of the Holling type, which is the upper limit (or theoretical maximum) of use, and \( b \) is the availability at which use is half of its maximum (Fig. 2). The use of a habitat varied distinctly between seasons and between the time of day and so do the parameters \( a \) and \( b \).

The estimated maximum relative use \( a \) was usually much greater than \( b \). If \( a \) is larger than \( b \), a specific habitat is selected for as long the availability is less than \( x^* = a - b \) (for a derivation see S2). The value of \( b \) indicates the strength of use irrespective of availability: the smaller \( b \) the greater is the use for small values of availabilities. Hence, the value of \( b \) allows conclusion about how fast the functional curve reaches saturation and is an indicator of the attraction of a habitat. However, the value of \( a \) quantifies the
potential maximum use of a habitat but needs to be regarded in the light of value \( b \) (see Appendix S2 and S10 for Details).

For instance, the probability of males using cultivated meadows in summer increased strongly with increasing availability for very low values of availability (< 0.03) with a very steep slope; for higher values of availability (> 0.1) the slope was almost 0 (Fig. 1). This strong proportional use for small values of availability is recognisable in the small value of \( b \) (Table 2). For cultivated meadows in summer at midnight \( b = 0.01 \), resulting in a very steep increase in the functional response curve. Compared to unmanaged meadows where \( b = 0.03 \), this increase is less pronounced at midnight and even more less at noon where \( b = 0.17 \). We found strong variations of the \( b \)-value for many of the habitats for different times of day and year and also between males and females (e.g. clearcuts, young stands, old deciduous and medium mixed stands, Table 2).

If \( b < a \) the value of \( b \) influences when the shift occurs from selective use to avoidance, which is the tipping point \( x^* = a - b \). This value shows strong differences between different habitats but also within habitats for different times of day and year (Table 2). For males in summer at midnight unmanaged meadows are selected for (proportional use > proportional availability) when availability is less than \( x^* = 0.26 \) and are avoided (proportional use < proportional availability) if the availability of unmanaged meadows exceeds 26% of the home range’s area. In summer at noon the tipping point is smaller (\( x^* = 0.22 \)), indicating that unmanaged meadows are used with a lesser intensity at noon than at midnight (Table 2).

**Discussion**

As predicted by our hypotheses, habitat use of roe deer is strongly characterised by functional response, with distinct variability in the shape of those responses among habitats and depending on month, daytime and, for a few cases, an individual’s sex. Thus, our results are consistent with a non-linear relationship between use and habitat availability, as this pattern occurred in most of the considered habitat types. Furthermore, the shapes of the curves could be linked to Holling’s equations and the functional response parameters in turn estimated. By comparing those parameters with respect to time of day, season, sex and different habitats, this approach could contribute to an easier understanding of the temporal variations in habitat use by large herbivores.

The values of the parameters describing the functional response curves can be interpreted in ecological terms in prey-predator-systems (58). Transferred to habitat selection behaviour of animals, they provide information about the functional relation between habitat availability and use, and especially about general habitat preference or avoidance behaviours either as a function or independent of habitat availability.

For type I, the slope describing the increase in the predation rate with increasing prey density (\( a \) in \( h_I(x) = ax \)) can be applied to habitat selection as well, as it also describes the linear increase in habitat use with increasing availability.

For type II and III, in \( h_{II}(x) = \frac{ax}{b^2 + x^2} \) and \( h_{III}(x) = \frac{ax^2}{b^2 + x^2} \), \( a \) is the asymptote that is approached as \( x \) increases. While it represents the maximum number of prey a predator can handle per unit time, when applied to habitat selection, it indicates the theoretical maximum habitat use at a specific time (season and time of day). The value of \( b \) was originally defined as the prey density at which a predator exhibits half of its maximum predation rate which is associated with the handling time. In the case of habitat selection, it is the availability at which habitat use is half-maximum at a specific time. Thus, the smaller the value of \( b \)
the greater the attraction of the habitat for the foraging animal as the saturation of the functional response
curve takes place for very small values of availabilities. Consequently, in the context of habitat selection
$b$ is associated with the attraction of a habitat for a species.

A type II functional response, indicative of a continuous decrease in selection strength with increased
habitat availability, was the most commonly observed pattern, especially in summer (Fig. 1). However, the
upper limit of use (denoted by $a$) and the degree of attraction (indicated by $b$) differed between different
habitats and over different time scales. Habitat selection by herbivores can involve a trade-off between
different needs, e.g. between food intake and risk avoidance which affect the proportion of time spent
in a habitat (15, 56). For instance, for roe deer, meadows satisfy their energy demands but at the same
time pose a higher risk as they do not provide much cover (59) whereas e.g. medium-aged mixed stands
offer shelter and forage but the quality and quantity of forage are lower (9, 60). Consequently, habitats
vary in the strength of the perceived trade-off that the animals are faced with due to their need to fulfill
sometimes conflicting demands and shapes of functional response are known to be more pronounced
when the strength of this trade-off situation, perceived by the animals, is increased (16). Hence, risk-
resource trade-offs may be the cause of functional response in habitat selection (15, 35) and Holling’s
types and associated parameters $a$ and $b$ can support to shed light on this relationship.

For roe deer in the BFNP, type II functional response patterns indicate saturation of use for relatively
small values of relative availability for some habitat types. For example, the use of cultivated meadows
(Fig. 1) by males in summer during the night was very high whereby the strong increase appears for very
low availabilities (half maximum use at availability $b = 0.01$) and keeps almost constant for increasing
availability with an upper limit of $a = 0.24$. Thus, male roe deer did not spend more than one fourth of
their time on a meadow during night. This was apparently enough to satisfy their needs and it did not
change if availability within the home range increased further which is linked to the strong trade-off the
animal is facing when using a habitat (16). The ratio $a/b$ (Table 2, Appendix 10) displays the strength
of the functional response, the greater the ratio the greater is the overall use. If the ratio is greater than
1 it means that use is greater than availability, hence selection takes place, for availabilities smaller than
$x^\ast = a - b$. A small ratio $a/b$ indicates a less pronounced or even absent functional responses which was
found for habitats with a low food/cover trade-off such as medium-aged mixed stands (Table 2, Fig. 1).

In type III responses, use is low at low availabilities but then increases more rapidly than it is the case
in a proportional use. The detection of habitats that evoked a type III functional response suggests that in
those cases availability influenced habitat use to a larger degree than an individual’s physiological needs.
In predator-prey dynamics, a type III response occurs in systems with more than one prey species and can
be explained by either a learning process or prey switching (61, 62). In the context of habitat selection in
herbivores, a type III response may occur if an individual has no other option than to become accustomed
to a habitat type. For more details on how to interprete the parameters $a$ and $b$ for Holling type III see
Appendix 2.

This study was based on a data set of roe deer from a specific study region, namely the BFNP. Even
though we are aware that habitat selection is a complex process involving a range of variables, we believe
that the here presented approach has the potential to support the detection of general trends in habitat
selection, which could foster the development of large-scale wildlife measures.
Conclusions

From an ecological perspective, the estimators $a$ for maximum use and $b$ for the attraction of a habitat can shed light on general trends in habitat selection or avoidance. While resource selection functions in the way commonly used fall short in displaying the effect of habitat availability on the selection coefficient, the here taken approach of using multicategorical logit models and relating the derived functional response curves to Holling’s types offers the opportunity to detect general trends in habitat selection and avoidance by taking into account habitat availability at different temporal scales. The application of Holling’s functional response type in habitat selection of animals allows to estimate the relevance of a habitat type for the species of concern and shed light on the cost-to-benefit ratio perceived by the species when using this habitat. This approach has the potential to offer a better comparability of habitat selection behaviour of animals between different study areas.

Supplementary information

Supplementary information accompanies this paper:

Appendix S1a: Roe Deer Capture and Radiotelemetry Data
Appendix S1b: Model selection & model fit
Appendix S2: Holling’s equation as applied to habitat selection
Appendix Fig. S3. AUC values for model selection
Appendix Fig. S4. Habitat selection by females
Appendix Fig. S5. Habitat selection by males
Appendix Fig. S6. Shapes of the functional response curves for females in June
Appendix Fig. S7. Shapes of the functional response curves for males in December
Appendix Fig. S8. Shapes of the functional response curves for females in December
Appendix S9. Overview tables of optimal models describing Holling types for males and females in June and December
Appendix S10: Overview of the effect of varying parameters $a$ and $b$ of the Holling’s type II on the functional response curve, linking the proportion of availability of a habitat with the proportion of its use.

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Availability of data and materials

The raw data used in this study are accessible via the eurodeer database www.eurodeer.org.

Ethics approval and consent to participate

None.

Authors’ contributions

CD, MH designed the study; MH organised and supervised data collection and management; CD performed the analysis and wrote an initial draft of the manuscript; all authors contributed to the revisions of the manuscript and gave final approval for its publication.
References

1. Manly, B., McDonald, L., Thomas, D., McDonald, T., Ecobichon, W.: Resource Selection by Animals: Statistical Design and Analysis for Field Studies, Chapman and Hall, London, ??? (2002).

2. Boyce, M., Verrier, P., Nielsen, S., Schmiegelow, F.: Evaluating resource selection functions. Ecological Modelling 157(2-3), 281–300 (2002).

3. Ewalt, M., Dupla, C., Heuch, M., Miller, J., Reineking, B.: LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of European roe deer. - Forests 5(6), 1374–1390 (2014).

4. Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M., Matthiopoulos, J.: The interpretation of habitat preference metrics under use-availability designs. Philosophical Transaction of the Royal Society B-Biological Sciences 365(1550), 2245–2254 (2010). doi:10.1098/rstb.2010.0088.

5. Holbrook, J.D., Olson, L.E., DeCesare, N.J., Hebblewhite, M., Squiers, J.R., Steenweg, R.: Functional responses in habitat selection: clarifying hypotheses and interpretations. Ecological Applications 29(3), 01852 (2015).

6. Boyce, M.S., McDonald, L.L.: Relating populations to habitats using resource selection functions. Trends in Ecology & Evolution 14(7), 269–272 (1999). doi:10.1016/S0169-5347(99)01593-1.

7. Gillies, C., Hebblewhite, M., Nielsen, S., Krauchuk, M., Frair, J., Saher, D., Stevens, C., Jerde, C.: Application of random effects to the study of resource selection by animals. Journal Of Animal Ecology 75(4), 887–898 (2006).

8. Hérard-Floch, I., Tremblay, J.P., Hansen, B.B., Solberg, E.J., Heim, M., Sæther, B.E.: Scale dependency and functional response in mouse habitat selection. Ecology 32(5), 849–859 (2009). doi:10.1111/j.1600-0587.2009.07837.

9. Bjørneraas, K., Hérard-Floch, I., Solberg, E.J., Sæther, B.E., van Moorter, B., Rolandsen, C.M.: Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oecologia 168(1), 231–243 (2012).

10. Morand, G., Fortin, D., Couturier, S., Duchene, T.: Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests. Journal of Applied Ecology 49(3), 611–620 (2012). doi:10.1111/j.1365-2664.2012.02134.x.

11. Johnson, D.: The comparison of usage and availability measurements for evaluating resource preference. Ecology 61(1), 65–71 (1980).

12. McLoughlin, P., Gaillard, J., Boyce, M., Benenfant, C., Messier, F., Duncan, P., Delorme, D., Van Moorter, B., Said, S., Klein, F.: Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88(12), 3192–3201 (2007).

13. Côté, M.L., Couturier, S., St-Laurent, M.-H., Drapeau, P., Dussault, C., Rudolph, T., Brodeur, V., Merk, J.A., Fortin, D.: Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. Journal of Applied Ecology 52(2), 496–504 (2015). doi:10.1111/1365-2664.1260.

14. Martin, J., Vouc’h, G., Bonnot, N., Cargnelutti, B., Chaval, Y., Loretet, B., Gouraud, M., Hoch, T., Plantard, O., Hewson, A.J.M., et al.: Temporal shifts in landscape connectivity for an ecosystem engineer, the roe deer, across a multiple-use landscape. Landscape Ecology 33(6), 937–956 (2018).

15. Godvik, I.M.R., Leu, L.E., Vlk, J.O., Velberg, V., Langvatn, R., Mysterud, A.: Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90(3), 699–710 (2009). doi:10.1890/08-0576.

16. Maflke, G., Dussault, C., Ouellet, J.-P., Laurian, C.: Linking trade-offs in habitat selection with the occurrence of functional responses for moose living in two nearby study areas. Oecologia 178(4), 965–977 (2012). doi:10.1007/s00442-012-2382-0.

17. Godvik, I.M.R., Langvatn, R., Mysterud, A., Møller, N., Calenge, C.: Same habitat composition but different use: evidence of context-dependent habitat selection in roe dear females. Scientific Reports 8 (2018).

18. Aebischer, N.J., Robertson, P.A., Kenward, R.E.: Compositional analysis of habitat use from animal radio-tracking data. Ecology 74(5), 1313–1325 (1993).

19. Worton, D.B., Shephard, T.E., Peterson, D.C.: Poisson point process models solve the pseudo-absence problem for presence-only data in ecological analysis. Annals of Applied Statistics 4(4), 2203–2204 (2010).

20. McGeoch, K., Han, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A.: Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31(6), 1161–1175 (2016).

21. Thurfjell, H., Côté, S., Boyce, M.: Applications of step-selection functions in ecology and conservation. - Movement Ecology 4, 4 (2014). doi:10.1186/2051-3933-2-4.

22. Hebblewhite, M., Merrill, E.: Modeling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45(3), 834–844 (2008). doi:10.1111/j.1365-2664.2008.01466.

23. Roever, C.L., Van Aarde, R.J., Leggett, K.: Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant. Ecology 85(11), 972–982 (2012).

24. Muff, S., Signer, J., Flebeg, J.: Accounting for individualspecific variation in habitat-selection studies: Efficient estimation of mixed-effects models using bayesian or frequentist computation. Journal of Animal Ecology 89(1), 80–92 (2020).
55. Wood, S.N.: Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC, ??? (2006)
56. Dupke, C., Bonenfant, C., Reineking, B., Hable, R., Zeppenfeld, T., Ewald, M., Henrich, M.: Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. Ecography 40(8), 1014–1027 (2017)
57. R Core Team: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (2017). R Foundation for Statistical Computing. https://www.R-project.org/
58. Bolker, B.M.: Ecological Models and Data in R. Princeton University Press, Princeton, New Jersey, ??? (2008)
59. Fied, A., DHI, L.: Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1) (2002)
60. Bonnot, N.C., Gourard, M., Hewison, A.J.M., Cardinet, B., Lortet, B., Chaval, Y., Morellet, N.: Boldness-mediated habitat use tactics and reproductive success in a wild large herbivore. Animal Behaviour 145, 107–115 (2018)
61. Real, L.: The kinetics of functional response. The American Naturalist 111 (978), 289–300 (1977)
62. Dawes, J., Souza, M.: A derivation of holling’s type I, II and III functional responses in predator–prey systems. Journal of theoretical biology 327, 11–22 (2013)

Figures

Figure 1 Shapes of functional response curves based on Holling’s types I, II or III for all habitats in June for 19 males roe deer during night (red dashed line) and day (green dot-dashed line) and the associated estimated optimal values for the parameters defining the Holling type. Black lines in the background of the coloured curves are the estimates based on multcategory logit models. Grey line indicates proportionality of use to availability.

Figure 2 Concept plot of the most familiar Holling’s type II functional response \( y(x) = \frac{ax}{b+x} \) for \( a = 0.8 \) and \( b = 0.15 \). \( x \) is the proportion of availability of a habitat in the home range, limited between 0 and 1, \( y(x) \) is the use of a habitat limited between 0 and \( a \), the upper bound of use and \( b \) the availability of a habitat at which the habitat is used half of the maximum (\( f(b) = \frac{a}{2} \)). Parameters \( a \) and \( b \) become ecologically valuable and interpretable when applying limit calculations (see Appendix S2, S10).

Tables

Table 1 Overview of the relative availability of habitat types in the study area, relative availability within the home ranges and relative use by roe deer in the Bavarian Forest National Park, in descending order of use.

| Habitat              | Availability in the study area | Availability in the home range | Use |
|----------------------|-------------------------------|-------------------------------|-----|
| Old deciduous        | 0.184                         | 0.230                         | 0.247|
| Old mixed            | 0.231                         | 0.393                         | 0.188|
| Old coniferous       | 0.220                         | 0.188                         | 0.170|
| Cultivated meadows   | 0.051                         | 0.060                         | 0.102|
| Medium mixed         | 0.075                         | 0.045                         | 0.079|
| Unmanaged meadows    | 0.020                         | 0.014                         | 0.064|
| Clearcuts            | 0.046                         | 0.024                         | 0.062|
| Young stands         | 0.020                         | 0.009                         | 0.047|
| Anthropogenic        | 0.027                         | 0.022                         | 0.018|
| Medium deciduous     | 0.015                         | 0.007                         | 0.014|
| Disturbance area     | 0.111                         | 0.008                         | 0.010|
Table 2 Parameters estimated for Holling’s equation fitted to the functional response curves describing the use of the available habitat types by male roe deer in the Bavarian Forest National Park in summer (June) at different times of day (noon/midnight). Associated curves are shown in Fig. 1. Holling’s equations for type I \( h_1(x) = ax \), where \( x \) is the availability of a habitat; for type II \( h_II(x) = \frac{ax}{b + x} \), and for type III \( h_III(x) = \frac{ax^2}{b + x^2} \). The fraction \( \frac{a}{b} \) indicates the selection strength independent of availability of a habitat: the greater the value the greater the general use. The value \( x^* = \frac{a}{b} \) for Holling type II is the availability at which use equals availability, hence the value of relative availability at which no selection occurs, which is the tipping point when selection switches to avoidance of a habitat.

| Habitat               | Sex | Month | Hour | type | a   | b   | a/b | x*  |
|-----------------------|-----|-------|------|------|-----|-----|-----|-----|
| Old mixed             | m   | 6     | 0 I  | I    | 0.71| 0   | 0   | 0   |
|                       |     |       | 12 I | I    | 0.94| 0   | 0   | 0   |
| Bark beetle area      | m   | 6     | 0 I  | I    | 0.40| 0   | 0   | 0   |
|                       |     |       | 12 II| I    | 0.39| 0.17| 2.34| 0.23|
| Unmanaged meadows     | m   | 6     | 0 II | II   | 0.29| 0.03| 9.16| 0.26|
|                       |     |       | 12 II| II   | 0.39| 0.17| 2.31| 0.22|
| Cultivated meadows    | m   | 6     | 0 II | III  | 0.24| 0.01| 22.67| 0.23|
|                       |     |       | 12 III| I    | 0.02| 0.04| 0.40| 0   |
| Clearcuts             | m   | 6     | 0 II | II   | 0.18| 0.07| 2.51| 0.11|
|                       |     |       | 12 II| II   | 0.20| 0.09| 2.35| 0.12|
| Young stands          | m   | 6     | 0 II | II   | 0.16| 0.12| 1.35| 0.04|
|                       |     |       | 12 II| II   | 0.20| 0.06| 3.52| 0.15|
| Old deciduous         | m   | 6     | 0 II | II   | 0.24| 0.18| 1.32| 0.06|
|                       |     |       | 12 II| II   | 0.30| 0.21| 1.45| 0.09|
| Old coniferous        | m   | 6     | 0 I  | I    | 0.37| 0   | 0   | 0   |
|                       |     |       | 12 I | I    | 0.46| 0   | 0   | 0   |
| Medium mixed          | m   | 6     | 0 III| III  | 0.19| 0.21| 0.90| 0   |
|                       |     |       | 12 II| II   | 0.82| 0.72| 1.14| 0.10|
| Medium deciduous      | m   | 6     | 0 II | II   | 0.13| 1.00| 0.13| 0   |
|                       |     |       | 12 II| II   | 0.00| 0.00| 0.87| 0   |
| Anthropogenic         | m   | 6     | 0 II | II   | 0.05| 1.00| 0.05| 0   |
|                       |     |       | 12 II| II   | 0.00| 1.00| 0.00| 0   |