

# Solving the sample size problem for resource selection functions

Garrett M. Street<sup>1,2</sup>  | Jonathan R. Potts<sup>3</sup>  | Luca Börger<sup>4,5</sup>  | James C. Beasley<sup>6</sup>  | Stephen Demarais<sup>1</sup> | John M. Fryxell<sup>7</sup>  | Philip D. McLoughlin<sup>8</sup>  | Kevin L. Monteith<sup>9</sup> | Christina M. Prokopenko<sup>10</sup> | Milton C. Ribeiro<sup>11</sup> | Arthur R. Rodgers<sup>12</sup> | Bronson K. Strickland<sup>1</sup> | Floris M. van Beest<sup>13</sup>  | David A. Bernasconi<sup>6</sup> | Larissa T. Beumer<sup>13</sup>  | Guha Dharmarajan<sup>6</sup>  | Samantha P. Dwinell<sup>14</sup>  | David A. Keiter<sup>6</sup> | Alexine Keuroghlian<sup>15</sup> | Levi J. Newediuk<sup>10</sup> | Júlia Emi F. Oshima<sup>11</sup>  | Olin Rhodes Jr.<sup>6</sup> | Peter E. Schlichting<sup>6</sup>  | Niels M. Schmidt<sup>13</sup>  | Eric Vander Wal<sup>10</sup>

<sup>1</sup>Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, MS, USA; <sup>2</sup>Quantitative Ecology and Spatial Technologies Laboratory, Mississippi State University, Mississippi State, MS, USA; <sup>3</sup>School of Mathematics and Statistics, University of Sheffield, Sheffield, UK; <sup>4</sup>Department of Biosciences, Swansea University, Swansea, UK; <sup>5</sup>Centre for Biomathematics, Swansea University, Swansea, UK; <sup>6</sup>Savannah River Ecology Laboratory, University of Georgia, Aiken, SC, USA; <sup>7</sup>Department of Integrative Biology, University of Guelph, Guelph, ON, Canada; <sup>8</sup>Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada; <sup>9</sup>Haub School of Environment and Natural Resources, University of Wyoming, Laramie, WY, USA; <sup>10</sup>Department of Biology, Memorial University of Newfoundland, St. John's, NL, Canada; <sup>11</sup>Instituto de Biosciências, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; <sup>12</sup>Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources and Forestry, ON, Canada; <sup>13</sup>Department of Bioscience, Aarhus University, Aarhus, Denmark; <sup>14</sup>Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY, USA and <sup>15</sup>IUCN/SSC Peccary Specialist Group, Campo Grande, Brazil

## Correspondence

Garrett M. Street

Email: gms246@msstate.edu

## Funding information

Natural Science and Engineering Research Council of Canada; Mississippi Department of Wildlife, Fisheries, and Parks; Parks Canada; Mississippi Agricultural and Forestry Experiment Station; Mississippi State University Extension Service; USDA Animal and Plant Health Inspection Service; U.S. Department of Energy; USDA National Wildlife Research Center; Wyoming Game and Fish Department; Bureau of Land Management; USDA-NIFA; USDA Wildlife Services; U.S. Forest Service; Forest and Wildlife Research Center; U.S. Fish and Wildlife Service; Ontario Ministry of Natural Resources and Forestry

Handling Editor: Chris Sutherland

## Abstract

1. Sample size sufficiency is a critical consideration for estimating resource selection functions (RSFs) from GPS-based animal telemetry. Cited thresholds for sufficiency include a number of captured animals  $M \geq 30$  and as many relocations per animal  $N$  as possible. These thresholds render many RSF-based studies misleading if large sample sizes were truly insufficient, or unpublishable if small sample sizes were sufficient but failed to meet reviewer expectations.
2. We provide the first comprehensive solution for RSF sample size by deriving closed-form mathematical expressions for the number of animals  $M$  and the number of relocations per animal  $N$  required for model outputs to a given degree of precision. The sample sizes needed depend on just 3 biologically meaningful quantities: habitat selection strength, variation in individual selection and a novel measure of landscape complexity, which we define rigorously. The mathematical expressions are calculable for any environmental dataset at any spatial scale and are applicable to any study involving resource selection (including sessile organisms). We validate our analytical solutions using globally relevant empirical data including 5,678,623 GPS locations from 511 animals from 10 species (omnivores, carnivores and herbivores living in boreal, temperate and tropical forests, montane woodlands, swamps and Arctic tundra).

3. Our analytic expressions show that the required  $M$  and  $N$  must decline with increasing selection strength and increasing landscape complexity, and this decline is insensitive to the definition of availability used in the analysis. Our results demonstrate that the most biologically relevant effects on the utilization distribution (i.e. those landscape conditions with the greatest absolute magnitude of resource selection) can often be estimated with much fewer than  $M = 30$  animals.
4. We identify several critical steps in implementing these equations, including (a) a priori selection of expected model coefficients and (b) regular sampling of background (pseudoabsence) data within a given definition of availability. We discuss possible methods to identify a priori expectations for habitat selection coefficients, effects of scale on RSF estimation and caveats for rare species applications. We argue that these equations should be a mandatory component for all future RSF studies.

#### KEYWORDS

bootstrap, habitat selection,  $p$ -value, power analysis, resource selection function, sample size, species distribution model, validation

## 1 | INTRODUCTION

Resource selection analysis (RSA) is a broad framework linking the distribution of animals to their preferences for specific habitat conditions and is a fundamental tool in animal ecology (Boyce & McDonald, 1999; Strickland & McDonald, 2006). Obtaining sufficient locations to ascertain the distribution of animals across landscapes is a fundamental requirement for RSA. Given that individual animals will differ in the magnitude and direction of preference for different components of a landscape (McLoughlin et al., 2010), it is necessary to obtain repeated localizations on multiple individuals, now commonly collected using animal-attached GPS sensors (Hebblewhite & Haydon, 2010). GPS data on animal movements are hence commonly employed for RSA and are often analysed using resource selection functions (RSFs; Boyce & McDonald, 1999; Elith & Leathwick, 2009; Hebblewhite & Haydon, 2010; Manly et al., 2002). RSFs are a class of exponential models of space use that estimate the probability distribution of animal locations using different resources/conditions in the landscape, taking into account the availability of each resource, and thereby provide a measure of the 'strength' of (behavioural) selection for or against each resource (Manly et al., 2002). RSFs are easily fitted using standard statistical models (commonly logistic or conditional logistic regression) applied to data on animal locations and resource distributions in the landscape and have become a cornerstone of research in spatial ecology (Manly et al., 2002; Elith & Leathwick 2009; Renner & Warton, 2013; Fieberg et al., 2021).

Given the prevalence of RSFs, it is surprising that the central question determining the validity of inferences obtained—how much data are needed to estimate a RSF for a given species?—has not been solved. This issue has been broached for occupancy analysis (Guillera-Arroita & Lahoz-Monfort, 2012) and generalized

linear mixed models (Johnson et al., 2015), and has been evaluated within individual RSF studies using simulations (Leban et al., 2001; Loe et al., 2012), yet no analytic expressions exist to determine the number of animals ( $M$ ) and relocations per animal ( $N$ ) required to obtain RSF outputs to a given degree of precision. While the accuracy and precision of RSFs generally increase with sample size, leading to a standard rule-of-thumb of  $M \geq 30$  needed for reliable ecological inference (Leban et al., 2001), this rough guideline is grounded in century-old thinking about statistics in the pre-computation world (James et al., 2013). Crucially, it is also oblivious to the ecological reality that a multitude of factors may affect selection strength and determine the required sample size (Manly et al., 2002; McLoughlin et al., 2010; Hebblewhite & Haydon, 2010). These include density dependence (i.e. certain habitats become less attractive when occupied by conspecifics; Fretwell & Lucas, 1969; McLoughlin et al., 2010; van Beest et al., 2016), trade-offs in selection for forage and cover under predation risk (Fortin et al., 2005; McLoughlin et al., 2010), temporal variations in resource dynamics (McLoughlin et al., 2010; Paolini et al., 2018) or the degree of habitat availability or heterogeneity in a landscape (Mysterud & Ims, 1998; McLoughlin et al., 2010; Paolini et al., 2018; van Beest et al., 2016). There is no consistency in RSF studies in the number of replicates used (Hebblewhite & Haydon, 2010), as the only alternative approaches to establish the number of replicates a priori are ecologically informed guesswork, or simply to collect as much data as possible.

The crux of the problem lies in the relationship between sample size and ecological complexity. It is suggested that more complex systems require more data to describe (Wisiz et al., 2008), yet a robust power analysis (Johnson et al., 2015) allowing examination of the relationship between RSF estimation, system complexity and data availability is crucially missing. This has obvious economic and

ethical implications if more animals are tagged and monitored than needed and affects research aimed at the conservation of species, which requires reliable estimates of animal–habitat relationships but where it is often impossible to monitor large numbers of animals. Here, we provide a solution to the sample size problem in RSFs by deriving analytic expressions for the values of  $M$  and  $N$  (the number of animals and relocations per animal respectively) required to estimate RSFs to a required degree of accuracy, taking into account landscape complexity and the strength of selection for the resources. We validate these expressions using simulations and a large dataset of GPS-tagged animals (including 10 species from different continents and biomes) and show that the most biologically relevant effects of landscapes on animal distributions can often be estimated with far fewer animals and locations than commonly stated.

## 2 | MATERIALS AND METHODS

We begin by describing mathematically how to determine the number of locations per animal ( $N$ ) and the number of animals ( $M$ ) for RSFs. Generally speaking, RSA seeks to parameterize a model of space use that has the following form (Boyce & McDonald, 1999):

$$u(\mathbf{x}) = \frac{A(\mathbf{x})W(\mathbf{x})}{\int_{\Omega} A(\mathbf{x}')W(\mathbf{x}')d\mathbf{x}'}, \quad (1)$$

where  $u(\mathbf{x})$  is the *utilization distribution* of the study species (i.e. the probability density function of the study animals' locations),  $A(\mathbf{x})$  is a function denoting the availability of the point  $\mathbf{x}$  to the animals,  $\Omega$  is the study area and  $W(\mathbf{x})$  is the RSF. (Note: throughout this manuscript, bold fonts imply that the quantity is a vector.) For the purposes of our analytic calculations, our RSF will be dependent on a single resource layer  $R(\mathbf{x})$ . This could denote, for example, the vegetation quality or prey availability at point  $\mathbf{x}$ . However, in general,  $R(\mathbf{x})$  represents a map of any environmental feature which is hypothesized to covary with space use. Although we only look at one resource layer at a time for our analytic calculations, we show in our empirical study (below) that the resulting formulae work when the RSF has multiple layers.

As is the standard method for RSA, we make three simplifying assumptions (Manly et al., 2002): (a) our weighting function is of the form  $W(\mathbf{x}|\beta) = \exp[\beta R(\mathbf{x})]$ , where  $\beta$  is a parameter to be estimated; (b) the availability kernel  $A(\mathbf{x})$  is a uniform distribution; and (c) relocations are independent. Consequently, our model of space use from Equation (1) becomes:

$$u(\mathbf{x}|\beta) = \frac{\exp[\beta R(\mathbf{x})]}{\int_{\Omega} \exp[\beta R(\mathbf{x}')]d\mathbf{x}'}. \quad (2)$$

The aim of this section is to understand how many independent samples are required to give an accurate parameterization of the model in Equation 2. Note that when applying our theory to empirical data, one will need to test that the assumption of independence between samples is reasonable. This is a standard assumption in resource selection

studies and the techniques for testing independence are no different for our theory than for resource selection in general. Much has already been written in the literature about this independence assumption (e.g. Gillies et al., 2006; Manly et al., 2002; Millsbaugh et al., 1998) and we refer the reader there for guidance in this regard.

### 2.1 | Locations from a single individual (N)

We first need to phrase the question ‘How many locations?’ in a concrete, mathematical way. Suppose we wish to test the null hypothesis  $H_0: \beta = 0$  against the alternative  $H_1: \beta \neq 0$  at a significance level  $p \in (0, 1)$ . An experiment to test this hypothesis involves measuring  $N$  samples and using (conditional) logistic regression to infer  $\beta$  and test the null hypothesis (as is the standard method for resource selection, e.g. Manly et al., 2002). We define  $N_{\alpha,p}(\beta)$  to be the minimum number of samples required so that we expect to reject the null hypothesis in  $100(1 - \alpha)\%$  of experiments. An approximate analytical formula for  $N_{\alpha,p}(\beta)$  is given as follows (derived in Appendix A):

$$N_{\alpha,p}(\beta) \approx \frac{(z_{\alpha} + z_p/2)^2}{\text{Var}[R(X_{\beta})]} \beta^{-2}. \quad (3)$$

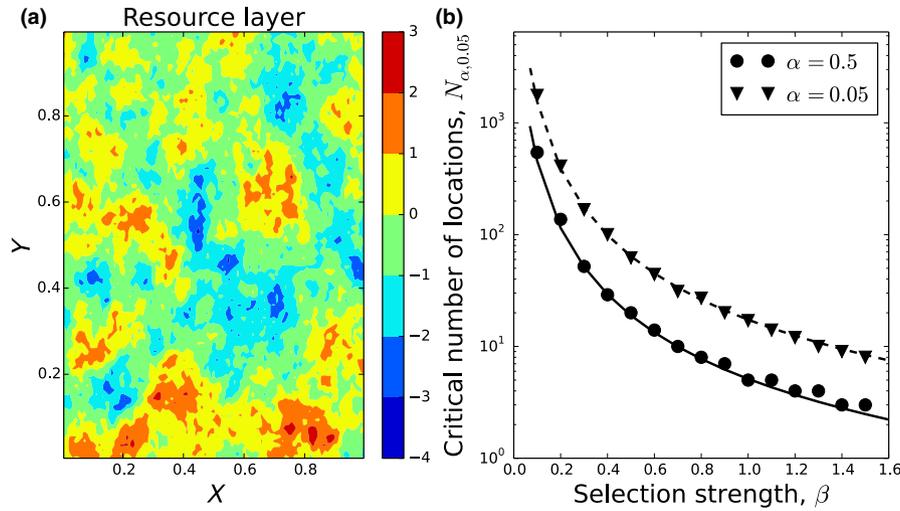
Here,  $z_{\alpha} = \Phi^{-1}(1 - \alpha)$  where  $\Phi(\cdot)$  is the cumulative distribution function for the standard normal distribution (e.g.  $z_{0.05} \approx 1.645$ ,  $z_{0.025} \approx 1.96$ ),  $X_{\beta}$  is a random variable whose probability density function is given by Equation 2, and  $\text{Var}[R(X_{\beta})]$  is the variance of  $R(X_{\beta})$ . An explicit functional expression for  $\text{Var}[R(X_{\beta})]$  can be written as follows:

$$\text{Var}[R(X_{\beta})] = \frac{\int_{\Omega} R^2(\mathbf{x}) \exp[\beta R(\mathbf{x})] d\mathbf{x}}{\int_{\Omega} \exp[\beta R(\mathbf{x})] d\mathbf{x}} - \left( \frac{\int_{\Omega} R(\mathbf{x}) \exp[\beta R(\mathbf{x})] d\mathbf{x}}{\int_{\Omega} \exp[\beta R(\mathbf{x})] d\mathbf{x}} \right)^2. \quad (4)$$

We call  $\text{Var}[R(X_{\beta})]$  ‘landscape complexity’. Critically, this form of landscape complexity is determined in part by multiplying the landscape layer by the expected  $\beta$ , so it should be understood as representing the landscape complexity *as viewed by the animal*.

The formula in Equation 3 is approximate due to two assumptions: (a) it relies on the standard error,  $\sigma$ , of the maximum likelihood function being approximately normally distributed and (b) it uses a standard result relating the standard error for the estimator of  $\beta$  to the second derivative of the log-likelihood function (see Appendix A for more details). Therefore, it is necessary to investigate the magnitude of these approximating assumptions using simulated data.

To test how effective the approximate expression from Equation 3 is at capturing the actual number of samples required to infer  $\beta$  with a given level of accuracy, we constructed a simulated resource layer which describes an example of the function  $R(\mathbf{x})$  (Figure 1a). This test layer is a Gaussian random field, previously used in the context of resource selection by Potts et al. (2014). It was generated by the R function `GaussRF()` from the `RandomFields` package (Schlather et al., 2016), using the exponential model with mean = 0, variance = 1, nugget = 0, and scale = 10, and consists of  $L = 100$  by  $L = 100$  pixels. By sampling  $N$  times from Equation 2 for various  $N$



**FIGURE 1** Performance of analytic expression on simulated data. Panel (a) shows a simulated resource layer,  $R(\mathbf{x})$ , which was used to construct the utilization distribution (Equation 2) from which the simulated animal locations were samples. The circles (resp. triangles) in Panel (b) show the empirically derived values of  $N_{0.5,0.05}(\beta)$  (resp.  $N_{0.05,0.05}(\beta)$ ), the minimum number of samples required so that there is a 50% chance (resp. 95% chance) of rejecting the null hypothesis that  $\beta = 0$  at a significance level of  $p = 0.05$ . The solid line (resp. dashed line) in Panel (b) shows the corresponding analytic approximations given by Equation 3 and the remarkable agreement with the empirically derived values

with  $R(\mathbf{x})$ , we can compute empirical values for  $N_{\alpha,p}(\beta)$  for different  $\beta$  (full method given in Appendix B). Comparison of these empirically derived values alongside the analytical expression from Equation 3 reveals remarkably strong agreement (Figure 1b). This suggests that Equation 3 gives an accurate estimation of the number of independent samples required to estimate  $\beta$ .

## 2.2 | Locations from multiple individuals ( $M$ )

Now we assume that there are  $M$  individuals and they each select resources with different  $\beta$ . To model this, let  $\beta_1, \dots, \beta_M \sim N(\beta, s^2)$  be independent draws from a normal distribution with mean  $\beta$  and variance  $s^2$ . (Note that this assumes that the individuals' responses to resources are normally distributed, which needs to be checked when applying our results to any specific study system). Then  $\beta_i$  is the coefficient of resource selection for individual  $i \in \{1, \dots, M\}$ . Suppose for each individual  $i$  we have gathered  $N_i$  locations. Let  $\hat{\beta}_i$  be the maximum likelihood estimator for  $\beta_i$ . Then the standard deviation of  $\hat{\beta}_i$  can be estimated as (Appendix A, Equation 15):

$$\sigma_i = \frac{1}{\sqrt{N_i \text{Var}[R(X_{\beta_i})]}}. \quad (5)$$

If  $\hat{\beta}$  is the mean of  $\hat{\beta}_1, \dots, \hat{\beta}_M$ , then  $\hat{\beta}$  is normally distributed as follows (Appendix C):

$$\hat{\beta} \sim N\left(\beta, \frac{1}{M^2} \sum_{i=1}^M \sigma_i^2 + \frac{s^2}{M}\right). \quad (6)$$

Thus  $\hat{\beta}$  is an unbiased estimator of  $\beta$ . Notice that the variance decays as  $M$  increases. If the practitioner has some prior expectation of the possible values of  $\beta$  and  $s^2$ , Equation 6 can be used to calculate the number of animals,  $M$ , required to obtain an empirical estimate of  $\beta$  to a given degree of accuracy.

As well as calculating an estimate of  $\beta$ , it is also possible to estimate  $s^2$ . The following is an unbiased estimator of  $s^2$  for  $M \geq 2$  (Appendix C):

$$\hat{s}^2 = \frac{1}{M-1} \sum_{i=1}^M \left( \hat{\beta}_i - \frac{1}{M} \sum_{j=1}^M \hat{\beta}_j \right)^2 - \frac{1}{M} \sum_{i=1}^M \sigma_i^2. \quad (7)$$

We could not derive a closed analytic formula for the uncertainty in the estimator given in Equation 7; however, we provide code for estimating this using random sampling (see Appendix D). In general, the estimator becomes more precise for lower  $\sigma_i$  and higher  $M$ . This is shown in Appendix D, where we also verify numerically Equations 6 and 7.

Equation 6 allows us to calculate the minimum number of animals,  $M_{\alpha,p}(\beta)$ , for which we would expect to reject the null hypothesis that  $\beta = 0$ , at significance level  $p$ ,  $100(1 - \alpha)\%$  of the time (two-tailed test).  $M_{\alpha,p}(\beta)$  is the minimum integer,  $M$ , that satisfies the following inequality:

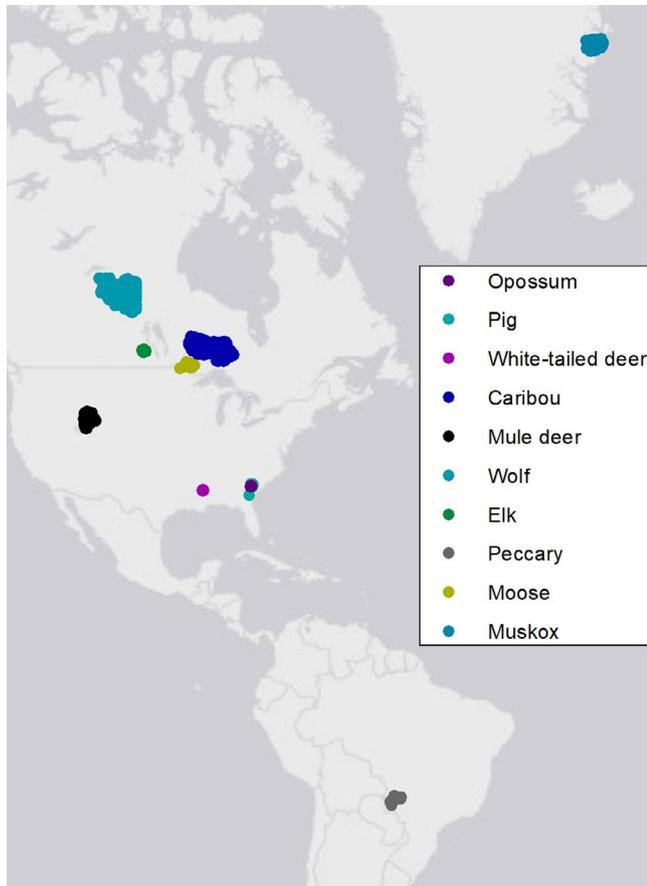
$$M \geq \frac{s^2(z_{p/2} + z_\alpha)^2 + \sqrt{s^4(z_{p/2} + z_\alpha)^4 + 4\beta^2(z_{p/2} + z_\alpha)^2 \sum_{i=1}^M \sigma_i^2}}{2\beta^2}. \quad (8)$$

Note that  $M_{\alpha,p}(\beta)$  is a non-decreasing function of  $s^2$ , meaning that more variation amongst individuals is likely to mean one has to sample a higher number of animals.

### 2.3 | Data and resource selection functions

Equations 3 and 8 give predicted values for the number of relocations  $N$  and the number of animals  $M$  required for RSF estimation. To test our analytical predictions, we compiled GPS-based relocation datasets from 10 separate species with accompanying landscape data in raster format (Table S1; Figure 2). Landscape data were either categorical (i.e. discrete landcover) or numeric (e.g. elevation, precipitation, etc.). To ensure comparability between model outputs for each species, we centred and scaled each numeric landscape raster in R using the `scale()` function with default parameters. We converted categorical landcover rasters to binary raster layers for each landcover classification of interest (e.g. deciduous forest, croplands, etc.) to acquire estimates of  $\text{Var}[R(X_\beta)]$  for a given categorical raster.

We generated a 1:1 sample of availability (i.e. 1 available location per animal relocation) within each animal's 99% home range as estimated using the function `kernelUD()` in R package `adehabitatHR` with the default bandwidth estimator. For each availability set, we extracted centred-and-scaled (numeric) and binary (categorical) landscape data to animal relocations and available locations and fit a RSF to each animal in each dataset using logistic regression (i.e. 511 individual models; Table S2). For simplicity, we used only linear main effects for each predictor in a given RSF; however, we emphasize



**FIGURE 2** Data distribution. Geographical locations of GPS datasets (5,678,623 GPS relocations) across 511 individually collared members of 10 species

that more complex effects (e.g. nonlinear and interaction terms) may be identically investigated using the appropriate nonlinear transformation or multiplicative product on the resource layer(s) prior to calculation. Note that, although our equations operate on a single resource layer at a time, our analysis uses RSFs with multiple layers. This procedure thus tests whether multiple layers may be analysed one-at-a-time to ascertain the number of animals and fixes required to estimate the  $\beta$ -value for each layer.

### 2.4 | Empirical validation: $M$

After fitting each RSF, we calculated the mean selection coefficient  $\bar{\beta}$  for each landscape layer across individuals within a species. Assuming  $\bar{\beta}$  was an accurate estimate of population-level selection  $\beta$ , we asked: how many animals  $M$  were necessary to estimate  $\beta$ ? We calculated  $\text{Var}[R(X_\beta)]$  for each centred-and-scaled or binary raster within each animal's 99% range according to Equation 4 and the resulting values of  $N$  according to Equation 3. We generated empirical distributions of  $\hat{\beta}$  and  $\hat{s}^2$  as described in Appendix D for  $M \in \{2, \dots, 30\}$  using the average  $N$  and  $\text{Var}[R(X_\beta)]$  as population-level estimates of each. We computed the empirical 95% intervals at a given  $M$  (i.e.  $\alpha = 0.05$ ). The value of  $M$  at which the empirical interval no longer contains 0 is the predicted minimum  $M$  necessary to estimate  $\beta$  with 95% confidence,  $M_{\text{pred}}$  (i.e. the minimum integer  $M_{0.05,0.05}(\beta)$ ; Equation 8).

For comparison with observation, we then resampled the estimated selection coefficients for each individual within a species. For a given  $M \in \{2, \dots, 30\}$  as above, we generated 4,000 samples of  $M_i$  observed selection coefficients and calculated  $\bar{\beta}$  for each (i.e. 4,000 mean selection coefficients assuming  $M_i$  animals). This represents the observed distribution of possible  $\bar{\beta}$  for  $M_i$  sampled animals, assuming the total pool of animals is a representative sample. Finally, for each  $M$ , we calculated the grand mean  $\bar{\beta}_G$  and the empirical 95% interval of  $\bar{\beta}$ . The value of  $M$  at which the empirical interval no longer contains 0 is the observed minimum  $M$  necessary to estimate  $\beta$  with 95% confidence,  $M_{\text{obs}}$ , and should correspond to  $M_{\text{pred}}$ .

### 2.5 | Empirical validation: $N$

The  $M$  validation procedure described above assumes that, on average, sufficient relocations  $N$  were available to estimate  $M$ . Now we consider: for a given individual-level selection coefficient  $\beta$ , do we have sufficient  $N$  to reject the null hypothesis for a given animal? We randomly sampled one animal from each dataset and calculated  $\text{Var}[R(X_\beta)]$  within the animal's 99% range using the animal's specific RSF model coefficients as  $\beta$ . From this, we calculated the predicted number of relocations  $N_{\text{pred}}$  necessary to estimate  $\beta$  given  $\text{Var}[R(X_\beta)]$  (i.e.  $N_{0.05,0.05}(\beta)$ ; Equation 3).

For comparison, we resampled  $N_{\text{sam}}$  relocations with replacement from the animal's dataset, where  $N_{\text{sam}} = * \frac{iN_{\text{total}}}{50}$ ,  $i \in \{1, \dots, 25\}$  and  $N_{\text{total}}$  is the total number of relocations recorded for that animal.

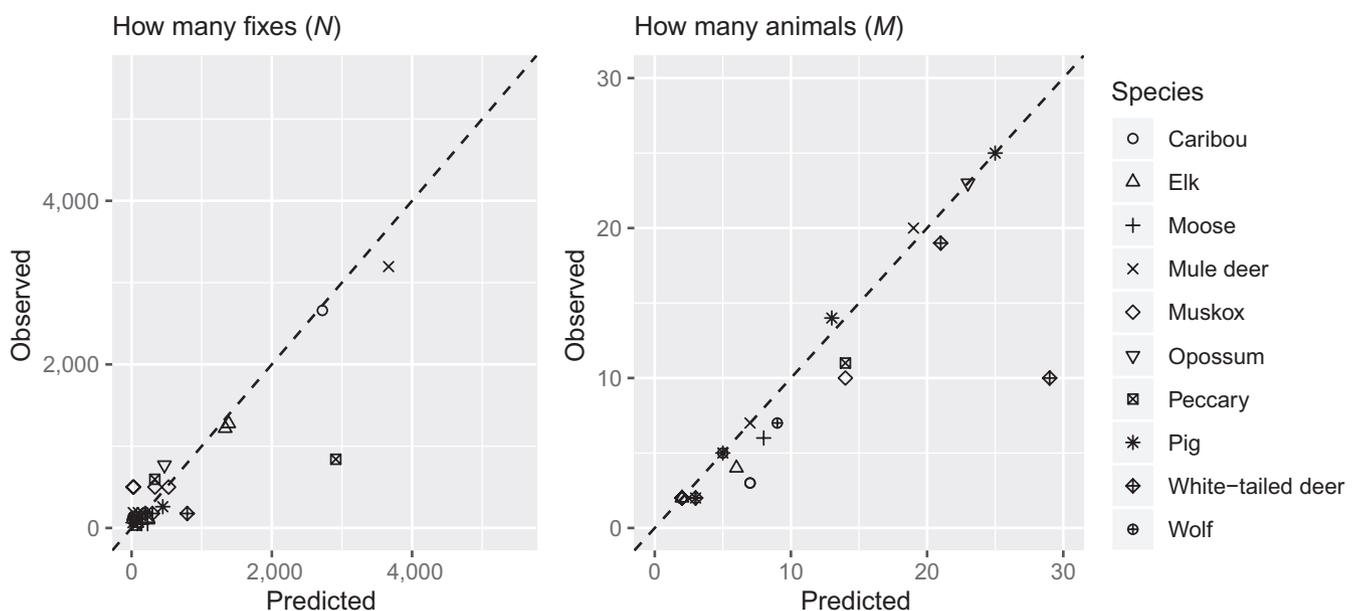
This unconventional sequence was selected because (a) it produced a comparable number of observed values of  $N$  to that in the  $M$  validation procedure (25 observed  $N$  vs. 29 pairings of  $M_{\text{pred}}$  and  $M_{\text{obs}}$ ) while (b) keeping the increments small enough to retain detail given that estimates of  $N$  can be orders of magnitude larger than those of  $M$ . We generated 4,000 samples of  $N_{\text{sam},i}$  relocations and fit an RSF to each individual sample (i.e. 4,000 RSFs assuming  $N_{\text{sam},i}$  relocations). We retained all originally generated available locations in each RSF so as to maintain a constant availability kernel between RSFs with different relocations. We then calculated the mean selection coefficient  $\bar{\beta}$  and its 95% empirical interval at a given  $N_{\text{sam}}$ . The value of  $N_{\text{sam}}$  at which the empirical interval no longer contains 0 is the observed minimum  $N$  necessary to reject  $H_0: \beta = 0$  at significance level  $p \leq 0.05$ ,  $N_{\text{obs}}$ , and should correspond to  $N_{\text{pred}}$ .

### 3 | RESULTS

Equations 3 and 8 at the basis of our methods provide analytically predicted values for the number of relocations  $N$  and the number of animals  $M$  required to parameterize an RSF. Simple 1-to-1 plots of  $N_{\text{pred}}$  versus  $N_{\text{obs}}$  and  $M_{\text{pred}}$  versus  $M_{\text{obs}}$  across all 10 species revealed strong agreement between observation and prediction (Figure 3). Interestingly, 1 outlier was identified for  $N$  and 1 for  $M$ . Visual inspection of the data revealed that these outliers occurred alongside availability samples within individual RSFs that did not properly describe the true spatial integral of resource availability (i.e.  $\int_{\Omega} A(\mathbf{x}')W(\mathbf{x}')d\mathbf{x}'$ ; Equation 1). That is, the 1:1 used/available sampling protocol undersampled the available space. Thus,  $N_{\text{pred}}$  and  $M_{\text{pred}}$  can be sensitive to insufficient spatial sampling of availability, and care should be taken to avoid such undersampling before applying these methods.

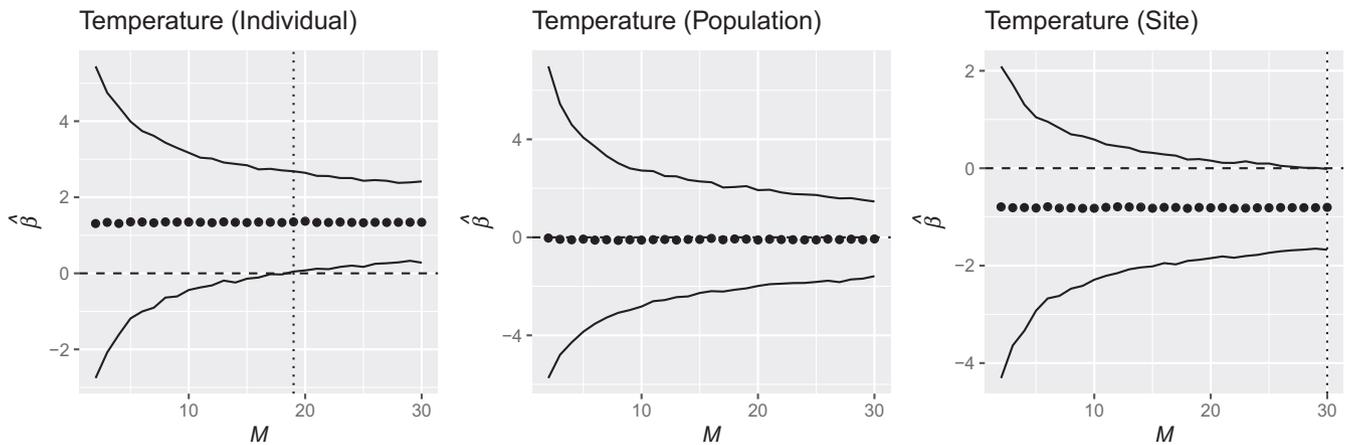
Given this, we then asked, what is the role of the definition of availability (sensu Johnson, 1980) in shaping these relationships? We estimated RSFs as described above using two additional availability definitions that varied the spatial extent of availability for a given animal: (a) within the entire collection of 99% kernel density estimates (KDEs; i.e. animals have access to resources within all KDEs equally) and (b) within the entire site (i.e. animals have access to all resources within the study site, including those outside of 99% KDEs). This mimics the problem of sufficiently sampling availability described above, but now availability is driven by conceptual or ecological definitions rather than by the sampling protocol itself. Similar consistency in  $\hat{\beta}$  was observed across  $M$  within a given definition of availability, but the sign and magnitude of  $\hat{\beta}$  varied with availability from individual- to site-level (Figure 4). Despite the change in sign and magnitude, Equation 8 is able to calculate  $M_{\text{pred}}$  consistent with observation across availability definitions. By inclusion, given that  $N_{\text{pred}}$  is a component of  $M_{\text{pred}}$  (see Equation 5), we also observe that Equation 3 is consistent with observation across availability definitions.

Lastly, we asked what are the primary drivers of  $N_{\text{pred}}$  and  $M_{\text{pred}}$  as estimated by Equations 3 and 8? A key outcome of our method is that this question can be answered analytically, by simply inspecting Equations 3 and 8. Equation 3 shows that  $N_{\text{pred}}$  is inversely correlated with both  $\text{Var}[R(X_{\beta})]$  and  $\beta^2$ , indicating that as either landscape variation or selection strength increase, so must  $N_{\text{pred}}$ . Similarly, because  $\beta^2$  is contained in the denominator of Equation 8,  $M_{\text{pred}}$  must decrease with increasing selection strength. To demonstrate this graphically, we plotted log-log regressions of  $N_{\text{pred}}$  and  $M_{\text{pred}}$  against  $\text{Var}[R(X_{\beta})]$  and  $\beta$ , respectively, using data from all 10 species to evaluate whether these analytical predictions bear out under real data scenarios (Figure 5). Per the analytical predictions, both  $N_{\text{pred}}$  and  $M_{\text{pred}}$  declined as their respective predictors (landscape variation or

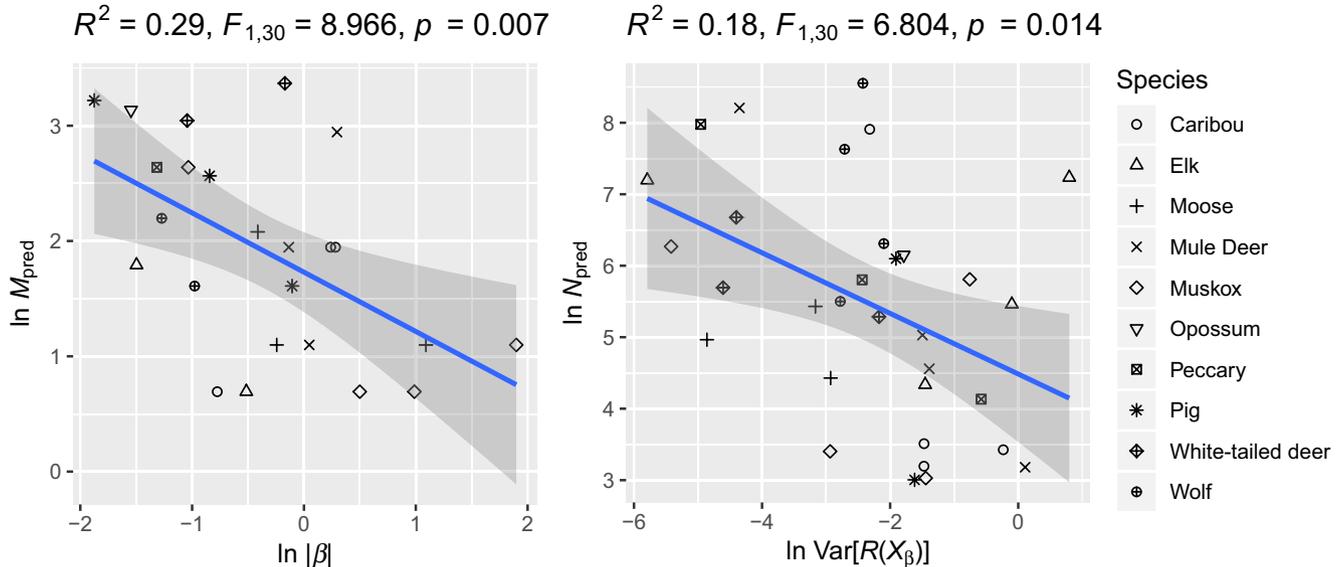


**FIGURE 3** One-to-one comparison of predicted and observed  $M$  and  $N$ . Two outliers are observed for  $N$  and one for  $M$  due to mismatch between sampled and true availability within the animals' 99% ranges. Dashed lines are those with gradient 1 crossing through the origin

## sMule deer: Temperature and scale



**FIGURE 4** Comparison of predicted  $M$  across orders of availability.  $M_{\text{pred}}$  (vertical dotted line) changes depending on whether availability for the RSF is defined at the scale of the individual (each animal has its own available locations within its own 99% KDE), population (all animals have equal access to resources within all animal's 99% KDEs) or site (all animals have equal access to resources across the entire site). If no vertical dotted line occurs, then  $M_{\text{pred}} > 30$



**FIGURE 5** Log-log regressions of predicted  $M$  versus  $\beta$  and predicted  $N$  versus  $\text{Var}[R(X_\beta)]$ . The predicted number of animals necessary  $M_{\text{pred}}$  declines with increasing absolute magnitude of selection (i.e. stronger effects require fewer animals to estimate), and the predicted number of relocations  $N_{\text{pred}}$  declines with increasing landscape complexity

habitat selection strength) increased. It is also worth noting that inclusion of both predictors within the same log-log regression (i.e.  $M_{\text{pred}}$  as a function of both  $\text{Var}[R(X_\beta)]$  and  $\beta$ ) returned  $R^2 = 1$ , as expected given that  $N_{\text{pred}}$  and  $M_{\text{pred}}$  are determined only by  $\text{Var}[R(X_\beta)]$  and  $\beta$ .

## 4 | DISCUSSION

It is common in studies using RSFs to assume that a sample size of  $M \geq 30$  animals tagged is necessary for consistent and reliable inference (Leban et al., 2001; Hebblewhite & Haydon, 2010). Furthermore, it has been suggested that more complex landscapes

(i.e. those with higher landscape variance  $\text{Var}[R(X_\beta)]$ ) require more relocations per animal  $N$  to characterize selection (Wis et al., 2008). Our analytical models and validation procedures return a rather different set of results. First, we found that  $M_{\text{pred}}$  was often (but not always) substantially  $< 30$ , and this prediction strongly agreed with observation based on resampling of GPS-based telemetry across a variety of ecologically contrasting species (Figure 3; Figures S1–S20). Strikingly, our analytical results show conclusively that  $M$  can only decline with increasing absolute magnitude of  $\beta$  (Equation 8). Although  $M$  indeed increases with increasing variation in individual selection (Equation 8), this indicates that the most biologically relevant effects (i.e. those with the greatest  $\beta$ ) can often be estimated with only a few animals (Figure 5).

This reveals important ethical and budgetary implications for wildlife studies. For example, consider the mule deer dataset containing 106 tagged individuals (Table S1). Our findings show that the strongest effects on the utilization distribution (i.e. selection for temperature, evergreen forest and shrublands) may be estimated with fewer than 20 animals (Figure S20), that is 80% fewer animals than were used. This means that, using a conservative estimate of US\$2,450 for each GPS collar and data fees (K. L. Monteith, pers. obs.), for the aspects of the study focussed on identifying the relevant resource drivers of animal distributions as in typical RSF studies, this project could have spent \$210,700 less than it did (excluding researcher/technician effort, which has significant costs in itself). Of course, it may still be necessary to tag more animals for aspects of the study beyond resource selection analysis, but this financial discrepancy is still worth bearing in mind as it is not a trivial amount. Compared to the popular approach of tagging as many animals as possible and constructing phenomenological models to identify ecological mechanisms post hoc (colloquially referred to as 'collar-and-follower'; Dunn, 2004; Fieberg & Johnson, 2015), our analytical results suggest researchers start with efforts aimed at constructing a priori hypotheses and associated models, then use our Equations 3 and 8 to estimate the number of animals and locations per animal required for the study aims (Johnson et al., 2015).

Second,  $N_{\text{pred}}$  (the number of independent relocations per individual) also strongly agreed with observation, with both predicted and observed  $N$  in the 1,000s or larger (Figure 3). This agrees with findings that within-replicate sample sizes should generally be large (e.g. Wisz et al., 2008); however, our analytical expressions also conclusively demonstrate that  $N$  is directly calculable (Equation 3) and as with  $M$  is expected to generally decline with increasing  $\text{Var}[R(X_\beta)]$  and  $\beta$ . These conclusions for both  $M$  and  $N$  are not only analytically proven but are additionally supported by real data bearing out the analytical predictions (Figures 3–5). As such, our findings demonstrate that not only are  $M$  and  $N$  imminently calculable given a known landscape and some expectation of  $\beta$ , but the expected trends in  $M$  and  $N$  with respect to landscape complexity and the strength of animal preference are opposite to those predicted by previous studies.

Why are our results contrary to so much of the preceding literature? One possibility could lie in the 'golden rule' of sample size, i.e. that  $M \geq 30$  is required for a sample size sufficient to invoke the central limit theorem and assume a roughly normal distribution of possible sample means (Aho, 2014, p. 154), or to ignore non-normality because a model structure is somehow 'robust' to non-normality (e.g. Hector, 2015, p. 48). This is reinforced by an absence of mathematical attention to the sample size question. Previous studies have used simulation or empirical analyses to explore sample size sufficiency within particular species or systems (e.g. Leban et al., 2001; Loe et al., 2012; Sequeira et al., 2019), leading to conclusions that are quite specific to a given study but then are widely adopted as inferring pattern across all systems. By defining the problem mathematically (i.e. at what values of  $M$  and  $N$  do we reject the null hypothesis  $100(1 - \alpha)\%$  of the time at significance  $p$ ?), we instead arrive at general analytical solutions that then may be tested with simulations

and empirical analyses that are specifically designed for those solutions, rather than relying on intuitive but incorrect assumptions about the relationships between landscape variation relative to selection strength and RSF sample size sufficiency.

Our calculations show that the required  $M$  and  $N$  for a given study are dependent entirely on  $\beta$  and  $\text{Var}[R(X_\beta)]$ . The latter can be directly calculated given a landscape and an expectation for  $\beta$ , but selecting an appropriate expected  $\beta$  is a critical step in estimating  $M$  and  $N$ . For a priori planning, this could be accomplished using expert knowledge and previous literature; however, there may be no conceivable prior expectation of  $\beta$  in some RSF exercises. In such a case, one may elect to perform, for example, a sensitivity analysis given a range of  $\beta$  to select conservative estimates of  $M$  and  $N$ . Furthermore, observe that  $\beta$  is often affected by a variety of ecological phenomena, including resource availability, competitor density and seasonal effects (McLoughlin et al., 2010; Mysterud & Ims, 1998; Paolini et al., 2018; van Beest et al., 2016). This implies that Equations 3 and 8 estimating  $N$  and  $M$ , respectively, are in fact hierarchical with dependencies not only on landscape variance (i.e.  $\text{Var}[R(X_\beta)]$ ) but also on landscape composition and structure as they determine  $\beta$ . In scenarios where we are uncertain about possible values of  $\beta$ , we may construct informed models suggesting likely values of  $\beta$  given an expectation for how the animal should behave as resource availability changes (e.g. generalized functional response models; Matthiopoulos et al., 2011). Such a hierarchical approach 'borrows' information from the functional response model to provide a more ecologically informed range of possible  $\beta$  for a sensitivity analysis (Hobbs & Hooten, 2015).

Our results also provide new insight into the importance of sufficient spatial sampling of availability. There was 1 outlier in the 1-to-1 comparison of  $N_{\text{pred}}$  and  $N_{\text{obs}}$ , and 1 in that of  $M_{\text{pred}}$  and  $M_{\text{obs}}$  (Figure 3). These occurred because the 99% range of the animals under observation was so large, and the underlying landscape rasters so finely grained, that our 1:1 use/availability sample did not accurately portray the spatial integral of availability  $\int_{\Omega} A(\mathbf{x}')W(\mathbf{x}')d\mathbf{x}'$  (Equation 1). This caused  $M_{\text{pred}}$  and  $N_{\text{pred}}$  to be based on a different, incomplete availability set compared to the fitted RSFs. This highlights a now well-established conclusion: the sampling intensity for availability in RSF-styled models should be as large as necessary to correctly characterize the availability integral. Previous RSF-styled studies (including SSF) have almost exclusively sampled availability as we did here using ratios (i.e. 1:1, 1:10, 1:100, etc.; e.g. Boyce & McDonald, 1999; Fortin et al., 2005; Street et al., 2016). This encourages potentially sampling at an intensity insufficient to approximate the spatial integral (as occurred here for outlying points in Figure 3; Benson, 2013). Our findings reinforce that availability sampling should be conducted in a regular (non-random) fashion at a spatial interval equal to the resolution of the underlying landscape data such that every possible location within the availability boundary is considered (Benson, 2013; Fieberg et al., 2021). This would produce an availability observation for every raster pixel and thus overlap between used and available locations. Although it is suggested that such overlap is to be avoided (e.g. Wisz et al., 2008), logically a used location must also be available otherwise it cannot be selected, and removing used

locations from availability can potentially omit important effects from the availability sample. Our equations indicate that this overlap is required by the mathematics of resource selection.

This finding reinforces that defining resource availability at the scale of the estimated model is a critical first step in planning a RSF. Our multiscale analysis of mule deer produced remarkably different estimates for  $M$  at each of the three definitions of availability (site-wide, population-wide and individual availability; Figure 4), indicating that failure to properly define the available space can lead to incorrect estimates of both  $M$  and  $N$ . This is not a new finding; the importance of properly defining what is available for an animal to select is a long-standing issue in RSA research (e.g. Boyce & McDonald, 1999; Fortin et al., 2005; Johnson, 1980). However, the difficulty of calculating  $M$  and  $N$  for planning a RSA study increases with the biological scale of the intended model. Site-wide availability assumes all animals have access to resources on the entire landscape and is similar in concept to first-order selection (i.e. where the species is located; Johnson, 1980), but availability may be sampled as a regular grid across the entire site. Population-wide availability refines the scale towards second-order selection (i.e. where animals situate their home ranges), but accurately defining a perimeter for the likely population range a priori within which to sample availability is non-trivial. This becomes even more difficult under individual availability; how can we anticipate the size and placement of individual home ranges? A feasible solution may be to delineate population boundaries and within this delineation generate random ranges with area determined by the literature and expert knowledge. This would enable calculation of an average theoretical availability for any animal in the study site with appropriate standard error. This could then be used to produce an average prediction for  $M$  and  $N$ , and associated confidence limits, across the average home range composition.

We approached this analysis with the aim of evaluating how many GPS-tagged animals  $M$  are needed for RSF estimation, but there are many RSF applications that do not seek  $M$  or require GPS-tagging (e.g. plant distributions). For example, RSFs estimated for rare species will typically lack sufficient data for individual-based estimation of the utilization distribution  $u(x)$  such that  $M$  is irrelevant and only  $N$  need be evaluated. RSFs can be sensitive to small sample sizes (Wiszl et al., 2008), yet they often generate accurate predictions for rare species with small datasets (McCune, 2016), suggesting that for some rare species smaller  $N$  is sufficient to achieve a robust model. Our findings permit evaluation of this. Consider a hypothetical scenario where an RSF is estimated for a rare species with 100 observations and  $\beta$  is recorded. Here, Equations 3–4 could be used to calculate  $N_{\text{pred}}$  as a post hoc metric of confidence assuming  $\beta$  is the true population/species-level average selection coefficient. If  $N_{\text{pred}} \leq 100$ , then one could trust the outcome of the RSF; conversely,  $N_{\text{pred}} > 100$  would indicate additional data collection is necessary. Where that is not possible, one could systematically adjust  $z_\alpha$  and  $z_{p/2}$  (Equation 3) to determine the confidence interval that rejects the null hypothesis  $H_0: \beta = 0$  and establish a degree of confidence for model outcomes. Although we performed validation using GPS-based datasets, Equation 3 is agnostic to how data are

collected and may also be applied to sessile organisms. Provided we can plausibly accept that  $\beta$  is roughly true and individual variation is either minimal or accommodated by the population-level  $\beta$  (presumably what has been estimated), our equations may be easily extended to evaluate almost any RSF-based study.

We must emphasize that although  $M$  may only decline with increasing  $\beta$ , Equation 3 allows for a turning point to occur such that  $N$  initially decreases with  $\beta$  but eventually increases at very large  $\beta$  (see Supplemental Information, Equation 25). When selection strength is particularly strong, smaller sample sizes make it much more likely to obtain perfect separation between used and unused resources. In such a case, one must collect more data to observe the animal not using a resource unit it should strongly prefer (or in the case of negative selection, to observe it using a resource it should strongly avoid). Practically, this means that sampling intensity for RSA is a greater concern for specialist organisms than generalists because specialists should exhibit typically larger  $\beta$  for preferred/avoided resource units than generalists. Although the equations identified here allow us to directly calculate  $N$  for any landscape and expected selection strength, we should generally expect that specialists will require larger  $N$  for precise RSF estimation.

The equations identified here explicitly evaluate the compatibility of a dataset with a given hypothetical model (i.e.  $\beta$ ). Calculating their solutions across gradients of  $N$  and  $M$  reveals how the number of data points (relocations) and number of replicates (animals) affect determination of compatibility. Rather than the values of  $N$  and  $M$  required to achieve statistical significance, we instead suggest these be used to determine the relevant sample sizes necessary to achieve 'consistent' results, that is if we increase sampling intensity would we see substantial change in estimated coefficients? From this perspective, we conclude that the number of animals  $M$  required to consistently estimate the most biologically relevant effects in an RSF can be well below commonly touted sample size thresholds (i.e.  $M \geq 30$ ), particularly when selection strength is strong (Figures 3 and 5). Moreover, the number of required relocations  $N$  can also be quite small but tends towards larger sample sizes when landscape variation is small. The sufficiency of samples sizes  $M$  and  $N$  is dependent entirely on the strength of selection ( $\beta$ ) and landscape variation with respect to selection strength ( $\text{Var}[R(X_\beta)]$ ). Rather than simply reporting sample sizes in RSF studies, researchers should pay explicit attention to the effect their sample size has on their findings. Regardless of study organism, ecosystem or scenario, our equations may be equally applied to any RSF-based study to evaluate the consistency of expected outcomes given a dataset of a particular size. This will partially address the so-called 'replicability crisis' by explicitly characterizing the consistency of model outputs in relation to sample sizes and effect sizes, thereby increasing reader (and reviewer) confidence in such studies. Similarly, editors and reviewers should abandon preconceived notions of what makes a sufficient sample size in RSF in favour of evaluating the sensitivity of findings to sample size based on the mathematical rules identified here, for it is also feasible (and indeed demonstrable) that consistent findings can be achieved with as few as  $N = 100$  relocations per animal and

$M = 2$  animals (Figure 3). Because  $M$  and  $N$  can be easily calculated provided knowledge of ecological and landscape effects, we argue that such calculations should henceforth be a mandatory component for all RSF studies.

## ACKNOWLEDGEMENTS

We thank the Movement Ecology Special Interest Group of The British Ecological Society for valuable discussion regarding this topic, in particular Marie Auger-Méthé. We also thank John Fieberg for providing a friendly review of an early iteration of this manuscript. GMS thanks the Mississippi Agricultural and Forestry Experiment Station (MAFES); the Forest and Wildlife Research Center (FWRC); the United States Department of Agriculture National Institute of Food and Agriculture (USDA NIFA); and the Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) for supporting this research and associated data collection. J.R.P. thanks the School of Mathematics and Statistics at the University of Sheffield for granting him study leave which has helped enable the research presented here. C.M.P., L.J.N. and E.V.W. respectfully acknowledge that Riding Mountain National Park is the traditional homeland of the Anishinabe People and the Métis Nation, within Treaty 2 territory and at the crossroads of Treaties 1 and 4. Contributions of S.P.D. and B.K.S. were partially supported by the Mississippi State University Extension Service (MSUES), FWRC and MDWFP. Contributions of J.C.B., O.R., P.E.S., G.D., D.A.K. and D.A.B. were partially supported by the USDA Animal and Plant Health Inspection Service (APHIS), Wildlife Services (WS), National Wildlife Research Center (NWRC) and U.S. Department of Energy (DOE) through Cooperative Agreement number DE-FC09-07SR22506 with the University of Georgia Research Foundation. Contributions of A.R.R. and J.M.F. were supported by the Ontario Ministry of Natural Resources and Forestry (OMNRF). Contributions of K.L.M. and S.P.D. were supported by Wyoming Game and Fish Department (WGFD), Bureau of Land Management (BLM), Muley Fanatic Foundation, Boone and Crockett Club, Wyoming Wildlife and Natural Resources Trust, Knobloch Family Foundation, Wyoming Animal Damage Management Board, Wyoming Governor's Big Game License Coalition, Bowhunters of Wyoming, Wyoming Outfitters and Guides Association, United States Forest Service (USFS) and United States Fish and Wildlife Service (USFWS). Contributions of C.M.P., L.J.N. and E.V.W. were supported primarily by Parks Canada Agency (Riding Mountain National Park of Canada) and the Natural Science and Engineering Research Council of Canada (NSERC). Contributions of F.M.v.B., L.T.B. and N.M.S. were supported by the AUFF Starting Grant (AUFF-F-2016-FLS-8-16).

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

G.M.S. conceived and directed the project and developed the validation and resampling framework, in collaboration with J.R.P. and L.B.; J.R.P. derived the analytic expressions, and G.M.S. and J.R.P. conducted the data analyses in collaboration with L.B.; G.M.S., J.R.P.

and L.B. wrote the manuscript. Remaining authors collected and contributed data and contributed equally to edits and revisions.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13701>.

## DATA AVAILABILITY STATEMENT

Data and sample code are available at FigShare <https://doi.org/10.6084/m9.figshare.11910831>.

## ORCID

Garrett M. Street <http://orcid.org/0000-0002-1260-9214>

Jonathan R. Potts <https://orcid.org/0000-0002-8564-2904>

Luca Börger <https://orcid.org/0000-0001-8763-5997>

James C. Beasley <https://orcid.org/0000-0001-9707-3713>

John M. Fryxell <https://orcid.org/0000-0002-5278-8747>

Philip D. McLoughlin <https://orcid.org/0000-0003-2286-2720>

Floris M. van Beest <https://orcid.org/0000-0002-5701-4927>

Larissa T. Beumer <https://orcid.org/0000-0002-5255-1889>

Guha Dharmarajan <https://orcid.org/0000-0001-8500-0429>

Samantha P. Dwinell <https://orcid.org/0000-0002-7043-3202>

Júlia Emi F. Oshima <https://orcid.org/0000-0003-1545-768X>

Peter E. Schlichting <https://orcid.org/0000-0003-2491-7940>

Niels M. Schmidt <https://orcid.org/0000-0002-4166-6218>

## REFERENCES

- Aho, K. A. (2014). *Foundational and applied statistics for biologists using R*. CRC Press.
- Benson, J. F. (2013). Improving rigour and efficiency of use-availability habitat selection analyses with systematic estimation of availability. *Methods in Ecology & Evolution*, 4, 244–251.
- Boyce, M. S., & McDonald, L. L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*, 14, 268–272.
- Dunn, W. C. (2004). More suggestions for raising the bar for conservation - A response to Anderson et al. *Wildlife Society Bulletin*, 32, 594–597.
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697.
- Fieberg, J., & Johnson, D. H. (2015). MMI: Multimodel inference or models with management implications? *Journal of Wildlife Management*, 79, 708–718.
- Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A 'how to' guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, 90, 1027–1043.
- Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behaviour shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86, 1320–1330.
- Fretwell, S. D., & Lucas, H. L. (1969). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, 19, 16–36.
- Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C. E., & Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, 75, 887–898.
- Guillera-Arroita, G., & Lahoz-Monfort, J. J. (2012). Designing studies to detect differences in species occupancy: Power analysis under imperfect detection. *Methods in Ecology & Evolution*, 3, 860–869.

- Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365, 2303–2312.
- Hector, A. (2015). *The new statistics with R: An introduction for biologists*. Oxford University Press.
- Hobbs, N. T., & Hooten, M. B. (2015). *Bayesian models: A statistical primer for ecologists*. Princeton University Press.
- James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An introduction to statistical learning with applications in R*. Springer.
- Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71.
- Johnson, P. C. D., Barry, S. J. E., Ferguson, H. M., & Müller, P. (2015). Power analysis for generalized linear mixed models in ecology and evolution. *Methods in Ecology & Evolution*, 6, 133–142.
- Leban, F. A., Wisdom, M. J., Garton, E. O., Johnson, B. K., & Kie, J. G. (2001). Effect of sample size on the performance of resource selection analyses. In J. J. Millspaugh & J. M. Marzluff (Eds.), *Radio tracking and wildlife populations* (chap. 11, pp. 291–307). Academic Press.
- Loe, L. E., Bonenfant, C., Meisingset, E. L., & Mysterud, A. (2012). Effects of spatial scale and sample size in GPS-based species distribution models: Are the best models trivial for red deer management? *European Journal of Wildlife Research*, 58, 195–203.
- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals: Statistical design and analysis for field studies* (2nd ed.). Kluwer Academic Publishers.
- Matthiopoulos, J., Hebblewhite, M., Aarts, G., & Fieberg, J. (2011). Generalized functional responses for species distributions. *Ecology*, 92, 583–589.
- McCune, J. L. (2016). Species distribution models predict rare species occurrences despite significant effects of landscape context. *Journal of Applied Ecology*, 53, 1871–1879.
- McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E., & Contasti, A. L. (2010). Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, 79, 4–12.
- Millspaugh, J. J., Skalski, J. R., Kernohan, B. J., Raedeke, K. J., Brundige, G. C., & Cooper, A. B. (1998). Some comments on spatial independence in studies of resource selection. *Wildlife Society Bulletin*, 26, 232–236.
- Mysterud, A., & Ims, R. A. (1998). Functional responses in habitat use: Availability influences relative use in trade-off situations. *Ecology*, 79, 1435–1441.
- Paolini, K. E., Strickland, B. K., Tegt, J. L., VerCauteren, K. C., & Street, G. M. (2018). Seasonal variation in preference dictates space use in an invasive generalist. *PLoS ONE*, 13, e0199078
- Potts, J. R., Auger-Méthé, M., Mokross, K., & Lewis, M. A. (2014). A generalized residual technique for analysing complex movement models using earth mover's distance. *Methods in Ecology and Evolution*, 5, 1012–1022.
- Renner, I. W., & Warton, D. I. (2013). Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. *Biometrics*, 69, 274–281.
- Schlather, M., Malinowski, A., Oesting, M., Boecker, D., Storkorb, K., Engelke, S., Martini, J., Ballani, F., Moreva, O., Auel, J., Menck, P., Gross, S., Ober, U., Ribeiro, P., Ripley, B. D., Singleton, R., Pfaff, B., & R Core Team. (2016). *Randomfields: Simulation and analysis of random fields, r package*. Retrieved from <http://CRAN.R-project.org/package=RandomFields>.
- Sequeira, A. M. M., Heupel, M. R., Lea, M. A., Eguíluz, V. M., Guarate, C. M., Meekan, M. G., Thums, M., Calich, H. J., Carmichael, R. H., Costa, D. P., Ferreira, L. C., Fernández-Gracia, J., Harcourt, R., Harrison, A.-L., Jonsen, I., McMahon, C. R., Sims, D. W., Wilson, R. P., & Hays, G. C. (2019). The importance of sample size in marine megafauna tagging studies. *Ecological Applications*, 29, e01947
- Street, G. M., Fieberg, J., Rodgers, A. R., Carstensen, M., Moen, R., Moore, S. A., Windels, S. K., & Forester, J. D. (2016). Habitat functional response mitigates reduced foraging opportunity: Implications for animal fitness and space use. *Landscape Ecology*, 31, 1939–1953.
- Strickland, M. D., & McDonald, L. L. (2006). Introduction to the special section on resource selection. *Journal of Wildlife Management*, 70, 321–323.
- van Beest, F. M., McLoughlin, P. D., Mysterud, A., & Brook, R. K. (2016). Functional responses in habitat selection are density dependent in a large herbivore. *Ecography*, 39, 515–523.
- Wis, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., & NCEAS Predicting Species Distributions Working Group. (2008). Effects of sample size on the performance of species distribution models. *Diversity & Distributions*, 14, 763–773.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Street, G. M., Potts, J. R., Börger, L., Beasley, J. C., Demarais, S., Fryxell, J. M., McLoughlin, P. D., Monteith, K. L., Prokopenko, C. M., Ribeiro, M. C., Rodgers, A. R., Strickland, B. K., van Beest, F. M., Bernasconi, D. A., Beumer, L. T., Dharmarajan, G., Dwinnell, S. P., Keiter, D. A., Keuroghlian, A., ... Vander Wal, E. (2021). Solving the sample size problem for resource selection functions. *Methods in Ecology and Evolution*, 00, 1–11. <https://doi.org/10.1111/2041-210X.13701>