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# Functional responses in habitat selection: clarifying hypotheses and interpretations

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*Abstract.* A fundamental challenge in habitat ecology and management is understanding the mechanisms generating animal distributions. Studies of habitat selection provide a lens into such mechanisms, but are often limited by unrealistic assumptions. For example, most studies assume that habitat selection is constant with respect to the availability of resources, such that habitat use remains proportional to availability. To the contrary, a growing body of work has shown the fallacy of this assumption, indicating that animals modify their behavior depending on the context at broader scales. This has been termed a functional response in habitat selection. Furthermore, a diversity of methods is employed to model functional responses in habitat selection, with little attention to how methodology might affect scientific and conservation conclusions. Here, we first review the conceptual and statistical foundations of methods currently used to model functional responses and clarify the ecological tests evaluated within each approach. We then use a combination of simulated and empirical data sets to evaluate the similarities and differences among approaches. Importantly, we identified multiple statistical issues with the most widely applied approaches to understand functional responses, including: (1) a complex and important role of random- or individual-level intercepts in adjusting individual-level regression coefficients as resource availability changes and (2) a sensitivity of results to poorly informed individual-level coefficients estimated for animals with low availability of a given resource. Consequently, we provide guidance on applying approaches that are insensitive to these issues with the goal of advancing our understanding of animal habitat ecology and management. Finally, we characterize the management implications of assuming similarity between the current approaches to model functional responses with two empirical data sets of federally threatened species: Canada lynx (*Lynx canadensis*) in the United States and woodland caribou (*Rangifer tarandus caribou*) in Canada. Collectively, our assessment helps clarify the similarities and differences among current approaches and, therefore, assists the integration of functional responses into the mainstream of habitat ecology and management.

*Key words: functional response; generalized linear mixed models; habitat availability; habitat selection; habitat use;* Lynx canadensis; Rangifer tarandus caribou; *resource selection function.*

## INTRODUCTION

Ecologists are interested in the mechanisms driving variation in the distribution and demography of animals. Studies of habitat selection, the process by which animals choose resources, provide a lens into such mechanisms by linking patterns of animal behavior to underlying resource availability (Johnson 1980). The selection process is assumed to result from innate or learned preferences that correspond to fitness benefits, and is commonly studied by monitoring the spatial behavior of animals (Gaillard et al. 2010, Aarts et al. 2012). Habitat selection is often quantified by statistically comparing environmental attributes at a sample of animal locations (habitat use) to another sample of environmental attributes at surrounding locations (availability; Johnson 1980, Manly et al. 2002, Lele et al. 2013) via a resource selection function (RSF; Boyce and McDonald 1999). However, estimating selection in this manner, with the intent to infer underlying mechanisms,

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is fraught with challenges (e.g., Manly et al. 2002, Aarts et al. 2008, Beyer et al. 2010, Lele et al. 2013).

One of these challenges is that animals may exhibit context-dependent habitat use or selection, such that habitat use varies across a sample of individuals because each individual is experiencing different environments (e.g., availability) and thus behaving differently. Mysterud and Ims (1998) were the first to explicitly characterize this phenomenon, which they termed a "functional response," in habitat use. This term was adapted from predation studies indicating that predator consumption rates (i.e., use) change according to variation in prey abundance (prey availability; Holling 1959). Characterizing a functional response in habitat use was an important contribution, but also indicated the tenuous nature of the ubiquitous assumption of constant habitat selection within a use–availability design (mentioned in Beyer et al. 2010, Lele et al. 2013). Indeed, this assumption has since proven widely unrealistic, as a growing number of studies have demonstrated functional responses in habitat use and selection (e.g., Hebblewhite and Merrill 2008, Moreau et al. 2012, Tardy et al. 2014, Holbrook et al. 2017*a*).

Characterizing functional responses provides a means to evaluate the assumption of constant habitat selection within use–availability designs and, perhaps more importantly, to reveal additional behavioral mechanisms that contribute to the distributions of animals. However, since the foundational article of Mysterud and Ims (1998), an array of ecological tests and analytical procedures has been applied to characterize functional responses. For instance, Mysterud and Ims (1998) pioneered the idea of a functional response by assessing how habitat use for an environmental resource changed as a function of resource availability (i.e., independent of an RSF). They demonstrated that eastern gray squirrels (*Sciurus carolinensis*) exhibited strong selection for habitat patches of food in the context of low availability, but when availability increased squirrels avoided food patches (Mysterud and Ims 1998). This pattern was presumably because of a trade-off whereby squirrels were balancing foraging opportunities in open habitats with proximity to security cover in forested habitats (Mysterud and Ims 1998). In just one year after Mysterud and Ims's (1998) foundational paper, Boyce and McDonald (1999) suggested an additional approach to evaluate functional responses, which was characterized as a two-staged approach: (1) fit an RSF for each animal and (2) use linear regression to evaluate how resource availability influenced the habitat selection coefficients as estimated via the RSF. In discussions following Boyce and McDonald (1999), Boyce et al. (1999) once again provided another approach for assessing functional responses by incorporating resource availability directly within a multivariate RSF, presumably via interactions between resource selection and availability.

Now 20 years later, there are many examples of ecologists implementing or expanding on each of these approaches. The ecological context for applying a particular technique appears to be associated with the underlying motivation of the ecologist. For instance, under the motivation of *understanding* the behavioral responses of animals, multiple studies have evaluated the influence of habitat availability on measures of habitat use (e.g., Mauritzen et al. 2003, Hansen et al. 2009, Pellerin et al. 2010, Laforge et al. 2015, Holbrook et al. 2017*a*), while others have assessed how availability influences selection coefficients derived from RSFs (e.g., Gillies et al. 2006, Hebblewhite and Merrill 2008, Moreau et al. 2012, Roever et al. 2012, Knopff et al. 2014) as well as how selection interacts with availability within a multivariate RSF (e.g., Godvik et al. 2009, Moreau et al. 2012, Tardy et al. 2014, Bastille-Rousseau et al. 2015, van Beest et al. 2016). Under a predominately *prediction* motivation, others have applied and extended the concept of functional responses to develop spatially and temporally transferable models that better predict species distributions in novel environments (e.g., Matthiopoulos et al. 2011, Aarts et al. 2013, Paton and Matthiopoulos 2016). The generalized functional response approach of Matthiopoulos et al. (2011) is a nice example, which demonstrated better (out-of-sample) predictive performance than traditional RSFs by allowing selection to interact with the availability of many different environmental resources. Indeed, there have been a diversity of approaches used to evaluate the question of functional responses in habitat ecology, but the selection of a particular approach seemingly depends on the motivation of the researcher.

Here, our objective was to evaluate the suite of approaches when the motivation is to *understand* functional responses of animals to key environmental resources. For instance, under this motivation one might ask for a forest-dependent species, "How does habitat use or selection of old-growth forest change as the availability of old-growth ranges from low to high?" We might expect the forest-dependent species to spend much more time in old-growth forest when it is less available on the landscape relative to when it is abundant, which would provide insight concerning the behavioral link between this species and old-growth forest. Our evaluation of current techniques to model functional responses is needed because they are assumed to generate similar results and conservation conclusions (van Beest et al. 2016). Therefore, we (1) reviewed the conceptual and statistical foundation of each approach, (2) assessed the strengths and weaknesses of each approach using simulated and empirical data sets, and (3) provided guidance for the study of functional responses with the goal of advancing ecological understandings of habitat relationships. Our simulations were constructed to capture the gradient in observed or described functional responses within the literature (Table 1). Our empirical data sets were collected from species of conservation concern, where the interpretation and ensuing conclusions could have significant management implications: (1)

TABLE 1. Ecological descriptions, example equations, and selected references for each functional response scenario we discovered in the literature.

| Scenario | Ecological description on the additive scale | Example equation on the additive scale | References |
|---|---|---|---|
| Proportional use/ generalist species | For a habitat generalist, habitat use will be proportional to availability (i.e., effectively random). This is the null hypothesis tested when evaluating functional responses. | $\bar{m}^U(x_1) = \bar{m}^A(x_1) + 0$ | Mysterud and Ims (1998), Roever et al. (2012) |
| Constant use | Constant use indicates that habitat use remains fixed across the gradient in availability. This is difficult to conceptualize in real populations, but nonetheless serves as a useful thought experiment | $\bar{m}^U(x_1) = 0 \times \bar{m}^A(x_1) + \text{constant}$ | Beyer et al. (2010) |
| Additive use | Additive use is a situation where a resource is always selected,† but a constant and additive function of proportional use because of some benefit. | $\bar{m}^U(x_1) = 1 \times \bar{m}^A(x_1) + \text{constant}$ | Holbrook et al. (2017*a*) |
| Relaxed selection/ specialist species | For a habitat specialist, one might expect stronger selection at low availabilities but, when the resource is abundant, habitat selection declines to approximate proportionality. | $\bar{m}^U(x_1) = 0.25 \times \bar{m}^A(x_1) + \text{constant}$ | Mauritzen et al. (2003), Holbrook et al. (2017*a*) |
| Increasing use | Increasing use is a situation where a resource is always selected,† but increasingly used (relative to random) as it becomes more available because of some benefit. | $\bar{m}^U(x_1) = 1.5 \times \bar{m}^A(x_1) + \text{constant}$ | Holbrook et al. (2017*a*); also increasing selection in Moreau et al. (2012), Tardy et al. (2014), van Beest et al. (2016) |
| Trade-off | A trade-off is where a resource (e.g., food) is selected at low availabilities, but as it crosses a threshold in availability the resource becomes avoided because of decreasing availability of an opposing resource (e.g., escape cover). | $\bar{m}^U(x_1) = 0.5 \times \bar{m}^A(x_1) + \text{constant}$ | Mysterud and Ims (1998), Godvik et al. (2009), van Beest et al. (2016) |
| Decreasing use | Decreasing use is a situation where a resource is always avoided,† but decreasingly used (relative to random) as it becomes more available because of some cost. | $\bar{m}^U(x_1) = 0.5 \times \bar{m}^A(x_1) - \text{constant}$ | Holbrook et al. (2017*a*); also decreasing selection in Hebblewhite and Merrill (2008) |
| Relaxed avoidance | Relaxed avoidance could occur if a disturbance is rare on the landscape resulting in strong avoidance when first encountered, but as the disturbance increases, avoidance decreases because of habituation or potential rewards. | $\bar{m}^U(x_1) = 1.5 \times \bar{m}^A(x_1) - \text{constant}$ | Knopff et al. (2014) |

*Note:* The abbreviations $\bar{m}^U(x_1)$ and $\bar{m}^A(x_1)$ indicate a vector (i.e., across individuals) of mean values for resource $x_1$ at used and available units, respectively.

†On the additive scale, we cannot determine increasing selection or avoidance. We need to know the multiplicative relationship between use and availability to determine increasing selection or avoidance.

threatened Canada lynx (*Lynx canadensis*) in the Northern Rocky Mountains, United States, and (2) threatened boreal woodland caribou (*Rangifer tarandus caribou*) in Alberta, Canada. Our overarching goal was to clarify similarities and differences among approaches and ultimately help integrate the assessment of functional responses into the mainstream of habitat ecology and management.

## METHODS

### *Assessing constant use: additive vs. multiplicative*

One distinction among the approaches to characterize functional responses is that constant use has been tested on both the additive and multiplicative scale (e.g., Mysterud and Ims 1998, Pellerin et al. 2010, Laforge et al. 2015, Holbrook et al. 2017*a*). These tests yield the same answer in the case of a 1:1 relationship, but generate important differences when selection or avoidance is evident. First, let us assume that $f^A(x_1) = (f^A(x_1)_1, f^A(x_1)_2, \ldots, f^A(x_1)_i)$ is a vector characterizing the available distribution and $f^U(x_1) = (f^U(x_1)_1, f^U(x_1)_2, \ldots, f^U(x_1)_i)$ is a vector of the use distribution across individual animals ($i$) for a continuous resource $x_1$ (e.g., Aarts et al. 2012: Fig. 1). These distributions can be summarized from a sample of observations by calculating the mean or median value of resource $x_1$ across available and used units (e.g., $\bar{m}^A(x_1), \bar{m}^U(x_1)$, respectively). With this in mind, the following two examples highlight the difference between the additive and multiplicative assessment of functional responses.

First, suppose individuals within species A exhibit a use distribution for a particular habitat type such that use remains 20% more than availability in an additive sense (e.g., 40% use at 20% availability, 50% use at 30% availability; Fig. 1). A test for a functional response on the additive scale will show a consistent and additive difference between use and availability and no functional response: $\bar{m}^U(x_1) = 1 \times \bar{m}^A(x_1) +$ constant, where the slope coefficient = 1 (Fig. 1). However, a test in the multiplicative sense (e.g., on the logarithmic scale) will show a decrease in the use/availability ratio and a negative functional response: $\log(\bar{m}^U(x_1)) = 0.64 \times \log(\bar{m}^A(x_1)) +$ constant, where the slope coefficient = 0.64 (Fig. 1). Alternately, suppose individuals within species B exhibit a use distribution such that use remains 50% more than availability in a multiplicative sense (e.g., 30% absolute use at 20% availability, 45% absolute use at 30% availability). Testing for a functional response in an additive sense would show an increasing difference between use and availability and a positive functional response: $\bar{m}^U(x_1) = 1.5 \times \bar{m}^A(x_1) +$ constant, where the slope coefficient = 1.5 (Fig. 1). However, the multiplicative test would show that the ratio between use/availability remains constant and thus no functional response: $\log(\bar{m}^U(x_1)) = 1 \times \log(\bar{m}^A(x_1)) +$ constant, where the slope coefficient = 1 (Fig. 1). This example demonstrates the importance of scale on the hypotheses associated with functional responses and the ensuing conclusions derived from such analyses.

### *Four approaches for modeling functional responses*

*Additive habitat use (approach 1).*—The simplest approach to modeling functional responses is to assess how the sample of use $(\bar{m}^U(x_1))$ changes with the sample of availability $(\bar{m}^A(x_1))$ on the additive scale. In this case, the null hypothesis with regard to a functional response is that the additive difference between use and availability is constant. Multiple studies (e.g., Pellerin et al. 2010, Laforge et al. 2015, Holbrook et al. 2017*a*) have recently applied this approach and the base model is as follows:

$$\bar{m}^U(x_1) = \theta_0 + \theta_1(\bar{m}^A(x_1)) \tag{1}$$

where, $\bar{m}^U(x_1)$ is a vector (i.e., across individuals) of mean values for resource $x_1$ at used units, $\bar{m}^A(x_1)$ is a vector (i.e., across individuals) of mean values for resource $x_1$ at available units, $\theta_0$ in the $y$ intercept, and $\theta_1$ is the slope of the functional response term. Statistical deviations from proportional habitat use (i.e., $\theta_1 = 1$) could indicate increasing habitat use ($\theta_1 > 1$) or decreasing habitat use ($\theta_1 < 1$). Additionally, as demonstrated in Holbrook et al. (2017*a*), curvilinear relationships are an important consideration and could be assessed by incorporating additional terms in the base model (e.g., polynomial regression).

*Multiplicative habitat use (approach 2).*—A second approach is to assess how habitat use changes across availability on the multiplicative scale, which was initially presented in Mysterud and Ims (1998). In this case, the null hypothesis is that habitat use is a constant multiplicative function of habitat availability, such that the ratio between $\bar{m}^U(x_1)$ and $\bar{m}^A(x_1)$ is constant. The ratio between $\bar{m}^U(x_1)$ and $\bar{m}^A(x_1)$ is equivalent to the Manly et al. (2002) selection ratio, $w_{x_1}$, which is proportional to the probability of selection (Aarts et al. 2012, Lele et al. 2013). Mysterud and Ims (1998) applied their approach in a situation of two habitat types with the logit transformation, but this could be extended to continuous resources by simply applying the natural logarithm

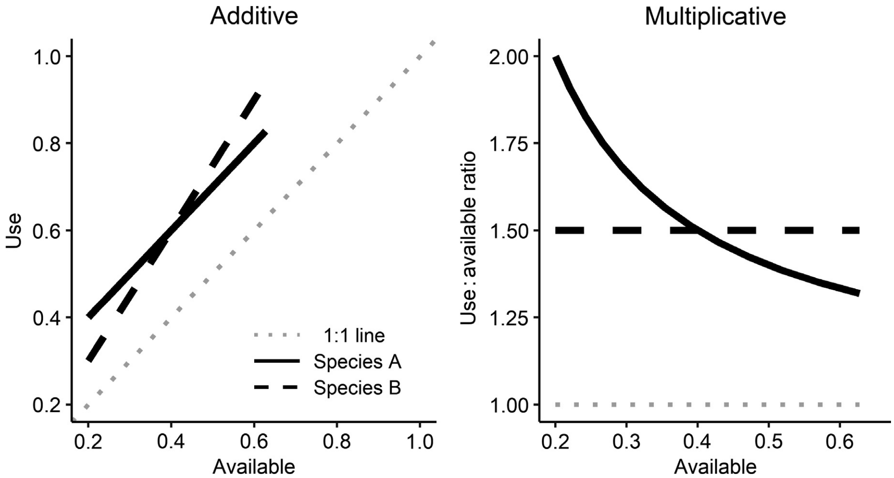

FIG. 1. Example demonstrating the difference between additive and multiplicative relationships when off the 1:1 line with respect to resource use (y-axis) and availability (x-axis). For instance, species A indicates proportional selection on the additive scale, but less than proportional on the multiplicative scale. Species B demonstrates increasing selection on the additive scale, but proportional selection on the multiplicative scale. The 1:1 line is where the additive and multiplicative scale are equal.

transformation to approach 1. The model for approach 2 is as follows:

$$\log(\bar{m}^U(x_1)) = \theta_0 + \theta_1(\log(\bar{m}^A(x_1))) \qquad (2)$$

where all components are the same as in approach 1 with the exception of the log transformation. The consequence of the log transformation is that when the ratio of use and availability remains constant (e.g., species B in Fig. 1), the slope ($\theta_1$) = 1. Thus, statistical deviations from a constant ratio between use and availability indicate a functional response in habitat selection (see Mysterud and Ims 1998). Similar to approach 1, curvilinear relationships could be assessed by incorporating additional terms in the base model.

*Habitat selection with selection coefficients (approach 3).*— A third approach is to characterize how individual-level selection coefficients (rather than $\bar{m}^U(x_1)$) change across availability using a resource selection function (RSF; Gillies et al. 2006, Hebblewhite and Merrill 2008, Moreau et al. 2012, Knopff et al. 2014). There are two treatments commonly used to generate estimates of individual-level coefficients, which will be used in a subsequent model to test for a functional response: (1) a generalized (i.e., logistic) linear mixed-effects model (GLMM) can be fit, including random intercepts and random coefficients for each individual (e.g., Hebblewhite and Merrill 2008) or (2) separate logistic models can be fit for each individual (i.e., two-stage approach; Boyce and McDonald 1999, Fieberg et al. 2010). As the first step in a two-stage approach, an estimating function for a single resource would take the following logistic form (Boyce et al. 2002):

$$\tau(x) = \frac{\exp(\beta_0 + \beta_1(x_{1i}))}{1 + \exp(\beta_0 + \beta_1(x_{1i}))} \qquad (3)$$

where $\beta_0$ is a vector of individual-level intercepts, $x_1$ is a vector of resource $x_1$ across individuals at used ($i$ = 1) and available units ($i$ = 0), and $\beta_1$ is a vector of individual-level selection coefficients for resource $x_1$. In the second step, the vector of individual coefficients ($\beta_1$, on the logit scale) are used in a different model to test for a functional response in selection by assessing whether the coefficients change with availability. Applying the logarithm to $\bar{m}^A(x_1)$ will preserve the multiplicative nature of the null hypothesis (e.g., Hebblewhite and Merrill 2008), which takes the following form:

$$\beta_1 = \theta_0 + \theta_1(\log(\bar{m}^A(x_1))) \qquad (4)$$

where, $\beta_1$ is a vector of individual-level selection coefficients for resource x$_1$, $\bar{m}^A(x_1)$ is a vector (i.e., across individuals) of mean values for resource $x_1$ at available units, $\theta_0$ is the $y$ intercept, and $\theta_1$ is the slope of the functional response term. Statistical deviations from proportionality (i.e., $\theta_1 = 0$) indicate a functional response. Conceptually, this approach (i.e., approach 3) seems similar to approach 2 in that both have null hypotheses of constant selection across changing availability. However, our results below demonstrate important differences when using selection ratios (approach 2) vs. individual-level coefficients (approach 3). Importantly, the estimation of individual coefficients with two-stage or GLMM modelling is affected by the concurrent estimation of individual intercepts, which are not part of approach 2.

*Habitat selection with RSF interaction (approach 4).*—A fourth approach, also involving RSFs in the form of GLMMs, is to evaluate the functional response explicitly within a GLMM by allowing individual-level habitat selection and availability for a particular resource to interact within a unified framework (Matthiopoulos et al. 2011, Moreau et al. 2012, Aarts et al. 2013, Tardy et al. 2014), which is different than the two-step process in approach 3. This modeling approach was presented in Tardy et al. (2014) where they used a logistic estimating function to generate regression coefficients, and plotted the marginal functional response across the gradient in $\bar{m}^A(x_1)$ using the log-linear RSF (Boyce et al. 2002):

$$w(x) = \exp(\beta_1(x_{1i}) + \theta_1(x_{1i} \times \bar{m}^A(x_1))) \qquad (5)$$

where $w(x)$ is the relative probability of selection, $\beta_1$ is the marginal RSF coefficient for resource $x_1$, $x_1$ is the vector of resource $x_1$ across individuals at used ($i$ = 1) and available units ($i$ = 0), and $\bar{m}^A(x_1)$ is a vector (across individuals) of mean values for resource $x_1$ at available units. Here, $\theta_1$ characterizes the functional response for resource $x_1$. Within this framework, information criteria are used to assess the support for the functional response represented by the interaction term (e.g., Godvik et al. 2009, Tardy et al. 2014, Mason and Fortin 2017). If there is no evidence of selection or avoidance (i.e., $\beta_1$ and $\theta_1 = 0$), the resulting predictions reduce to exp (0) and $w(x) = 1$. Thus, a predicted value of $w(x) = 1$ indicates proportional use and serves as a reference for interpreting functional responses in selection.

### Simulating and analyzing functional response scenarios

To evaluate the similarities and differences among the four approaches we simulated data sets characterizing different functional responses we identified in the literature (Table 1). We believe our review of the literature captured an exhaustive list of the different scenarios of functional responses previously documented or described. We conceptualized each scenario on the additive scale of use and availability and provided ecological descriptions, example equations, and selected references (Table 1).

We used program R (R Core Team 2017) to develop all scenarios (Simulation_Rcode, see *Data Availability*).

For each scenario, we simulated one continuous resource for 50 individuals, with 1,000 simulated GPS locations (i.e., used units) and 1,000 simulated random locations (i.e., available units) per individual. We used a range between 0 and 1 to indicate the proportion of a habitat type for a particular resolution or window size, which is a common resource in resource selection analyses. To generate available resource values, we first created an evenly spaced sequence of 50 mean values of availability, with a minimum of 0.25 and maximum of 0.60, chosen to provide an ideal and balanced range (i.e., not extremely low or high) at which to assess the suite of functional responses. For each individual, we then generated 1,000 random (i.e., available) values from a normal distribution, with the mean set to one of the values in the sequence between 0.25 and 0.6 and the standard deviation set to 0.2. To generate used resource values, we used a sequence of mean values created specifically for each functional response scenario (Table 1). For example, mean values for the proportional use scenario were created identically to the availability values, while the values for the additive use scenario used the same minimum and maximum sequence but added 0.2 to every value. The constant use scenario was created using a mean of 0.5 for every individual. The specialist, increasing use, trade-off, decreasing use, and relaxed avoidance scenarios were all created by adding varying amounts to each value in the original availability sequence (Simulation_Rcode, see *Data Availability*). If resource values were randomly generated above 1 or below 0, which could happen in some scenarios at the ends of the availability range (e.g., low or high), we replaced these values with 1 or 0, respectively, to maintain consistency in the resource distribution.

We then analyzed each scenario with the four modeling approaches aforementioned (Table 1, Simulation_Rcode: see *Data Availability*). We used linear and log-linear regression for approach 1 and approach 2, respectively. For the sake of simplicity we did not include curvilinear models with approach 1 or 2, but in real-world situations we would certainly incorporate curvilinear responses because (by definition) habitat use will equal availability at the extremely low or high end of availability. We computed 95% CIs to determine if there was evidence of a functional response (e.g., $\theta_1 \neq 1$) for approach 1 and 2. For approach 3, we estimated a mixed-effects RSF (i.e., logistic GLMM), with random intercepts and coefficients for each individual (e.g., Hebblewhite and Merrill 2008). We then used individual-specific coefficients in a subsequent log-linear regression to test the null hypothesis that $\theta_1 = 0$ ($\alpha = 0.05$). Finally, for approach 4, we estimated a more complex mixed-effects RSF including an interaction term (i.e., $\theta_1(x_{1i} \times \bar{m}^A(x_1))$) that characterized a functional response in habitat selection. We calculated AIC for a reduced model without $\theta_1$ and compared that to the full model including $\theta_1$. A value of $\Delta\text{AIC} > 2$ provided support for a functional response, which we verified with a 95% CI around the estimate of $\theta_1$. We performed all analyses in R (R Core Team 2017; Empirical_Rcode: see *Data Availability*).

### *Evaluating functional responses with real-world data: the case of Canada lynx and woodland caribou*

We then applied the four modeling approaches to evaluate functional responses in real-world data sets. We applied each approach to a data set collected on Canada lynx in the Northern Rockies, United States (Holbrook et al. 2017*a*) and another collected on boreal woodland caribou in Alberta, Canada (DeCesare et al. 2012). Both cases concern threatened species for which interpretations of animal responses to changing landscapes have important conservation implications.

Canada lynx data were collected in northwestern Montana, United States, during winter (i.e., November to March) between 1998 and 2015 (University of Montana IACUC permits 4-2008 and TE053737-1). All animals ($n$ = 63 adults; 27 females and 36 males) were equipped with GPS telemetry collars and resource use was measured at locations using 30-min fix intervals every other day. The GPS data were cleaned using standard procedures and winter use areas were constructed using 95% minimum convex polygons (see Holbrook et al. 2017*a* for details). Used locations ranged from 113 to 2,972 locations per lynx and random locations were sampled within individual use areas following a 1:1 allocation of used to available for each lynx. We measured two landscape resources at each location to assess functional responses by Canada lynx: (1) proportion of advanced regenerating forest at 250-$\text{m}^2$ resolution, and (2) predicted probability of snowshoe hare occupancy (from Holbrook et al. 2017*b*). We predicted lynx would exhibit consistent selection for regenerating forests and demonstrate increasing selection for snowshoe hare occupancy as it became rarer on the landscape (i.e., specialist response in Table 1).

The woodland caribou data were collected from the A la Pêche population in west-central Alberta, Canada, during 2001–2009. These data are a subset of those included within a previous study of resource selection in woodland caribou (see DeCesare et al. 2012). Adult female caribou ($n$ = 21 during summer, $n$ = 26 during winter) were captured with winter helicopter net-gunning and fitted with GPS telemetry collars. Capture protocols were approved by the University of Montana Institutional Animal Care and Use Committee (Animal Use Protocol 059-09MHWB-122209), University of Alberta Animal Care Committee (Protocol SCHM-2005-61), and Parks Canada Animal Care Committee (JNP-2009-4052). Resource use by caribou was sampled using GPS location data with 3- or 4-h fix intervals and averages of 2,288 (range = 591–3,660) and 2,854 (range = 602–6,115) locations per individual during summer and winter, respectively. Resource availability was sampled with random locations within seasonal use areas (i.e., 95% fixed kernel; DeCesare et al. 2012) following a 1:1 allocation of used to available for each caribou. A single resource, the density of linear features (seismic lines, roads, pipelines, and hiking trails; km/km$^2$), was estimated at used and available locations using circular neighborhoods of 70 m radii surrounding each location. Caribou avoid linear disturbances because they facilitate increased encounter rates with their primary predator, gray wolves (*Canis lupus*; DeCesare et al. 2012). Caribou were previously found to respond (i.e., avoid) most strongly to linear features at this radius of 70 m when studying third-order habitat selection (DeCesare et al. 2012).

We evaluated functional responses within our case studies using the same techniques as mentioned previously (see *Simulating and analyzing functional response scenarios*). However, for approach 3, we used both a GLMM RSF (e.g., Hebblewhite and Merrill 2008) and individual-specific RSFs (e.g., DeCesare et al. 2012, Knopff et al. 2014) to generate individual-level selection coefficients to test whether both methods yielded equivalent results.

In addition, functional responses within our own case studies, as well as others (e.g., Moreau et al. 2012, Knopff et al. 2014), suggested the potential for high influence of individuals with low availability of a given resource. The precision of individual coefficients decreases at low availability to the point where coefficients are inestimable for a resource that is neither used nor available (Beyer et al. 2010). Population-level estimates of average resource selection patterns across individuals often involve using inverse-variance weights to weight individual coefficients according to their relative precision (DeCesare et al. 2012). However, to our knowledge, this approach has not been applied in the evaluation of functional responses. While individual coefficients in our simulated data did not vary in precision, those estimated from real-world data do. Therefore, we applied approach 3 with both unweighted (i.e., approach 3A) and weighted (i.e., approach 3B) individual coefficients to assess how individual-level precision would affect the evaluation of functional responses. We used the methods of Murtaugh (2007) to estimate coefficient weights, $W_i$, for each individual $i$ as

$$W_i = \frac{1/[\mathrm{SE}(\beta_i)]^2}{\sum_i^N (1/[\mathrm{SE}(\beta_i)]^2)} \tag{6}$$

where $\beta_i$ is the individual-level selection coefficient. We then incorporated these weights in the model presented in Eq. 4 to place higher confidence on those coefficients with higher precision. Including $W_i$ in Eq. 4 will alter the precision of the regression such that observations with higher weights will increase the precision whereas observations with lower weights will have the opposite effect.

Finally, we also incorporated second and third degree polynomials into our applications of approaches 1 and 2 to test for curvilinear functional responses (e.g., Pellerin et al. 2010, Holbrook et al. 2017*a*). As mentioned by Mysterud and Ims (1998), disproportionate habitat use can occur in some parts of the range of availability and not in others. Moreover, habitat use will, by definition, equal availability at the extremely low or high end of availability; thus, curvilinear responses are an important consideration. For approach 1 and 2 we assessed the relative fit of each model (i.e., linear, second-degree polynomial, and third-degree polynomial) to our data using a likelihood-ratio test ($\alpha = 0.05$). Support for a curvilinear model indicated a functional response in habitat use, which we then assessed by plotting the relationships and associated 95% CIs. Finally, we back-transformed the log-linear predictions from approach 2 to the additive scale for visual display and interpretation (e.g., as in Fig. 1 of Mysterud and Ims 1998). All analyses were conducted in program R (R Core Team 2017; Empirical_Rcode: see *Data Availability*).

## RESULTS

### Simulated functional responses

Our analyses revealed differences in functional responses across the four modeling approaches (see Fig. 2, Table 2, Appendix S1: Table S1). First, approaches 3 and 4 fail to explicitly highlight habitat use, per se. Indeed, in many cases habitat use remained constant or increased as availability increased, while the functional responses for approach 3 and 4 were negative, indicating either a trade-off situation, decreasing selection, or increasing avoidance (Fig. 2; constant, specialist, trade-off, and decreasing scenarios). Thus, there are merits to assessing patterns of use concurrently with those of selection, particularly when important resources are abundantly available and consequently unlikely to appear statistically important when assessing selection alone (Beyer et al. 2010, Aarts et al. 2013, Holbrook et al. 2017*a*). Second, when using solely approach 1, it was impossible to identify how *selection* was changing. For instance, one can interpret whether habitat use remained above the 1:1 line, which indicated *consistent* selection, but the strict assumption of *constant* selection could not be evaluated. Under approach 1, both the increasing and decreasing scenarios indicated that habitat use deviated from random expectation, but approach 2 revealed that selection and avoidance, respectively, were additive functions of availability (Fig. 2, Table 2). These differences were a result of the additive and multiplicative scales (e.g., Fig. 1). In contrast, however, one can better infer how selection or avoidance changes if habitat use tends toward, or crosses, the 1:1 line as availability increases. For instance, all four approaches indicated decreasing selection or avoidance for the constant, specialist, trade-off, and avoidance scenarios (Fig. 2). Finally, approaches 2, 3, and 4 agreed when interpreting selection, with the

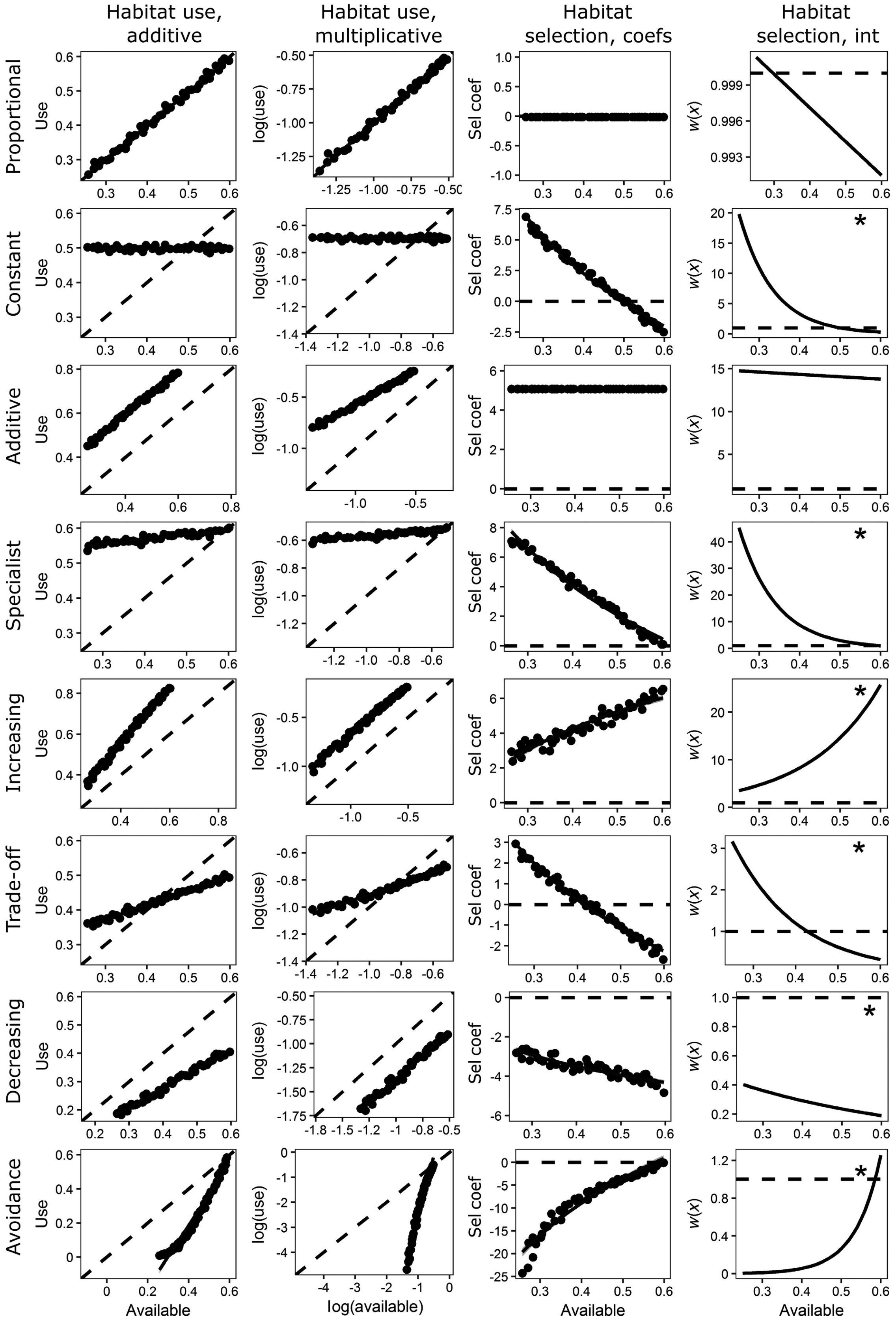
Habitat use, additive
Habitat use, multiplicative
Habitat selection, coefs
Habitat selection, int
Proportional
Constant
Additive
Specialist
Increasing
Trade-off
Decreasing
Avoidance
Use
log(use)
Sel coef
w(x)
*
Available
log(available)

FIG. 2. Functional responses in habitat use and selection across eight generated scenarios and four modeling approaches. Note the column of "Habitat use, additive" reflects the data generated from the descriptions in Table 1. The four modeling approaches are as follows: approach 1 (habitat use, additive), approach 2 (habitat use, multiplicative), approach 3 (habitat selection, coefficients), and approach 4 (habitat selection, interaction). Dashed lines indicate proportional habitat use, black dots indicate each simulated individual ($n$ = 50), and w(x) is the relative probability of selection. Approach 1, 2, and 3 include 95% CIs but given the low variation are not visible, and asterisks in approach 4 indicate statistical support ($P \leq 0.05$) for a functional response.

exception of the additive, increasing, and decreasing scenarios (Fig. 2, Table 2).

We also documented some important similarities across approaches. For instance, all four approaches indicated no functional response when habitat use followed null conditions (i.e., use was proportional to availability; proportional scenario in Fig. 2). Moreover, approaches 3 and 4 produced the same general conclusion across all scenarios (Fig. 2, Table 2). Finally, the explicit test of functional responses tended to agree across approaches and scenarios with only two exceptions associated with approach 2 (i.e., increasing and decreasing scenarios; Table 2).

### *Real-world functional responses: the case of Canada lynx and woodland caribou*

In our Canada lynx and woodland caribou case studies we also observed inconsistencies across modeling approaches. When applying approach 1, Canada lynx exhibited increasing habitat use with increasing availability of advanced regenerating forest, and habitat use increasingly deviated from random expectations (Fig. 3A, Table 3, Appendix S2: Table S1). While approach 2 demonstrated increasing habitat use with increasing availability, both approach 2 and approach 3 (with weighted coefficients) suggested constant selection and no functional response (Fig. 3A, Table 3, Appendix S2: Table S1). However, the unweighted version of approach 3 (both individual-level models and mixed-effects models) and approach 4 indicated evidence of decreasing selection for regenerating forest as it became more available (Fig. 3A, Table 3, Appendix S2: Table S1, Appendix S3: Fig. S1). In addition, after exponentiating the predictions from approach 2 back to the additive scale, the conclusion from approach 1 and 2 was similar with the exception of the log-normal errors in approach 2 (see Fig. 3A and Appendix S3: Fig. S1).

TABLE 2. Interpretation of functional responses observed in habitat use and selection across our simulated scenarios using the four different modeling approaches.

| Scenario | Additive habitat use (approach 1) | Multiplicative habitat use (approach 2) | Habitat selection with coefficients (approach 3) | Habitat selection with RSF interaction (approach 4) |
|---|---|---|---|---|
| Proportional use/generalist | (0) proportional use | (0) proportional use | (0) no selection | (0) no functional response |
| Constant use | (−) constant habitat use | (−) constant habitat use | (−) selected at low availabilities and avoided at high availabilities | (−) selected at low availabilities and avoided at high availabilities |
| Additive use | (0) additive use and consistent selection† | (−) increasing use but decreasing selection | (0) constant selection | (0) constant selection |
| Relaxed selection/ specialist species | (−) increasing use, but selection is relaxed | (−) increasing use, but selection is relaxed | (−) relaxed selection | (−) relaxed selection |
| Increasing use | (+) use is increasingly deviating from random and selection is consistent† | (0) increasing use and additive selection | (+) increasing selection | (+) increasing selection |
| Trade-off | (−) increasing use, but selected at low availabilities and avoided at high availabilities | (−) increasing use, but selected at low availabilities and avoided at high availabilities | (−) selected at low availabilities and avoided at high availabilities | (−) selected at low availabilities and avoided at high availabilities |
| Decreasing use | (−) increasing use, use is increasingly deviating from random, and avoidance is consistent† | (0) increasing use and additive avoidance | (−) increasing avoidance | (−) increasing avoidance |
| Relaxed avoidance | (+) increasing use, but avoidance is relaxed | (+) increasing use, but avoidance is relaxed | (+) relaxed avoidance | (+) relaxed avoidance |

*Notes:* Negative, positive, and no functional responses are indicated by −, +, and 0, respectively. See Appendix S1: Table S1 for the statistical summary that provides the basis for these interpretations. RSF, resource selection function.

†On the additive scale, we cannot determine increasing selection or avoidance. We need to know the multiplicative relationship between use and availability to determine increasing selection or avoidance.

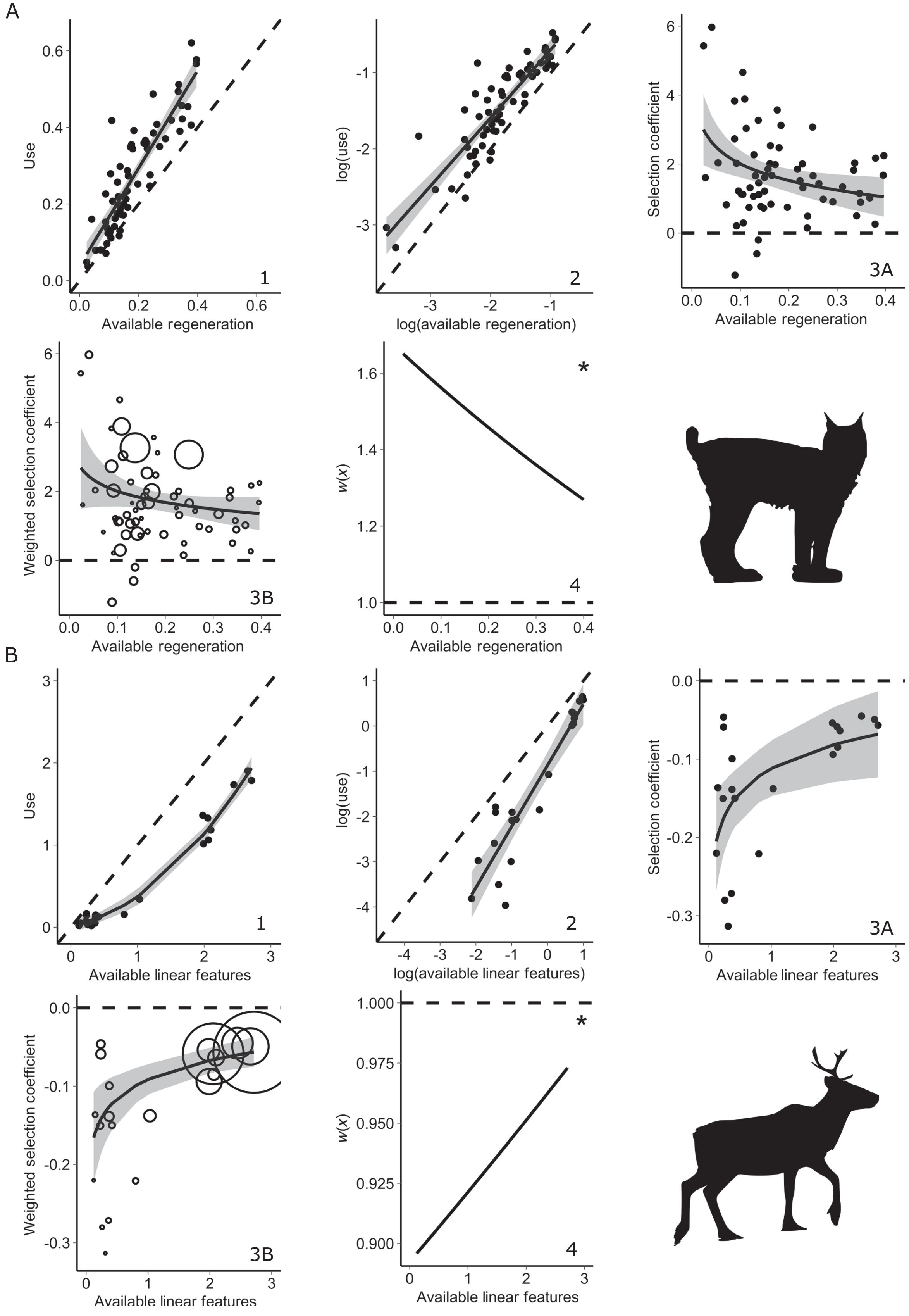
A
Use
Available regeneration
0.0
0.2
0.4
0.6
1
log(use)
log(available regeneration)
-3
-2
-1
2
Selection coefficient
Available regeneration
0
2
4
6
3A
Weighted selection coefficient
Available regeneration
3B
w(x)
Available regeneration
1.0
1.2
1.4
1.6
*
4
B
Use
Available linear features
0
1
2
3
1
log(use)
log(available linear features)
-4
-3
-2
-1
0
1
2
Selection coefficient
Available linear features
0.0
-0.1
-0.2
-0.3
3A
Weighted selection coefficient
Available linear features
3B
w(x)
Available linear features
0.900
0.925
0.950
0.975
1.000
*
4

FIG. 3. Functional responses in habitat use and selection exhibited (A) by Canada lynx (*Lynx canadensis*; $n = 64$) during winter for regenerating forest and (B) by female woodland caribou (*Rangifer tarandus caribou*; $n = 21$) during summer for linear feature density. The four modeling approaches are presented, including the unweighted (i.e., 3A) and weighted (i.e., 3B) variation of approach 3. Circles in 3B indicate individuals and the size of the circle highlights the relative precision in selection coefficients (i.e., larger circles = higher precision). Dashed lines indicate proportional habitat use and black dots indicate individuals. Approaches 1, 2, and 3 include 95% CIs; statistical support ($P \leq 0.05$) for a functional response for approach 4 is indicated with an asterisk.

Canada lynx exhibited functional responses characterized as relaxed selection for increasing snowshoe hare occupancy across all approaches (Table 3, Appendix S4: Fig. S1). The best model capturing the functional response when applying approach 1 and 2 was a curvilinear relationship. These responses indicated that habitat use by Canada lynx increased with availability, but use approached proportionality on the high end of availability (Table 3, Appendix S2: Table S1, Appendix S4: Fig. S1).

Woodland caribou exhibited similar functional responses to linear feature density across summer and winter, but once again there was variation across modeling approaches. Approach 1 indicated that caribou exhibited a functional response and that habitat use increasingly deviated from random expectation and linear features were consistently avoided (Fig. 3B, Table 3, Appendix S2: Table S1). In contrast, approach 2 and 4 (in the summer) indicated that avoidance of linear features by caribou relaxed as linear feature density increased (Fig. 3B, Table 3, Appendix S2: Table S1). However, the pattern from approach 2 was similar to approach 1 after exponentiating the predictions back to the additive scale (see Fig. 3B, Appendix S3: Fig. S2 and Fig. 3B), suggesting a negative functional response by caribou to linear feature density.

Finally, in some cases we observed different patterns within approach 3 when applying unweighted (e.g., individual-level models and mixed-effects models) and weighted selection coefficients to assess functional responses in woodland caribou. For instance, when using unweighted coefficients during the winter we observed a pattern of relaxed avoidance with proportional habitat selection at the highest availability of linear features (Table 3, Appendix S4: Fig. S1B). However, when using weighted selection coefficients that accounted for sampling variation of individuals exposed to low availability, we observed a pattern of constant avoidance across the gradient in linear feature density (Table 3, Appendix S4: Fig. S1B). Similarly, when using unweighted coefficients during the summer, we observed relaxed avoidance and nearly proportional habitat selection at the highest densities of linear features (Fig. 3B, Table 3). When applying weighted coefficients we still observed relaxed avoidance, but the distribution of error across the gradient in availability suggested avoidance remained well below proportional habitat selection (Fig. 3B, Table 3). These differences in responses

TABLE 3. Interpretation of functional responses observed in habitat use and selection for Canada lynx (*Lynx canadensis*) and woodland caribou (*Rangifer tarandus caribou*) across the four different modeling approaches.

| Species/ resource | Additive habitat use (approach 1) | Multiplicative habitat use (approach 2) | Habitat selection with coefficients (approach 3A) | Habitat selection with weighted coefficients (approach 3B) | Habitat selection with RSF interaction (approach 4) |
|---|---|---|---|---|---|
| Canada lynx | | | | | |
| Regeneration | (+) increasing use, use is increasingly deviating from random, and selection is consistent† | (0) increasing use, and constant selection | (–) relaxed selection | (0) constant selection | (–) relaxed selection |
| Snowshoe hare occupancy | (–) increasing use, but selection is relaxed | (–) increasing use, but selection is relaxed | (–) relaxed selection | (–) relaxed selection | (–) relaxed selection |
| Woodland caribou | | | | | |
| Linear feature density (summer) | (–) increasing use, use is increasingly deviating from random, and avoidance is consistent† | (+) increasing use, but avoidance is relaxed | (+) relaxed avoidance | (+) relaxed avoidance | (+) relaxed avoidance |
| Linear feature density (winter) | (–) increasing use, use is decreasingly deviating from random, and avoidance occurs at higher availabilities | (+) increasing use, but avoidance is relaxed | (+) relaxed avoidance | (0) constant avoidance | (0) no functional response |

*Notes:* Variations of approach 3 (i.e., unweighted and weighted selection coefficients) are highlighted by 3A and 3B, respectively. Negative, positive, and no functional responses are indicated by –, +, and 0, respectively. See Appendix S2: Table S1 for the statistical summary that provides the basis for these interpretations.

†On the additive scale, we cannot determine increasing selection or avoidance. We need to know the multiplicative relationship between use and availability to determine increasing selection or avoidance.

provided evidence that applying unweighted selection coefficients to characterize functional responses could be misleading. Indeed, after accounting for variation in precision via weighted coefficients, woodland caribou showed relatively stable avoidance of linear feature density.

## Discussion

Our results highlighted key differences among approaches when evaluating functional responses, the consequences of which could be profound in terms of conservation conclusions and recommendations. This is best illustrated with our woodland caribou data set. Using the most broadly applied approaches (i.e., approach 3 and 4), we might have concluded a mechanism of relaxed avoidance (e.g., Table 1) for woodland caribou responses to linear features, such that habitat selection was proportional to availability at the highest densities of linear features (Fig. 3B, Appendix S4: Fig. S1B). Under this mechanism, caribou appeared to strongly avoid linear features when first encountered, but relaxed their avoidance (to proportional habitat selection), possibly through an inferred process of habituation. Instead, after accounting for poor precision at low values of availability, we now argue that this result was generated erroneously because of the previously unrecognized effect of including estimates of selection at low values of availability. That is, the precision of caribou-specific selection coefficients increased with increasing availability of linear features (see circles in Fig. 3B), which generated imprecise estimates of selection at low availabilities. This influences the functional response pattern because a set of poorly informed estimates are used to set the reference point (i.e., $y$-intercept) of the population-level response. However, by directly assessing habitat use (approach 1) and weighting selection coefficients (approach 3B), we were able to identify that use increasingly deviated from random expectations and that avoidance remained relatively constant as caribou experienced increasing densities of linear features (Fig. 3B, Appendix S4: Fig. S1B). Thus, threatened woodland caribou likely exhibit consistent avoidance of linear features (rather than habituation), which aligns with abundant literature across the boreal region of the globe showing negative effects of human disturbance on woodland caribou (Vors and Boyce 2009). This example illustrates the ecological and conservation consequences of underappreciating the nuances when evaluating functional responses.

There are multiple reasons (beyond the additive and multiplicative scales) why the four approaches to modeling functional responses produced contrasting results. The first substantial difference is that habitat use is distinct from habitat availability, whereas habitat selection (i.e., as in approach 3 and 4) is a mathematical function of availability (Beyer et al. 2010, Aarts et al. 2013). Consequently, a negative functional response in habitat selection can be generated without any change in an animals' habitat use, as illustrated in our simulated scenario of constant use (Fig. 2). A negative functional response in habitat selection is often interpreted as a trade-off scenario, whereby the animal behaviorally selects and *uses* a resource at low availability (i.e., patches of food) but avoids and reduces *use* at high availability (i.e., abundant food but little cover) because of increased risk (e.g., Godvik et al. 2009); however, *use* cannot be inferred from this analysis. Our results indicate that assessing habitat use along with habitat selection would aid the interpretation of functional responses.

Second, the characterization of habitat selection differs between approach 2 and approaches 3 and 4 because of the estimation of individual-level intercepts (although commonly disregarded in RSF applications; Lele et al. 2013) when estimating selection coefficients (from Eq. 3). We found that these intercepts themselves also change with availability (as did Gillies et al. 2006), which confounds the comparison of individual selection coefficients when testing for a functional response. This is not the case when using approach 2 to evaluate habitat selection. The degree to which individual intercepts vary with availability can itself vary across different functional response scenarios. For example, across all scenarios and case studies, the correlation ($|r_{\text{Pearson}}|$) between individual-level intercepts (i.e., $\beta_0$ from Eq. 3) and $\bar{m}^A(x_1)$ was between 0.73–1.00 and 0.20–0.85, respectively. Within our case studies, the correlation between $\beta_0$ and $\bar{m}^A(x_1)$ decreased as among-individual variation in selection increased (indexed via residual sum-of-squares under approach 3). Together, this demonstrated that *both* the intercepts and selection coefficients can change with changing availability, but to varying degrees depending on the consistency of the functional response pattern. Consequently, this means that approaches 3 and 4 do not provide an isolated test of constant selection as in approach 2. Rather, approaches 3 and 4 test functional responses somewhere in between the concept of additive (approach 1) and multiplicative (approach 2) habitat use, which is likely why approach 1, 3, and 4 agree, but differ from approach 2, under the additive, increasing, and decreasing scenarios (Fig. 2). Collectively, appreciating the technical differences between approaches, as well as between the concepts of habitat use and selection, are essential to understand animal responses to changing environmental conditions.

In addition, the resolution of interpretation varies markedly across the different approaches. For example, approach 1 allows interpretation of how habitat use changes and, if habitat use tends toward the 1:1 random use line, how habitat selection changes as availability increases (e.g., relaxed selection and relaxed avoidance; Fig. 2, Table 2). However, if habitat use tends away from the 1:1 line, then increasing selection or avoidance cannot be inferred. Under this circumstance, the functional response has to be interpreted in the context of the 1:1 random use line (e.g., in Fig. 1); for example, see our interpretation of the increasing use scenario (Table 2). Approach 2 presents a unique opportunity because it allows interpretation of changing habitat use (e.g., going up, down, or constant; Fig. 2) as well as changes in habitat selection as availability increases (Table 2, Table 3). Moreover, when predictions are exponentiated from approach 2 onto the additive scale (as in Fig. 1 of Mysterud and Ims 1998), the interpretation is similar to approach 1. Thus, approach 2 is perhaps the most flexible in terms of assessing functional responses. Finally, approach 3 and 4 only allow interpretation of changes in selection or avoidance as availability increases (Table 2, Table 3), conditioned on accounting for a portion of the functional response via the individual-level intercepts that are part of the estimation process.

### *Ecological insights from case studies*

The functional responses for Canada lynx and woodland caribou highlighted ecological insights into context-dependent habitat selection. All four approaches indicated that Canada lynx exhibited relaxed selection for predicted occupancy of snowshoe hares, but approach 1 demonstrated that lynx generally do not use areas below a 0.6 probability of hare occupancy. Lynx also exhibited selection for advanced regenerating forests, but the functional response observed varied by approach. Because of the two main issues associated with approaches 3 and 4 (i.e., imprecise estimates of selection at low availability and individual-level intercepts accounting for a portion of the functional response), we based our conclusion on approaches 1 and 2. Therefore, lynx increasingly use and consistently select advanced regenerating forests across the gradient in availability (Fig. 3). This conclusion is consistent with previous work and supports the mechanism of lynx as a specialist predator that focuses on snowshoe hares and their habitats (Squires et al. 2010, Holbrook et al. 2017*a*).

Among woodland caribou, approach 1 and the exponentiation of approach 2 indicated that caribou's use of linear features increasingly deviated from random expectation in a negative direction as linear feature density increased (Fig. 3B). Additionally, weighted selection coefficients under approach 3 suggested caribou exhibited relatively consistent avoidance across the gradient in linear feature density. As mentioned previously, we concluded that caribou exhibit a negative response to linear features, which was similar to other studies demonstrating the impacts of human alterations on woodland caribou behavior and demography (DeCesare et al. 2012, Mason and Fortin 2017).

### *Conclusions and practical guidance*

We conclude by providing guidance on future assessments of functional responses in habitat ecology and management, which we have organized around two questions. First, "What is the goal of my study: prediction, extrapolation, or understanding?" If prediction or extrapolation, perhaps the researcher is primarily interested in *predicting* animal distributions in spatially or temporally novel environments. In this case, the definition of a functional response might be more practically couched within the RSF framework, such that RSF coefficients are not static and are allowed to vary depending on the study location or time period. Under this framework, we would suggest techniques similar to approach 4 that have demonstrated superior predictive ability using out-of-sample data (i.e., Matthiopoulos et al. 2011, Aarts et al. 2013, Paton and Matthiopoulos 2016). The generalized functional response model of Matthiopoulos et al. (2011) is a flexible example that can incorporate interactions between selection and availability for many different resources. However, if the goal of the study is to *understand* how animals respond to changing environmental conditions, we suggest either approach 1, 2, or both. In contrast to some previous studies (e.g., Hebblewhite and Merrill 2008, McLoughlin et al. 2010), we would not suggest using unweighted selection coefficients within approach 3 or using approach 4 because of the issues revealed by our evaluation: (1) inability to distinguish between changing habitat use or availability in the presence of a negative functional response, (2) imprecise estimation of selection at low availability, and (3) individual-level intercepts can be highly correlated with availability and account for an unknown portion of the functional response. If selection coefficients are the main focus, however, we suggest weighting coefficients as one means of accounting for imprecision at low availability.

If one accepts our recommendations by using approach 1 or 2, deciding between these two options leads us to the second question, "Which concept of a functional response am I most interested in testing: habitat use, habitat selection, or both?" If the answer is habitat selection or both, we recommend approach 2. One can easily test if habitat use is a constant multiplicative function of availability such that the selection ratio remains constant (i.e., multiplicative test in Fig. 1), but can also exponentiate the predictions to assess how additive habitat use changes with availability (as in approach 1). However, multiplicative changes in use may not be an intuitive null hypothesis in certain scenarios, such as when a resource is at the extremes (low or high) of availability (e.g., Kertson and Marzluff 2010). Alternatively, evaluating how an animal modifies its habitat use relative to random expectation (i.e., approach 1) might be a more appealing assessment of a functional response.

Regardless of the approach, there are some important considerations fundamental to assessing functional responses. First, the gradient in resource availability is an important concept, which is also related to the level of animal exposure for a given resource. If the gradient is narrow or at the low end of availability, testing for a functional response may not be useful because (1) animals might not be effectively exposed to the resource or (2) there is little variation to evaluate a behavioral response. Indeed, the premise of a functional response requires both animal exposure and variation in availability. Second, curvilinear functional responses are an important consideration because disproportionate use or selection can occur over a portion of the availability gradient. This is particularly true because, by definition, habitat use has to equal availability on the extremes of availability; in other words, use will tend toward the proportional line if a resource approaches absence or 100% availability. Third, some researchers have assessed how selection or use for resource A (e.g., forest) changes as availability of resource B (e.g., meadow) increases (e.g., Moreau et al. 2012, Tardy et al. 2014). This is an interesting approach to assess trade-off situations, but seemingly makes the inherent assumption that resource A and B are inversely correlated. If they are not, which might be the case in complex landscapes, the interpretation of functional responses becomes difficult. Thus, we suggest explicitly testing for the inverse nature of the resources if trade-offs are expected. Finally, there are methodological factors within a traditional use–availability design that could influence assessments of functional responses (e.g., Aarts et al. 2008). For instance, estimating use and availability are sensitive to issues such as defining availability (e.g., Beyer et al. 2010), bias and error in animal locations (e.g., Frair et al. 2010), and variation in the underlying measurements (or spatial predictions) of environmental resources under question (Aarts et al. 2008). Heterogeneity associated with all of these components could influence or attenuate functional responses in real data sets and therefore should be considered.

Twenty years ago Mysterud and Ims (1998) provided a conceptual advancement concerning context-dependent habitat relationships, which was termed a functional response in habitat use. Many studies since then have expanded our knowledge of functional responses in habitat ecology, but have implemented a variety of analytical procedures that were assumed to generate similar conclusions and management recommendations (van Beest et al. 2016). Our evaluation here has demonstrated that the commonly applied approaches are distinctly different and the choice of method can influence the conservation conclusions. Therefore, careful consideration is warranted when selecting a particular approach. Perhaps the most conservative strategy would be to evaluate how both habitat use and selection change as animals are exposed to differing resource availabilities. It is our hope that our evaluation of approaches and subsequent recommendations assist the transition of functional responses into the mainstream of habitat ecology. Understanding how animals respond to changing environmental conditions is important for both ecology and management, and functional responses are an important tool to help characterize those responses.

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## LITERATURE CITED

Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. Estimating space-use and habitat preferences from wildlife telemetry data. Ecography 31:140–160.

Aarts, G., J. Fieberg, and J. Matthiopoulos. 2012. Comparative interpretation of count, presence-absence and point methods for species distribution models. Methods in Ecology and Evolution 3:177–187.

Aarts, G., J. Fieberg, S. Brasseur, and J. Matthiopoulos. 2013. Quantifying the effect of habitat availability on species distributions. Journal of Animal Ecology 82:1135–1145.

Bastille-Rousseau, G., J. R. Potts, J. A. Schaefer, M. A. Lewis, E. H. Ellington, N. D. Rayl, S. P. Mahoney, and D. L. Murray. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. Ecography 38:1049–1059.

Beyer, H. L., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. The interpretation of habitat preference metrics under use-availability designs. Philosophical Transactions of the Royal Society B 365:2245–2254.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.

Boyce, M. S., L. L. McDonald, and B. Manly. 1999. Replay from M.S. Boyce, L.L. McDonald, and B.F.J. Manly. Trends in Ecology and Evolution 14:490.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

DeCesare, N. J., et al. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1068–1083.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of the Royal Society B 365:2233–2244.

Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B 365:2187–2200.

Gaillard, J., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B 365:2255–2265.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90:699–710.

Hansen, B. B., I. Herfindal, R. Aanes, B. Sæther, and S. Henriksen. 2009. Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. Oikos 118:859–872.

Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834–844.

Holbrook, J. D., J. R. Squires, L. E. Olson, N. J. DeCesare, and R. L. Lawrence. 2017*a*. Understanding and predicting habitat for wildlife conservation: the case of Canada lynx at the range periphery. Ecosphere 8:e01939.

Holbrook, J. D., J. R. Squires, L. E. Olson, R. L. Lawrence, and S. L. Savage. 2017*b*. Multiscale habitat relationships of snowshoe hares (*Lepus americanus*) in the mixed conifer landscape of the Northern Rockies, USA: cross-scale effects of horizontal cover with implications for forest management. Ecology and Evolution 7:125–144.

Holling, C. S. 1959. Some characteristics of simply types of predation and parasitism. Canadian Entomologist 7:385–398.

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

Kertson, B. H., and J. M. Marzluff. 2010. Improving studies of resource selection by understanding resource use. Environmental Conservation 38:18–27.

Knopff, A. A., K. H. Knopff, M. S. Boyce, and C. C. St. Clair. 2014. Flexible habitat selection by cougars in response to anthropogenic development. Biological Conservation 178: 136–145.

Laforge, M. P., R. K. Brook, F. M. van Beest, E. M. Bayne, and P. D. McLoughlin. 2015. Grain-dependent functional responses in habitat selection. Landscape Ecology 31:855–863.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. Journal of Animal Ecology 82:1183–1191.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Mason, T., and D. Fortin. 2017. Functional responses in animal movement explain spatial heterogeneity in animal-habitat relationships. Journal of Animal Ecology 86:960–971.

Matthiopoulos, J., M. Hebblewhite, G. Aarts, and F. Fieberg. 2011. Generalized functional responses for species distributions. Ecology 92:583–589.

Mauritzen, M., S. E. Belikov, A. N. Boltunov, A. E. Derocher, E. Hansen, R. A. Ims, Ø. Wiig, and N. Yoccoz. 2003. Functional responses in polar bear habitat selection. Oikos 100:112–124.

McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology 79:4–12.

Moreau, G., D. Fortin, S. Couturier, and T. Duchesne. 2012. Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests. Journal of Applied Ecology 49:611–620.

Murtaugh, P. A. 2007. Simplicity and complexity in ecological data analysis. Ecology 88:56–62.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1435–1441.

Paton, R. S., and J. Matthiopoulos. 2016. Defining the scale of habitat availability for models of habitat selection. Ecology 97:1113–1122.

Pellerin, M., C. Calenge, S. Saïd, J.-M. Gaillard, H. Fritz, P. Duncan, and G. Van Laere. 2010. Habitat use by female western roe deer (*Capreolus capreolus*): influence of resource availability on habitat selection in two contrasting years. Canadian Journal of Zoology 88:1052–1062.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Roever, C. L., R. J. van Aarde, and K. Leggett. 2012. Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant. Ecography 35:972–982.

Squires, J. R., N. J. DeCesare, J. A. Koble, and L. F. Ruggiero. 2010. Seasonal resource selection of Canada lynx in managed forests of the Northern Rocky Mountains. Journal of Wildlife Management 74:1648–1660.

Tardy, O., A. Massé, F. Pelletier, J. Mainguy, and D. Fortin. 2014. Density-dependent functional responses in habitat selection by two hosts of the raccoon rabies virus variant. Ecosphere 5:132.

van Beest, F. M., P. D. McLoughlin, A. Mysterud, and R. K. Brook. 2016. Functional responses in habitat selection are density dependent in a large herbivore. Ecography 39:515–523.

Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626–2633.

## SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1852/full

## DATA AVAILABILITY

Example R code and data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.47174j0