BIOLOGGING

Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation

Stefanie Muff[1,2] (iD) | Johannes Signer[3] (iD) | John Fieberg[4] (iD)

[1]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

[2]Department of Mathematical Sciences, Norwegian University of Science and Technology (NTNU), Trondheim, Norway

[3]Wildlife Sciences, Faculty of Forest Science and Forest Ecology, University of Goettingen, Göttingen, Germany

[4]Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN, USA

Correspondence
Stefanie Muff
Email: stefanie.muff@uzh.ch

John Fieberg
Email: jfieberg@umn.edu

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Abstract

1. Popular frameworks for studying habitat selection include resource-selection functions (RSFs) and step-selection functions (SSFs), estimated using logistic and conditional logistic regression, respectively. Both frameworks compare environmental covariates associated with locations animals visit with environmental covariates at a set of locations assumed available to the animals. Conceptually, slopes that vary by individual, that is, random coefficient models, could be used to accommodate inter-individual heterogeneity with either approach. While fitting such models for RSFs is possible with standard software for generalized linear mixed-effects models (GLMMs), straightforward and efficient one-step procedures for fitting SSFs with random coefficients are currently lacking.

2. To close this gap, we take advantage of the fact that the conditional logistic regression model (i.e. the SSF) is likelihood-equivalent to a Poisson model with stratum-specific fixed intercepts. By interpreting the intercepts as a random effect with a large (fixed) variance, inference for random-slope models becomes feasible with standard Bayesian techniques, or with frequentist methods that allow one to fix the variance of a random effect. We compare this approach to other commonly applied alternatives, including models without random slopes and mixed conditional regression models fit using a two-step algorithm.

3. Using data from mountain goats (*Oreamnos americanus*) and Eurasian otters (*Lutra lutra*), we illustrate that our models lead to valid and feasible inference. In addition, we conduct a simulation study to compare different estimation approaches for SSFs and to demonstrate the importance of including individual-specific slopes when estimating individual- and population-level habitat-selection parameters.

4. By providing coded examples using integrated nested Laplace approximations (INLA) and Template Model Builder (TMB) for Bayesian and frequentist analysis via the R packages `R-INLA` and `glmmTMB`, we hope to make efficient estimation of RSFs and SSFs with random effects accessible to anyone in the field. SSFs with individual-specific coefficients are particularly attractive since they can provide

insights into movement and habitat-selection processes at fine-spatial and temporal scales, but these models had previously been very challenging to fit.

1 | INTRODUCTION

Ecologists have long been interested in understanding how animals select habitat and the resulting fitness consequences from different space-use strategies (Gaillard et al., 2010). Importantly, optimal behavioural strategies may depend on intrinsic factors specific to the individual, such as its age, sex and body condition (Lesmerises & St-Laurent, 2017), as well as extrinsic factors, including climatic conditions (Raynor, Beyer, Briggs, & Joern, 2017), local predator communities (Heithaus, 2001), competition for resources (Rosenzweig, 1991), or local availability of different habitat types (Mysterud & Ims, 1998). Interestingly, individuals from the same species often adopt different habitat-use strategies (e.g., Leclerc et al., 2016), suggestive of behavioural phenotypes or "personalities" (Stamps, 2007); these differences may also have a strong genetic component (Jaenike & Holt, 1991). Thus, understanding the causes and consequences of among-animal variation in habitat selection is key to addressing fundamental questions in ecology and evolution, including the extent to which individuals develop specialized, individual niches that are narrower than that of the population (Bolnick et al., 2002; Sheppard et al., 2018).

Modern biotelemetry devices have made it possible to monitor habitat use of multiple animals at finer temporal and spatial scales, providing unique opportunities to study variation in individual behaviours and habitat-selection strategies (Cagnacci, Boitani, Powell, & Boyce, 2010). Popular publications by Gillies et al. (2006) and Dingemanse and Dochtermann (2013) have argued for the use of random effects (i.e. random parameters drawn from a common statistical distribution) to model individual variation in the context of habitat-selection and behavioural studies, respectively. Random effects allow individual coefficients to be "tied together" via an assumption that they come from a common population. These models offer a powerful approach to studying inter-individual variability, because they explicitly allow intercepts and/or slopes in the respective regression models to vary by individual, while at the same time taking advantage of the shared information that is present in the data from different individuals (Fieberg, Rieger, Zicus, & Schildcrout, 2009). An added benefit of these models is that they can accommodate non-independent data arising from having multiple observations on the same individual. By contrast, treating all observations as though they are independent would result in optimistic standard errors and confidence intervals, leading to what Hurlbert (1984) referred to as *pseudoreplication*.

1.1 | Habitat-selection analyses using resource-selection and step-selection functions

Habitat-selection analyses typically compare environmental covariates at locations visited by an animal to environmental covariates at a set of locations assumed available to the animal (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). Historically, most analyses of animal telemetry data focused on what Johnson (1980) called 3rd order selection, with available points sampled randomly or systematically from within an animal's estimated home range. In the wildlife literature, the combined observed and available locations are typically analysed using *logistic regression*, with specific focus on estimating the exponential of the linear predictor (with the intercept removed) referred to as a RSF. Warton and Shepherd (2010) provided context for interpreting RSFs by showing that slope parameters in logistic regression models are asymptotically equivalent to slope parameters in an IPP model. The IPP assumes that the intensity function is a log-linear function of the covariates; thus, regression parameters describe relationships between environmental covariates and the relative density of observed locations in space, assuming all locations in the spatial domain are equally accessible or available to the animal. Fithian and Hastie (2013) further showed that equivalence between logistic regression and an IPP only holds when the model is correctly specified or when available points are "infinitely" weighted. Interestingly, several other modelling approaches, including the maximum entropy method (Maxent, Phillips, Anderson, & Schapire, 2006), weighted distribution theory (Lele & Keim, 2006) and resource utilization functions (Millspaugh et al., 2006), have also been shown to be equivalent to fitting an IPP model (Aarts, Fieberg, & Matthipoulos, 2012; Fithian & Hastie, 2013; Hooten, Hanks, Johnson, & Alldredge, 2013; Renner & Warton, 2013).

Recent methodological development has focused on modelling habitat selection at finer temporal and spatial scales, in part driven by concerns associated with serial autocorrelation of animal locations, as points close in time are also expected to be close in space (Arthur, Manly, McDonald, & Garner, 1996; Fortin et al., 2005; Rhodes, McAlpine, Lunney, & Possingham, 2005). Recognizing that not all areas of the availability domain (typically the home range of the animal) are equally available at all time points, Fortin et al. (2005) suggested resampling step lengths (distances between successive observed locations) and turn angles (deviations from previous bearings) to generate random movements and hence available points conditional on the previously observed locations. This process results in stratified datasets with a different set of available

points associated with each observed location. The combined (stratified) observed and available location data are typically analysed using *conditional logistic regression*, with the exponential of the linear predictor referred to as a SSF. Forester, Im, and Rathouz (2009), Duchesne, Fortin, and Rivest (2015) and Avgar, Potts, Lewis, and Boyce (2016) further refined this approach and demonstrated the utility of using common statistical distributions to model and simulate step lengths and turn angles. Specifically, they showed that it was possible to fit the equivalent of a biased random walk model when random points were generated using specific statistical distributions and when movement-related covariates (e.g. turn angles, step length, log-step-length) were included in conditional logistic regression models. These methods have recently been implemented in the `amt` R package (Signer, Fieberg, & Avgar, 2019), making SSFs an exciting and accessible approach for studying habitat selection at the scale of the movement step.

1.2 | Use of random effects in resource-selection and step-selection functions

Gillies et al. (2006) recommended using logistic regression models with individual-specific random intercepts to account for unequal sample sizes, and individual-specific random coefficients (briefly denoted as *random coefficients* or *random slopes*) to account for individual-specific differences when fitting RSFs. Similarly, Hebblewhite and Merrill (2008) recommended random intercepts to account for correlation within nested groupings of locations from socially structured populations (e.g. repeated observations from individual wolves and observations from wolves in the same pack). Gillies et al. (2006) and Hebblewhite and Merrill (2008) further emphasized that random coefficients could be used to model variation in habitat selection attributable to differences in habitat availability, referred to as a *functional response* (Beyer et al., 2010; Mysterud & Ims, 1998). Soon thereafter, Matthiopoulos, Hebblewhite, Aarts, and Fieberg (2011) and Aarts, Fieberg, Brasseur, and Matthiopoulos (2013) developed a formal framework for modelling functional responses using a combination of random effects and fixed effects constructed from the first few moments (mean, variance) of habitat covariates.

Most modern statistical software platforms provide methods for fitting generalized linear mixed-effects models (e.g. logistic regression with random intercepts and slopes) and, therefore, allow for the possibility of studying individual-specific variation in studies focused on 3rd order habitat selection. However, a literature search that we carried out on all papers that cited Gillies et al. (2006), published between January 2016 and May 2018 and claiming to use random effects in an RSF (*n* = 69), revealed that less than 20% of all publications included individual-specific random slopes in their models, while the majority of them only specified an individual-specific random intercept. This is interesting because random intercept-only models are often not sufficient to account for pseudoreplication (Schielzeth & Forstmeier, 2009). Further, in applications of RSFs, the variability in the intercepts is largely driven by differences in the ratio of used to available points, which is under control of the analyst

(Fieberg, Matthiopoulos, Hebblewhite, Boyce, & Frair, 2010). We will come back to this point later in the paper.

In the context of SSFs, Duchesne, Fortin, and Courbin (2010) argued for incorporating individual-specific slopes to allow the influence of habitat covariates to depend on what is locally available to the animal (i.e. for functional responses). Unfortunately, conditional logistic regression models that include individual-specific random slopes are extremely challenging to fit, especially with large numbers of strata (Craiu, Duchesne, Fortin, & Baillargeon, 2011). To circumvent this problem, Craiu et al. (2011) developed a two-step estimation approach to fitting mixed-effects models. This approach works well when the number of strata per individual is large, but frequently fails (or leads to numerical instabilities) when one or several individuals do not have enough variability in the encountered locations. As one of its main limitations, it is not possible to use this two-step approach in cases where one or more individuals do not encounter all factor levels of a categorical predictor.

1.3 | Objectives

Our overarching goal of this paper is to provide both new and established users of RSFs and SSFs with a coherent framework to formulate and fit the respective statistical models. In particular, the objectives are to: (a) reiterate the importance of including random slopes in habitat-selection models, both for RSFs and SSFs; (b) reiterate the importance of weighting available points when fitting logistic regression models to estimate RSFs; and (c) present computationally efficient and consistent methods for fitting both RSFs and SSFs with random effects. To allow fitting of SSFs, we propose to reformulate the conditional logistic regression model as a (likelihood-equivalent) Poisson model, where stratum-specific intercepts are included and efficiently modelled as a random effect with a fixed large prior variance. We will explain why fixing the variance is important, and why, for the same reason, random intercept variances in RSFs should also be fixed at a large value, instead of estimated. We illustrate how all models discussed here can easily be fit using R (R Core Team, 2018), either employing a Bayesian approach via integrated nested Laplace approximations (INLA, Rue, Martino, & Chopin, 2009) using the R interface `R−INLA`, or in a frequentist approach using Template Model Builder (TMB) via the `glmmTMB` R package (Brooks et al., 2017; Magnusson et al., 2017). To illustrate the efficiency and accuracy of these methods, we reanalysed data from a study on mountain goats (*Oreamnos americanus*; Lele & Keim, 2006) and Eurasian otters (*Lutra lutra*; Weinberger, Muff, de Jongh, Kranz, & Bontadina, 2016) and carried out a simulation study to compare the reformulated Poisson model for SSFs to existing two-step procedures. We provide ready-to-use R code to replicate all of our analyses (Muff, Signer, & Fieberg, 2019).

2 | BACKGROUND ON ANALYSING RSFS AND SSFS

Both RSFs and SSFs quantify habitat selection by comparing environmental covariates associated with locations that animals visit

(encoded as $y = 1$) with environmental covariates at a set of locations assumed available to the animal (encoded as $y = 0$). The main difference between the RSF and the SSF approach is that the latter conditions (i.e. "matches") the set of available points on the current location of the animal, resulting in a stratified dataset, whereas RSFs use a single set of (pooled) available locations for each animal, with these locations usually generated by sampling randomly or systematically from within an animal's home range (e.g., Manly et al., 2002). The sampling scheme used to generate available points dictates how the respective data should be analysed (Warton & Aarts, 2013): While RSFs can be estimated by fitting a standard logistic regression model, SSFs need to account for the fact that a unique set of available points is chosen for (or "matched to") each observed location, which can be accomplished by fitting a conditional logistic regression model. In the latter case, each observed location thus forms a stratum along with its set of matched available locations. We give a short overview of the two different regression models that are typically used to estimate RSFs and SSFs.

2.1 | RSFs: logistic regression model

Assume we have $n = 1, ..., N$ individuals and a set $j = 1, ..., J_n$ of used and available locations for animal n. In the absence of any random effects, the probability that a point y_{nj} with covariate vector x_{nj} is used, $\Pr(y_{nj} = 1 \mid x_{nj}) = \pi_{nj}$, can then be modelled as

$$\text{logit}\left(\pi_{nj}\right) = \boldsymbol{\beta}^\top x_{nj}, \quad y_{nj} \sim \text{Bern}\left(\pi_{nj}\right), \tag{1}$$

with logistic (logit) link and $\boldsymbol{\beta}^\top$ being the transposed of the covariate vector $\boldsymbol{\beta}$ that is the target of interest (Warton & Shepherd, 2010). Standard GLM software, such as the `glm()` function in R, can be used to estimate $\boldsymbol{\beta}$. An extension of model (1) to include individual-specific random effects is conceptually straightforward, and the respective mixed model can for example be fit by the `glmer()` function from the `lme4` package (Bates, Mächler, Bolker, & Walker, 2015).

It is important to note that, unlike prospective sampling designs involving a binary response variable, the y_{nj} in RSF designs are not Bernoulli random variables. Rather, the Bernoulli likelihood formed by (1) results in a set of estimating equations that produce consistent estimators of β in an equivalent log-linear IPP model (Warton & Shepherd, 2010). This equivalence holds whenever the RSF model is correctly specified, or when the number of available points is sufficiently large (Warton & Shepherd, 2010). However, using a sufficiently large number of available points is computationally inefficient, and in fact, Fithian and Hastie (2013) elegantly show that the same convergence limit is obtained when instead infinite weights are assigned to all available points. For the respective weighted logistic regression approach, the likelihood for the available "background" samples (i.e. $y = 0$) is weighted with a weight W, while the used points ($y = 1$) keep weight 1. Fithian and Hastie (2013) demonstrated how, for $W \to \infty$, the likelihood converges to the IPP likelihood. In our experience, values of $W = 1,000$

typically lead to good approximations, but larger values may be tried to check for convergence. Weights are easily incorporated into most GLM software (e.g. `glm()` or `glmer()`). We do not reiterate the logistic regression likelihood here, but refer the reader to Hosmer and Lemeshow (2000) for more on logistic regression, and to Warton and Shepherd (2010) and Fithian and Hastie (2013) for a description and justification of its use for studying habitat selection.

2.2 | SSFs: conditional logistic regression model

Assume we have $n = 1, ..., N$ individuals with realized steps at time points $t = 1, ..., T_n$, with $j = 1, ..., J_{n,t}$ locations that were either used or available to animal n at time step t. Note that, for notational simplicity, we may replace $J_{n,t}$ by J, because it is common practice to match a constant number of available points to each observed location (e.g. 10 available for 1 used location). Used and available locations associated with each step form a choice set or *stratum*. This implies that the probability the nth animal selects the jth unit with habitat-specific covariates x_{ntj} at time point t, given the set of possible choices $x_{nt\cdot} = \{x_{nt1}, ..., x_{ntJ}\}$, is

$$\Pr\left(y_{ntj} = 1 \mid x_{nt\cdot}\right) = \pi_{ntj} = \frac{\exp\left(\boldsymbol{\beta}^\top x_{ntj}\right)}{\sum_{i=1}^{J} \exp\left(\boldsymbol{\beta}^\top x_{nti}\right)}, \tag{2}$$

with covariate vector $\boldsymbol{\beta}$ that is the target of estimation. A popular and computationally efficient way to fit the discrete choice model (2) in the context of habitat-selection studies is by interpreting it as a specific version of the stratified proportional hazards model (Manly et al., 2002; McDonald, Manly, Nielson, & Diller, 2006). In the absence of random effects, this "Cox trick" provides a framework for efficient inference using maximum likelihood (ML), for instance via the `clogit()` function from the `survival` package in R (Therneau, 2015b), although any function to fit the Cox proportional hazard survival model can be used.

3 | MIXED-EFFECTS MODELLING OF RSFS AND SSFS

3.1 | The importance of random slopes

Virtually all habitat-selection studies monitor multiple animals, and the respective data are combined and modelled jointly. However, it is well known that such a sampling design generally leads to pseudoreplication due to non-independence among the data points from the same individual (see e.g., Duchesne et al., 2010; Fieberg et al., 2010; Gillies et al., 2006). Generalized linear mixed models (GLMMs) offer a powerful approach to properly account for correlated measurements taken on the same animal, while also allowing for differences in the intercepts and/or slopes among animals due to individual-specific preferences and/or differences in habitat availability that induce functional responses in habitat selection (Aarts et al., 2013; Hebblewhite & Merrill, 2008; Matthiopoulos et al., 2015, 2011; Mysterud & Ims, 1998).

TABLE 1 Estimates for the slopes of elevation ($\hat{\beta}_{ele}$) and aspect ($\hat{\beta}_{asp}$), and for the variances of the random effects $\hat{\sigma}^2_{intercept}$, $\hat{\sigma}^2_{ele}$, $\hat{\sigma}^2_{asp}$ from four models fit to data from 10 GPS-collared mountain goats. Models M1 – M3 were fit with an unweighted likelihood. Model M4, which is the recommended model, was fit with weighted logistic regression (W = 1,000) and fixed intercept variance ($\sigma^2_{int} = 10^6$). All models were fit using `glmmTMB()`

Model	$\hat{\beta}_{ele}$	$\hat{\beta}_{asp}$	$\hat{\sigma}^2_{intercept}$	$\hat{\sigma}^2_{ele}$	$\hat{\sigma}^2_{asp}$
M1 (random intercept)	0.12 (0.05)		0.008		
M2 (random intercept)	0.14 (0.03)	0.52 (0.02)	0.013		
M3 (random intercept + slopes)	0.07 (0.38)	0.66 (0.11)	0.96	1.40	0.10
M4 (random intercept + slopes)	0.12 (0.31)	0.65 (0.11)		0.93	0.12

Our literature review on the RSF papers mentioned in the introduction suggests that it is common practice to include individual-specific random intercepts, but not random slopes when modelling habitat selection. This is remarkable for three reasons: First and most importantly, random intercept-only models cannot (by definition) account for among-individual variation in the regression *slopes*; that is, they cannot account for functional responses. Further, the slope estimator from a logistic model that omits random effects is a biased estimator of the mean slope in the population, a fact that has been discussed repeatedly in the statistical and ecological literature (e.g., Fieberg et al., 2009; Muff, Held, & Keller, 2016). Second, omitting individual-specific random slopes when they actually do vary between individuals induces too little uncertainty in the estimated parameters (e.g., Schielzeth & Forstmeier, 2009). Consequently, it is possible that researchers end up with too high confidence in their potentially biased estimators of effect sizes. The problem is particularly acute when there are lots of observations for each animal, which is typically the case in telemetry studies. And third, the intercept in RSF models reflects the probability of a location being used when all covariates are set equal to 0 and is thus heavily influenced by the ratio of used versus available points (Fieberg et al., 2010). Given that it is common to use a predefined, constant ratio of used to available points for all animals (e.g. 10 available points per used point), it is not surprising that random intercept estimators will sometimes return an among-animal variance component of 0. We demonstrate all of these issues by comparing RSF models with and without random slopes that we fit to data from mountain goats in Section 4.1. Moreover, the first two issues are also relevant for SSF models, as pointed out by, for example Duchesne et al. (2010), and are illustrated here with an analysis of Eurasian otters and with a simulation study in Sections 4.2 and 4.3, respectively.

3.2 | Computational challenges for SSFs

Fitting a GLMM is generally known to be a difficult and computationally demanding task, and the user can choose among various model fitting procedures (an overview is given by e.g. Bolker et al., 2009, Table 1). Note, however, that while standard logistic mixed models (i.e. RSFs) can be fit with several available software packages and functions (such as `lme4::glmer()`), random-effects modelling is even more challenging for SSFs, that is, for conditional logistic regression, especially when the number of cases per stratum is greater than 1, or when the strata are unbalanced (Craiu et al., 2011). Given that proportional hazard (i.e. survival) models are commonly used to analyse SSFs with only fixed effects, it seems natural to interpret random-effects SSF models as survival models with random effects (denoted as *frailty models*), for which R solutions, for example `coxme::coxme()` or `mclogit::mclogit()`, exist (e.g. Elff, 2016; Therneau, 2015a). Unfortunately, computation quickly becomes prohibitive for telemetry data with large numbers of strata.

To address these challenges, several approaches to circumvent direct random-effects estimation have been proposed, such as the use of generalized estimating equations (GEEs, Craiu, Duchesne, & Fortin, 2008) or a two-step estimation approach (Craiu et al., 2011). GEEs, however, provide marginal parameter estimates that are analogous to those obtained from models without random effects, which are known to underestimate the true effect sizes experienced by individual animals (Fieberg et al., 2009; Lee & Nelder, 2004; Muff et al., 2016); thus, we do not generally recommend them for habitat-selection studies. The two-step approach is an efficient alternative that combines estimates of individual-specific regression parameters from standard ML methods for independent data with an expectation—maximization algorithm in conjunction with conditional restricted maximum likelihood (REML). It is available via the `Ts.estim()` function from the `TwoStepCLogit` package in R (Craiu, Duchesne, Fortin, & Baillargeon, 2016). This approach is an approximate method that works best when the number of strata per animal is large (Craiu et al., 2011). However, the data must fulfil certain regularity conditions, namely all animals must have encountered all levels of a categorical covariate, as it is otherwise not possible to obtain the individual-specific estimates from the first step that are needed for the second step of the procedure. Despite this major limitation of the two-step estimation method, it is one of the most popular approaches for fitting SSFs with random effects, while fitting such models is currently considered unfeasible with standard GLM or GLMM software.

3.3 | An efficient alternative for SSFs

We will now illustrate how relatively simple model reformulations allow one to fit mixed conditional logistic regression models in a standard GLMM. Starting (for notational simplicity) with the fixed effects-only model introduced in Equation 2, we take advantage of the fact that the conditional logistic regression model is a special case

of a multinomial model (e.g., McCullagh & Nelder, 1989) and that as such it is likelihood-equivalent to the Poisson model

$$E\left(y_{ntj}\right) = \mu_{ntj} = \exp\left(\alpha_{nt} + \boldsymbol{\beta}^{\top}\boldsymbol{x}_{ntj}\right), \quad \text{with} \quad y_{ntj} \sim \text{Po}\left(\mu_{ntj}\right) \quad (3)$$

(Chen & Kuo, 2001; McCullagh & Nelder, 1989; Whitehead, 1980), where α_{nt} is the stratum-specific intercept of animal n at time point t. Since a predefined fixed number of used points (usually one) is allowed within a stratum, the probability of use, conditional on the used and available locations in the stratum, is

$$\text{Pr}\left(y_{ntj} = 1 | \boldsymbol{x}_{nt\cdot}\right) = \pi_{ntj} = \frac{\exp\left(\alpha_{nt} + \boldsymbol{\beta}^{\top}\boldsymbol{x}_{ntj}\right)}{\sum_{i=1}^{J} \exp\left(\alpha_{nt} + \boldsymbol{\beta}^{\top}\boldsymbol{x}_{nti}\right)} = \frac{\exp\left(\boldsymbol{\beta}^{\top}\boldsymbol{x}_{ntj}\right)}{\sum_{i=1}^{J} \exp\left(\boldsymbol{\beta}^{\top}\boldsymbol{x}_{nti}\right)}, \quad (4)$$

where the last equality holds because the stratum-specific intercepts α_{nt} cancel out. This illustrates that model (3) is maximizing the same likelihood-kernel as the conditional logistic model given in (2). Thus, model (3), which is sometimes denoted as the *conditional Poisson* model, and conditional logistic regression models give equivalent parameter estimates, $\hat{\beta}$, and also the same standard errors (for a mathematical derivation see e.g., McCullagh & Nelder, 1989, Chapter 6.4.2). Note that these considerations are not limited to the presence of only one used point per stratum, but are valid for multinomial data with any number of cases per stratum, and even hold when the different strata in a dataset contain an unequal number of cases. In addition, the reformulation also works when random effects are added to the linear predictors in (3), in which case any convenient GLMM software can be used to fit the resulting mixed Poisson model. This option to fit SSFs has already been pointed out by Duchesne et al. (2010), but it has only rarely been used to analyse mixed conditional logistic regression models that arise from habitat-selection studies (but see Bruun & Smith, 2003).

The obvious disadvantage of formulation (3) – and a potential reason why the approach is rarely used – is that a large number of stratum-specific fixed intercepts α_{nt} must be estimated, which might again make the procedure prohibitive for movement data with tens of thousands of realized steps, given that each step induces a stratum and thus a separate intercept. Luckily, the α_{nt} are not actually of interest, and it is computationally more convenient and efficient to interpret them as a random effect $\alpha_{nt} \sim N(0, \sigma_{\alpha}^{2})$. However, it is well known that estimates of random effects will, on average, be too small in absolute terms, a phenomenon that is known as 'shrinkage towards an overall mean' in the statistics literature (e.g., Robinson, 1991; Snijders & Bosker, 1999). While shrinkage has, in general, many desirable properties, it would introduce a bias into the SSF analysis (see illustration in Section 4.3). The trick to avoid shrinkage in the α_{nt} values, while still taking advantage of the efficiency of a random-effects model, is to not allow the variance σ_{α}^{2} to be freely estimated, but instead to fix it at a large value to ensure that stratum-specific intercepts are not pulled towards 0, but are estimated essentially like fixed-effects parameters.

This idea is easy to implement in a Bayesian approach, where such information can be specified in the priors. In fact, exactly

such models with fixed intercept variance have been previously implemented in a Bayesian setting under the multinomial modelling framework; see for example the WinBUGS manual section 9.7 (Lunn, Thomas, Best, & Spiegelhalter, 2000). Adding random effects to the linear predictor leads to the mixed Poisson model

$$E\left(y_{ntj}\right) = \mu_{ntj} = \exp\left(\alpha_{nt} + \boldsymbol{\beta}^{\top}\boldsymbol{x}_{ntj} + \boldsymbol{u}_{n}^{\top}\boldsymbol{z}_{ntj}\right), \quad \text{with} \quad y_{ntj} \sim \text{Po}\left(\mu_{ntj}\right), \quad (5)$$

with individual-specific random slopes $\boldsymbol{u}_{n}^{\top}$, design vector $\boldsymbol{z}_{ntj}$ (typically a sub-vector of $\boldsymbol{x}_{ntj}$) and $\alpha_{nt} \sim N(0, \sigma_{\alpha}^{2})$ with σ_{α}^{2} fixed at a large value, for example 10^{6}. It may be prudent to verify that the results are robust when even larger values of σ_{α}^{2} are used.

For the Bayesian analyses presented here, we will take advantage of INLA via its R interface `R-INLA`. INLA avoids sampling by accurately approximating posterior marginal distributions (Rue et al., 2009), and it has therefore become a popular and efficient alternative to MCMC or likelihood-based inference, in particular for GLMMs (Fong, Rue, & Wakefield, 2010). Importantly, while fixing a variance in a Bayesian analysis is straightforward and natural, it is of course also possible in a likelihood framework. Model (5) can therefore also be fit with frequentist GLMM software, provided that there is an option to constrain σ_{α}^{2} to a fixed, large value to avoid shrinkage of the intercepts. To our knowledge, this is currently not implemented in `glmer()` in the `lme4` package in R, but it is possible with the `glmmTMB` package (Brooks et al., 2017; Magnusson et al., 2017). Consequently, we will fit frequentist GLMMs using `glmmTMB::glmmTMB()` to estimate SSFs according to model (5).

It may seem a logical consequence to suggest infinitely weighted Poisson regression to estimate the model parameters of Equation 5 for SSFs, given that infinitely weighted logistic regression is recommended for RSFs. However, the assumptions that hold for RSFs are violated because strata (which are the sampling-units of SSFs) only contain very few available points ($y = 0$); thus, the large-sample properties of RSFs do not apply to the case of SSFs, and convergence to the IPP is therefore not guaranteed (see e.g. assumptions of Theorems 3.2 and 3.3 in Warton & Shepherd, 2010). As a consequence, weighting introduces a bias, unless the use to availability ratio is very small. We will illustrate this point with a simulation (see Section 4.3 and Figure S1 in the Appendix).

3.4 | Individual-specific intercepts in RSFs

As mentioned in Section 3.1, the (individual-specific) intercept term in an RSF is largely determined by the sampling ratio of used and available points for each individual (Warton & Shepherd, 2010, Theorem 3.2). However, the intercept is also influenced by the probability that a point is used (vs. available) for the case when all covariates are set equal to 0. If all covariates $\boldsymbol{x}$ in Equation 1 have been mean-centred, for example, this reflects an "average" point in the habitat ensemble of all individuals. Thus, even in the presence of equal sampling ratios for all individuals, individual-specific intercepts may still vary due to differences in the distribution of habitat covariates within each individual's home range (e.g. varying availability of

woodland). Importantly, in the same way that the intercept is used to *condition on* habitat availability at the current position of an individual in an SSF, the intercept conditions on the habitat availability in the home range of the respective individual in an RSF. As a consequence, we recommend that individual-specific intercepts should not be shrunk towards an overall mean, but instead should also be given a large, fixed prior variance just like the stratum-specific intercepts in SSF models in Section 3.3.

4 | APPLICATIONS

The code and data for all analyses in this Section are available at the Data Repository of the University of Minnesota (Muff et al., 2019).

4.1 | Habitat selection of mountain goats: an RSF analysis

To reiterate the problems with fitting random intercept-only models, we considered data collected from GPS-collared mountain goats in British Columbia, previously analysed by Lele and Keim (2006) with fixed effects-only models, and available in the `ResourceSelection` R package (Lele, Keim, & Solymos, 2017). This dataset consists of use and availability locations for each of 10 different mountain goats, with a use to available ratio of 1:2 for each goat, and a total number of 6,338 used points. Because such a low use to available ratio is generally considered inadequate (see e.g., Northrup, Hooten, Anderson, & Wittemeyer, 2013), we employ the example here purely for illustration purposes. We first fit a RSF containing a single predictor, elevation (centred and scaled to have mean 0 and *SD* 1) along with a random intercept (variance not fixed) for each goat. The model was fit with an unweighted logistic regression using `glmmTMB::glmmTMB()` and returned a variance estimate for the among-animal variability in intercepts very close to 0 (Table 1, model M1), reflecting that the differences in the intercepts are mainly determined by the use to available ratio, as pointed out in Sections 3.1 and 3.4. Interestingly, a variance estimate of exactly 0 was obtained when using default settings in the `lme4::glmer()` function (results not shown), reflecting the challenge of estimating such a small variance.

We next considered RSFs that included elevation plus a centred and scaled measure of aspect and compared the estimates from a random intercept-only model (model M2) to those from a model containing independent random intercepts and slopes (model M3), both fit with `glmmTMB()`. In model M3, the standard errors associated with the slope coefficients for aspect and elevation were an order of magnitude larger than when they were not allowed to vary by individual in model M2. These results clearly demonstrate the problems noted by Schielzeth and Forstmeier (2009), namely that random intercept-only models tend to underestimate standard errors of (potentially biased) fixed-effects parameters. Finally, we fit the weighted logistic regression model (using $W = 1,000$) with random intercept and slopes, with fixed

intercept variance at 10^6 (model M4), because this is the procedure we recommend. Weighting the likelihood and fixing the variance of the intercepts in M4 led to a noticeable increase in the estimate of β_{ele} and a decrease in the estimate of σ^2_{ele} with respect to the unweighted model, while it had little effect on the estimated values of β_{asp} and σ^2_{asp}. Very similar results to model M4 were obtained when we carried out a Bayesian analysis using `R-INLA`, and also when the model was fit with an intercept variance that could be freely estimated (results therefore not shown, but see data and code for all analyses).

4.2 | Habitat selection of otters: an SSF analysis

We reanalysed data collected and presented by Weinberger et al. (2016) involving nine radio-collared otters that were tracked between 6 months and 3 years in the European Alps. To fit SSFs to these data, each observed location was matched with nine random (available) points generated by resampling step lengths and turning angles from their empirical distribution (Fortin et al., 2005). Due to the absence of an efficient alternative, the original analysis was performed with a two-step estimation method provided by the `TwoStepCLogit::Ts.estim()` function. The original model included 12 covariates and random effects for all of them. Here, however, we only included the variables of main interest, namely the factorial covariate *habitat type* (with levels *main discharge*, *reservoir* and *residual water*), and the continuous variable *river width*. Moreover, because Forester et al. (2009) showed that the addition of a distance function to the linear predictor is required to reduce bias in the parameter estimators, we included *step length* as an additional covariate. The data contained a total of 41,670 data points with 4,167 realized steps, where the latter thus corresponds to the number of strata.

For illustration, we started by fitting fixed effects-only models. To this end, the well-established stratified Cox model was fit via the `survival::clogit()` function. The respective results were compared to the outcome from the conditional Poisson model as given by Equation 3, where the stratum-specific intercepts are implicitly estimated by modelling them as a random intercept with a fixed variance $\alpha_{nt} \sim N(0, 10^6)$; we also re-ran the models with $\alpha_{nt} \sim N(0, 10^{12})$ to verify that results were robust to this choice. We estimated the parameters both with the frequentist approach using `glmmTMB`, and with the Bayesian approach using `R-INLA`, with independent $\beta \sim N(0, 10^4)$ priors for all components in the vector of slope parameters. This led to parameter estimates that were essentially indistinguishable from those obtained via the stratified Cox model (Table 2), illustrating that the conditional Poisson model is equivalent to the conditional logistic model and that we can circumvent the estimation of the stratum-specific fixed intercepts by a random effect with large fixed variance. Note that this equivalence does not hold when σ^2_α is freely estimated instead, and that this would lead to invalid results, as will be illustrated in the simulation below (Section 4.3). Computation times were on the order of a few seconds for all procedures.

TABLE 2 Estimated slopes for reservoir ($\hat{\beta}_{RESE}$), residual water ($\hat{\beta}_{REST}$) and river width ($\hat{\beta}_{Width}$) and for the corresponding variance parameters of the Eurasian otter example when using the Cox model (clogit), the Poisson model with stratum-specific intercept (cPois) fit with R-INLA or glmmTMB(), and the two-step procedure Ts.estim() (Two-step). For the INLA output, posterior means are given for the slope estimates, and posterior modes for the variances

Slope estimates	$\hat{\beta}_{RESE}$	$\hat{\beta}_{REST}$	$\hat{\beta}_{Width}$
I. Fixed-effects models			
clogit	−0.07 (0.07)	−0.38 (0.10)	0.16 (0.04)
cPois (INLA)	−0.07 (0.07)	−0.38 (0.10)	0.16 (0.04)
cPois (glmmTMB)	−0.07 (0.07)	−0.39 (0.10)	0.16 (0.04)
II. Mixed-effects models (random intercept & slopes)			
Two-step	0.04 (0.17)	−0.24 (0.24)	0.10 (0.12)
cPois (INLA)	0.02 (0.18)	−0.33 (0.22)	0.11 (0.14)
cPois (glmmTMB)	−0.004 (0.14)	−0.35 (0.16)	0.12 (0.11)
Variance estimates (mixed models only)	$\hat{\sigma}^2_{RESE}$	$\hat{\sigma}^2_{REST}$	$\hat{\sigma}^2_{Width}$
Two-step	0.17	0.35	0.08
cPois (INLA)	0.08 (0.02, 0.78)	0.10 (0.03, 1.02)	0.05 (0.02, 0.47)
cPois (glmmTMB)	0.07 (0.01, 0.64)	0.10 (0.01, 1.12)	0.07 (0.02, 0.28)

Note: Values in parentheses are *SE* (for the slope estimates) and 95% credible intervals (for the variances); Ts.estim() does not provide measures of uncertainty for variance parameters.

Next, we included independent individual-specific random slopes for all covariates (except for step length). We again estimated parameters with glmmTMB and R-INLA, using the conditional Poisson model (5). For the Bayesian model, the same priors as above were used for the fixed effects and the intercept α_{nt}. In addition, PC priors PC(3, 0.05) were assigned to the precisions of the remaining random slopes (note that priors in the Bayesian framework are typically given to precisions, not variances), but results were insensitive to this choice. PC priors were recently proposed as robust and intuitive alternatives to inverse gamma priors and were shown to have excellent robustness properties with respect to the choice of their hyperprior parameters (Simpson, Rue, Riebler, Martins, & Sørbye, 2017). PC priors are parameterized as PC(μ, α), where the interpretation of the parameters (μ, α) is that Pr($\sigma > \mu$) = α for the standard deviation σ; thus, the user can specify how likely it is (0 < α < 1) that σ is larger than a specific value μ > 0.

Results from the conditional Poisson models were compared to the outcome of the two-step procedure via Ts.estim(), where it was also assumed that the random effects were independent. These results (Table 2) illustrate two important points: First, the inclusion of individual-specific random slopes in the Poisson regression model leads to different parameter estimates and to much larger standard errors for the slope estimates than when fixed effects-only models are used, which again confirms that fixed effects-only models tend to give overly precise standard errors and biased estimators of regression parameters in the presence of inter-individual heterogeneity. And second, the reformulation of the conditional logistic regression model as a Poisson model with random stratum-specific intercept, as given in (5), leads to feasible estimation of mixed-effects parameters in a single modelling step. While computations with other single-step R procedures, such as adding random effects (frailties) to survival models using coxme::coxme(), were unfeasible even when only 1,000 out of the more than 4,000 strata were used (we interrupted the sessions after 24 hr of non-convergence), glmmTMB() terminated in roughly 5 s and R-INLA in 70 s on an Intel Core i7-6500U 4 x 2.50 GHz processor for the full dataset. On the other hand, the Ts.estim() procedure was still considerably faster (about 0.5 s), but we note that the parameter estimates from the approximate two-step procedure are not in very good agreement with those from the (correctly specified) Poisson model, especially for β_{REST} and σ^2_{REST}. Finally, to illustrate that the two-step procedure fails when at least one individual does not encounter all levels of a factorial variable, we artificially removed all strata that contained either used or available points falling in residual water for the individual that had the fewest visits to this habitat type (a total of 12 strata were removed). As expected, the Ts.estim() procedure could not be run, while stable results were obtained from fitting the Poisson model.

4.3 | Simulation analysis of an SSF design

To more systematically compare different estimation approaches for SSFs, we simulated and analysed data with known true coefficient values. The simulation of movement tracks involved two continuous covariates: *elevation* and *habitat*. We simulated elevation and habitat as independent unconditional Gaussian Random Fields (GRF; as implemented in Ribeiro & Diggle, 2016) with range σ^2 = 0.1 and a partial sill of π = 50 to obtain smooth and realistic surfaces for the two covariates. Each setup was replicated 500 times to obtain a sampling distribution of the estimated coefficients and to investigate bias and variance of the different estimators.

We simulated movements of 20 animals according to a biased random walk starting at the centre of the landscape at time *t* = 0. To

find the position at time $t + 1$, each animal n was given 200 candidate locations, where the coordinates for each candidate location were determined by drawing a random step length from an exponential distribution with rate parameter $\lambda = 1$, and a random turning-angle from a uniform distribution. One candidate location was then selected at random with probability proportional to $\boldsymbol{\beta}^{\top}\boldsymbol{x}$, where $\boldsymbol{x}$ are the covariate values at the end point of each potential step, and $\boldsymbol{\beta}^{\top}$ is the vector of selection coefficients (–4, 4). Animals were assigned individual-specific slopes for both variables, generated from uncorrelated Gaussian distributions with mean (-4,4) and variances $\sigma^2_{\text{ele}} = 10$ and $\sigma^2_{\text{hab}} = 5$. For each animal, we simulated 200 time steps, and each observed step was paired with nine random (control) steps. Following Forester et al. (2009), we generated random steps with step lengths from an exponential distribution with rate $\lambda = 1/(2\bar{l})$, with $\bar{l}$ equal to the mean realized step length, and with the direction of random steps drawn from a uniform distribution distribution of turning angles between $-\pi$ and π. We then included step length (l) in the linear predictor to correct for the bias due to the way we generated random step lengths (i.e. exponential with $\lambda = 1/(2\bar{l})$ rather than $\lambda = 1$).

These data were analysed with the mixed conditional Poisson model of Equation 5 using `R-INLA` and `glmmTMB` including random slopes for elevation and habitat. The variance of the stratum-specific intercept was fixed to $\sigma^2_\alpha = 10^6$. To illustrate that fixing this variance is important, we also fit the same model with σ^2_α estimated instead (only with `glmmTMB` to avoid redundancy). For INLA, we used $N(0, 10^3)$ priors on the fixed effects, and $1/\sigma^2_{\text{ele}} \sim$ PC(10, 0.01) and $1/\sigma^2_{\text{hab}} \sim$ PC(5, 0.01) priors on the precisions of the random effects.

As a comparison, we also estimated regression parameters using the two-step approach implemented in `Ts.estim()` assuming independent slopes, and fit fixed-effects-only models with Cox models using the `clogit()` function.

The Poisson models with fixed σ^2_α fit with `R-INLA` and `glmmTMB` retrieved consistent estimators of the fixed-effects parameters, and the two-step estimator was also nearly unbiased (Figure 1). This was not true, however, when the stratum-specific intercept variance was estimated by the model rather than fixed at 10^6, in which case all estimators were heavily biased. Importantly, we also observe that ignoring random effects leads to biased estimators of fixed-effects parameters when, like here, there is inter-individual heterogeneity in the slopes. All variance estimators were slightly underestimated for all methods, namely because the step-length variable in the predictor absorbs some of the variability in the selection coefficients. In fact, we were able to obtain less biased variance estimators when we omitted the step-length variable (see Figure S2 in the Appendix). The impact of including step length in the linear predictor on the variance estimators is interesting and unexpected, and it is an apparent contrast to Forester et al. (2009), where the inclusion of step length is recommended to avoid bias in fixed-effect parameters. This trade-off between bias in the estimators of fixed effect parameters and the variance parameters deserves more attention in future research. Finally, as pointed out in Section 3.3, weighted regression models resulted in biased estimators except for very large numbers of random steps per stratum (Figure S1 in the Appendix); therefore, weighted alternatives were not further investigated here.
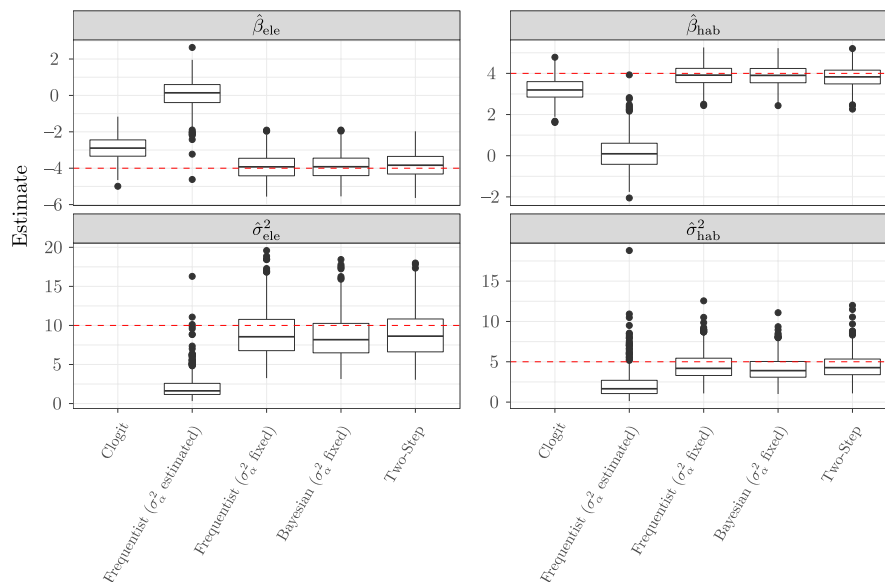

FIGURE 1 Sampling distribution for estimated SSF coefficients from conditional logistic regression without random effects using the `clogit()` function, from the conditional Poisson regression model with random coefficients using either a frequentist (`glmmTMB`) or a Bayesian approach (`R-INLA`), and from a two-step approach implemented in the `Ts.estim()` function. In the Bayesian case, the estimates are the posterior means for the fixed effects and the posterior modes for the variances. The frequentist approach was implemented both with $\sigma^2_\alpha = 10^6$ fixed (as recommended) or by estimating σ^2_α (for illustration). Boxplots show the distribution of the estimates from 500 replications. Variance estimates $\hat{\sigma}^2_{\text{hab}} > 20$ were removed for better visibility (only affects frequentist with σ^2_α estimated). The horizontal red dashed lines indicated the true value used for the simulations

5 | DISCUSSION

Recent technological advances have made it possible to track a wider range of species for longer durations, leading to an explosion of high-temporal resolution location data (Kays, Crofoot, Jetz, & Wikelski, 2015). For example, Movebank, an online platform for storing, managing, and sharing data now includes about 1.2 billion locations from over 5,500 studies of 850 different taxa (Kranstauber et al., 2011; Wikelski & Kays, 2018). The widespread availability of fine-scale temporal data is fuelling the development of new statistical approaches for modelling animal movement data (e.g., Hooten, Johnson, McClintock, & Morales, 2017; Jonsen et al., 2018) and also provides unique opportunities to study among-individual variability in movement and habitat-selection patterns. Step-selection functions are appealing because they provide an objective approach to determining habitat availability based on movement characteristics of the study species (Fortin et al., 2005; Thurfjell, Ciuti, & Boyce, 2014). Although fitting step-selection models to individual animals is straightforward, efficient standard estimation procedures for models fit to multiple animals have been lacking, hindering our ability to quantify among-animal variability in their habitat-selection patterns. Mixed-effects models are an attractive option, but these models are well acknowledged to be computationally challenging to fit in this context (Duchesne et al., 2010).

We proposed to fit RSFs and SSFs in a unified, standard GLMM framework, which is possible by combining three statistical results. First, we make use of the fact that the conditional logistic regression model, which needs to be fit to derive SSFs, is actually a multinomial model, and as such, it is likelihood-equivalent to a Poisson model. This renders mixed-effects modelling for SSFs equivalent to fitting any Poisson GLMM, which implies that incorporating individual-specific variation in SSFs is no more challenging than doing so for RSFs. Second, because individual- or stratum-specific intercepts are not actually of interest in RSFs or SSFs, and because they are determined by sampling ratios and habitat availability, these intercepts should be treated as fixed effects, or equivalently and

more efficiently, as random effects with large, fixed variance. Doing so prevents these intercept parameters from being shrunk towards the overall mean. The magnitude of the shrinkage, and hence bias, may be minimal for RSFs that include many observations for each individual (as in the goat example of Section 4.1), but can be substantial for SSFs which tend to include only a few observations in each stratum (Figure 1). And third, we reiterated that the logistic regression likelihood to estimate RSFs should always be weighted with a large weight W on the available points, in order to ensure convergence to the IPP likelihood which is guaranteed for $W \rightarrow \infty$ (Fithian & Hastie, 2013).

Fixing the individual- or stratum-specific intercept variance is particularly straightforward in a Bayesian framework, where the user is required to specify priors on all unknown parameters. To ensure efficient Bayesian inference, we have relied on the INLA approach via the R–INLA interface. Of course, all models discussed here can also be approached via MCMC sampling, although this may be very inefficient. We include an MCMC implementation of an SSF analysis to fisher (*Pekania pennanti*) data using the Stan language (Carpenter et al., 2017) in the data repository that accompanies this article. For that example, Stan required an order of magnitude more time to converge than INLA (Stan ≈ 38 min for two parallel chains with 2000 iterations each, INLA ≈ 1 min). Users that prefer frequentist inference should choose a software package that allows to fix a random effect variance to a prespecified value. Here, we fit these models using glmmTMB, which provides fast inference, and has previously proven useful for analysing large telemetry data sets (Jonsen et al., 2018). Table 3 gives an overview of models and procedures that we recommend for efficient and accurate inference on either fixed-effects or random-effects RSFs and SSFs.

Prior to now, fitting random coefficient SSFs was often only computationally feasible via two-step procedures that combine estimates of individual-specific habitat-selection inference (Craiu et al., 2011), a strategy what was proposed for habitat-selection inference more generally (e.g., Fieberg et al., 2010; Hooten, Buderman, Brost, Hanks, & Ivan, 2016). An advantage of using Ts.estim is that

	RSF designs	SSF designs
Example	Mountain goats (Section 4.1)	Eurasian otters (Section 4.2)
Fixed effects models		
	Logistic regression	Conditional logistic / conditional Poisson regression (model (3) in text)
R procedures	inla(), glm(), glmmTMB()	clogit() function or inla()/glmmTMB() for Poisson models with stratum-specific random effect and large fixed variance σ_α^2
Mixed effects models		
	Mixed logistic regression	Mixed conditional Poisson regression (model (5) in text)
R procedures	inla(), glmer(), glmmTMB()	inla(), glmmTMB(), Ts.estim()

TABLE 3 Overview of sampling designs and procedures in R that we recommend for efficient computation. Note that we recommend to carry out RSF analyses using the *infinitely weighted* version, while unweighted regression is recommended for SSFs

it is typically much faster than `glmmTMB` or `R-INLA`, as illustrated by the computation times of the otter data analysis in Section 4.2. However, it must be kept in mind that `Ts.estim` is an approximate procedure that does not guarantee consistent results and that it may fail to converge or even does not run, for example when at least one animal does not encounter all habitat types. Moreover, it might be worth noting that `Ts.estim` does not return any information-theoretic measures like AIC, BIC or DIC to help guide model selection. Still, for very large datasets and models, where GLMMs may demand too much computational power, it certainly remains a convenient and efficient alternative. Regarding efficiency, we have also seen that frequentist analyses with `glmmTMB` can be considerably faster than the Bayesian route using `R-INLA`. In fact, efficiency gain will rarely be the reason to choose Bayesian over likelihood inference. An interesting benefit of Bayesian procedures is that they give (marginal) posterior distributions of all parameters, whereas frequentist approaches usually only return point estimates and standard errors for fixed effect parameters, but no measures of uncertainty for variance parameters (although `glmmTMB` is a notable exception). In addition, various modelling extensions, such as spatial or temporal dependencies (e.g., Lindgren, Rue, & Lindström, 2011) or measurement error in covariates (e.g., Muff, Riebler, Held, Rue, & Saner, 2015), are often much more straightforward to incorporate, or even only computationally feasible, in a Bayesian setup.

Although the importance of including random coefficients in regression models of habitat-selection studies has been stressed repeatedly (Duchesne et al., 2010; Gillies et al., 2006), our literature review suggests that random-effects models are often understood as models that merely include a random intercept. Here, we have reiterated and illustrated that such practice may lead to too high confidence in results that are potentially biased. By providing coded examples using `R-INLA` and `glmmTMB`, we hope to make efficient estimation of RSFs and SSFs with random effects accessible to anyone in the field. SSFs with individual-specific coefficients are particularly attractive since they can provide insights into movement and habitat-selection processes at fine-spatial and temporal scales (Avgar et al., 2016; Signer et al., 2019), but these models had previously been very challenging to fit.

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AUTHORS' CONTRIBUTIONS

J.F., S.M. and J.S. conceived the research idea; S.M. developed the statistical framework; S.M., J.F. and J.S. conceived the design and analysis of the data; J.S. developed and ran the simulations and conducted the literature review; and S.M. and J.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code for all examples and simulations presented here are available through the Data Repository of the University of Minnesota (https://www.lib.umn.edu/datamanagement/drum) of the paper (https://doi.org/10.13020/8bhv-dz98, see Muff et al., 2019). The repository also includes a short tutorial including data not presented here.

ORCID

Stefanie Muff https://orcid.org/0000-0002-8425-0757
Johannes Signer https://orcid.org/0000-0002-1771-7775
John Fieberg https://orcid.org/0000-0002-3180-7021

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