A 'How-to' Guide for Interpreting Parameters in Resource- and Step-Selection Analyses

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Abstract

1. Resource-selection and step-selection analyses allow researchers to link animals to their environment and are commonly used to address questions related to wildlife management and conservation efforts. Step-selection analyses that incorporate movement characteristics, referred to as *integrated step-selection analyses*, are particularly appealing because they allow modeling of both movement and habitat-selection processes.

2. Despite their popularity, many users struggle with interpreting parameters in resource-selection and step-selection functions. Integrated step-selection analyses also require several additional steps to translate model parameters into a full-fledged movement model, and the mathematics supporting this approach can be challenging for biologists to understand.

3. Using simple examples, we demonstrate how weighted distribution theory and the inhomoge-

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22 neous Poisson point-process model can facilitate parameter interpretation in resource-selection

23 and step-selection analyses. Further, we provide a "how to" guide illustrating the steps

24 required to implement integrated step-selection analyses using the `amt` package.

25 4. By providing clear examples with open-source code, we hope to make resource-selection and

26 integrated step-selection analyses more understandable and accessible to end users.

27 **Keywords**: habitat selection, inhomogeneous Poisson point-process, integrated step-selection

28 analysis, resource-selection function, spatial hazards, step-selection function, telemetry, relative

29 selection strength

Introduction

31 New technologies (e.g., improved Global Positioning System [GPS] collars) and advances in remote

32 sensing have made it possible to collect animal location data on unprecedented spatial and temporal

33 scales (Kays, Crofoot, Jetz, & Wikelski, 2015; Robinson et al., 2020), which in turn has fueled

34 the development of new methods for modeling animal movement and for linking individuals to

35 their environments (Guisan, Thuiller, & Zimmermann, 2017; Hooten, Johnson, McClintock, &

36 Morales, 2017). Two of the most popular approaches for analyzing telemetry data, resource-selection

37 and step-selection analyses, compare environmental covariates at locations visited by an animal

38 ("used locations") to environmental covariates at a set of locations assumed available to the animal

39 ("available locations") using logistic and conditional logistic regression, respectively (Boyce &

40 McDonald, 1999; Fortin et al., 2005; Thurfjell, Ciuti, & Boyce, 2014). These methods are widely

41 available in most statistical software packages, and thus, they provide a robust and easy-to-implement

42 framework for analyzing habitat-selection patterns; note, here and elsewhere, we have used the term

43 *habitat-selection* rather than *resource-selection* to highlight our broader interest in modeling the

44 effects of a diverse set of environmental variables (e.g., those capturing risks and environmental

45 conditions in addition to resources), but we will often use these terms interchangeably. Despite

46 their popularity, our collective experience has been that most users struggle to interpret parameters

47 in these models. Further, it seems that papers attempting to address this issue have had limited

48 success, and in some aspects may have increased confusion (see e.g., Keating & Cherry, 2004;

49 Johnson, Nielsen, Merrill, McDonald, & Boyce, 2006; Lele, Merrill, Keim, & Boyce, 2013; Avgar,

Lele, Keim, & Boyce, 2017; Chamaille-Jammes, 2019).

Here, we highlight how point-process models and weighted distribution theory provide simple and effective frameworks for interpreting regression parameters in resource-selection and step-selection analyses. In the sections that follow, we begin by reviewing recent research connecting resource-selection functions to point-process models and weighted distribution theory. Using these connections, we demonstrate correct interpretation of parameters using simple examples of models fit to GPS locations of fisher (*Pekania pennanti*) from upstate New York (LaPoint et al., 2013a, 2013b). We then provide a short review of step-selection analyses, including their history and methods for parameter estimation. Step-selection analyses are particularly appealing because: 1) they provide an objective method for defining habitat availability in terms of movement constraints; 2) they relax the assumption that locations are statistically independent; and 3) by including movement characteristics (e.g., functions of step length and turn angle) as predictors, they provide a means to model both movement and habitat selection processes (termed an *integrated step-selection analysis* by Avgar, Potts, Lewis, & Boyce, 2016). Recognizing that many biologists may find the mathematics supporting integrated step-selection analyses intimidating, we aim to provide a "how to" guide demonstrating the steps required to implement the approach using the `amt` package (Signer, Fieberg, & Avgar, 2019). This demonstration is expanded upon using coded examples in the supplementary appendices, which we encourage the reader to explore. We end with a short discussion highlighting challenges related to statistical dependencies and model transferability.

Resource-Selection Analyses

Logistic Regression

Much of the confusion surrounding the interpretation of parameters in resource-selection analyses can be attributed to the use of logistic regression in a non-standard way. Logistic regression is most easily understood as a model for binary random variables that can take on one of two values (0 or 1) with probability that depends on one or more explanatory variables (Hosmer, Lemeshow, & Sturdivant, 2013).

Consider, for example, a prospective study designed to infer how various environmental characteristics

influence whether a habitat patch will be used by one or more animals. In this case, we may randomly select n habitat patches and monitor them to determine if they are used ($y_i = 1$) or not ($y_i = 0$) for $i = 1, 2, \ldots, n$. Logistic regression allows us to model the probability that each patch will be used, $P(y_i = 1) = p_i$, as a logit-linear function of patch-level predictors $(X_{i1}, \ldots, X_{ip})$ and regression parameters $(\beta_1, \ldots, \beta_p)$:

$$y_i \sim \text{Bernoulli}(p_i)$$

$$\text{logit}(p_i) = \log\left(\frac{p_i}{(1 - p_i)}\right) = \beta_0 + \beta_1 X_{i1} + \ldots \beta_p X_{ip}$$

After having fit a model, we can exponentiate the regression coefficients, $\exp(\beta_k)$, to quantify how the odds of use, $p/(1 - p)$, change as we increase the kth predictor by 1 unit while holding all other predictors constant. We can also use the inverse-logit transformation (eqn. (1)) to estimate the probability that a patch will be used, given its set of spatial predictors:

$$p_i = \frac{\exp(\beta_0 + \beta_1 X_{i1} + \ldots \beta_p x_{ip})}{1 + \exp(\beta_0 + X_{i1}\beta_1 + \ldots X_{ip}\beta_p)} \tag{1}$$

The logit transformation ensures that p will be constrained between 0 and 1 for all values of the predictor variables.

Contrast this approach with how logistic regression is used to study habitat selection. In a typical habitat-selection study, logistic regression models are fit to separate samples of used and available sample units, groups that are not mutually exclusive (i.e., available habitat patches may also be used). We will refer to the combined locations as *use-availability* data. In this case, y_i is no longer a Bernoulli random variable since p_i depends on the ratio of used to available points (which is under control of the analyst). Further, most analyses of telemetry data involve point-level sampling in continuous space rather than discrete sample units. In this case, the probability associated with any point is necessarily 0 to ensure the distribution integrates to 1 over all of available space. Thus, it is perhaps not surprising that there has been considerable confusion and controversy surrounding the use of logistic regression with use-availability data (e.g., Keating & Cherry, 2004; Johnson et al.,

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98 2006; Chamaille-Jammes, 2019).

99 Various arguments have been constructed to justify the use of logistic regression when analyzing

100 use-availability data (Manly, McDonald, Thomas, McDonald, & Erickson, 2002; Johnson et al.,

101 2006; Aarts, MacKenzie, McConnell, Fedak, & Matthiopoulos, 2008), but a significant breakthrough

102 came when Warton & Shepherd (2010) made a connection between logistic-regression and an

103 inhomogeneous Poisson point-process (IPP). An IPP is a model for random locations or events in

104 space, where the expected spatial density of the locations depends on spatial predictors (see next

105 section, **Inhomogeneous Poisson Point-process Model**). Warton & Shepherd (2010) showed

106 that as the number of available points is increased towards infinity, the slope parameters in logistic

107 regression models will converge to the slope parameters in an IPP model. Interestingly, several

108 other popular approaches for analyzing species distribution data, including MaxEnt (Phillips &

109 Dudík, 2008; Elith et al., 2011), weighted distribution theory with an exponential link function

110 (Lele & Keim, 2006), and resource utilization functions (Millspaugh et al., 2006), have been shown

111 to be equivalent to fitting an inhomogeneous Poisson point-process model (Warton & Shepherd,

112 2010; Aarts, Fieberg, & Matthiopoulos, 2012; Fithian & Hastie, 2013; Hooten, Hanks, Johnson, &

113 Alldredge, 2013; Renner et al., 2015).

114 Instead of focusing on p_i, as is typical in prospective studies, logistic regression applied to use-

115 availability data should simply be viewed as a convenient tool for estimating coefficients in a

116 *resource-selection function*, $w(x; \beta) = \exp(X_{i1}\beta_1 + \ldots X_{ip}\beta_p)$ (Boyce & McDonald, 1999; Boyce et

117 al., 2002). As we will see in the next section, this expression is equivalent to the intensity function

118 of an IPP model, but with the intercept (the log of the baseline intensity) removed; the baseline

119 intensity gives the expected density of points when all covariates are 0. Because resource-selection

120 functions do not include this baseline intensity, they are said to measure "relative probabilities

121 of use" or, alternatively, said to be "proportional to the probability of use" (Manly et al., 2002).

122 Although the term *probability of use* sounds appealing, it is important to remember the challenges

123 with defining probability at the point-level. Further, although probability of use is easily defined for

124 discrete sample units (e.g. grid cells), these probabilities should increase with the size of the spatial

125 unit and also with the study duration (Lele & Keim, 2006; Lele et al., 2013). Thus, with telemetry

126 studies, it seems more natural to model spatial (or spatio-temporal) "hazards" or rates of use in

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127 continuous space (and time), from which "probability of use" can be determined by integrating these

128 hazards over whatever spatial (and temporal) unit is deemed appropriate. Point-process models

129 allow us to do just that!

Inhomogeneous Poisson Point-Process (IPP) Model

131 The IPP model provides a simple framework for modeling the density of points in space as a

132 log-linear function of spatial predictors through a spatially-varying intensity function, $\lambda(s)$:

$$\log(\lambda(s)) = \beta_0 + X_1(s)\beta_1 + \ldots X_p(s)\beta_p \tag{2}$$

133 where s is a location in geographic space, and $X_1(s), \ldots, X_p(s)$ are spatial predictors associated with

134 location s. The intercept, β_0, determines the log-density of points (within a small homogeneous area

135 around s) when all $X_i(s)$ are 0, and the slopes, $\beta_1, \ldots, \beta_p$, describe the effect of spatial covariates on

136 the log density of locations in space. The IPP model can be understood by listing its key features

137 and assumptions, namely:

138 1. The number of locations in an area G, n_G, is given by a Poisson random variable with mean

139 $\mu_G = \int_G \lambda(s)ds$.

140 2. Locations are independent (any clustering can be explained by spatial covariates).

141 If all available spatial predictors are measured only at a coarse scale (e.g., at a set of gridded or

142 rasterized cells), then fitting the IPP model is equivalent to fitting a Poisson regression model (Aarts

143 et al., 2012). Specifically, one may treat the counts, y_i, in n discrete spatial units ($i = 1, \ldots, n$), as

144 a set of independent Poisson random variables with means $= \lambda(s_i)|G_i|$ where $\lambda(s_i)$ is given by eqn.

145 (2) and $|G_i|$ is the area of grid cell i. Note that $\log(E[y_i]) = \log(\lambda(s_i)|G_i|) = \log(\lambda(s_i)) + \log(|G_i|)$;

146 thus, the log-link used in Poisson regression implies the area, $|G_i|$, should be included as an offset

147 (a predictor variable with with regression coefficient fixed at a value of 1).

148 When spatial predictors are available at the point-level, as will be the case whenever constructing

149 "distance to" predictors (e.g., distance to nearest road, water source, etc), it will be advantageous

150 to model the locations in continuous space. In telemetry studies, the absolute density of points

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151 will be determined by the frequency and duration of data collection. Thus, β_0 will not be of

152 biological interest, and it will be appropriate to focus efforts on estimating and interpreting the

153 slope coefficients, $\beta_1, \ldots, \beta_p$, which determine relationships between the spatial covariates and the

154 relative density of locations throughout the study area (Fithian & Hastie, 2013). As is the case with

155 linear and generalized linear models (e.g., Poisson regression), we can estimate parameters using

156 maximum likelihood. This technique requires writing down an expression, called the *likelihood*, that

157 captures the data generating mechanism in terms of one or more parameters. With telemetry data,

158 it makes sense to work with the conditional likelihood of the IPP model (Aarts et al., 2012), i.e.,

159 the likelihood of the observed locations in space, conditional on there being n observed locations in

160 total. The conditional likelihood is given by:

$$L(\beta_1, \ldots, \beta_p | s_1, \ldots, s_n) = \prod_{i=1}^{n} \frac{\lambda(s_i)}{\int_{s \in G} \lambda(s) ds} \tag{3}$$

161 where the product is over the n observed locations, $\lambda(s_i)$ is the intensity function evaluated at

162 observation i, and the integral in the denominator evaluates the intensity function over the spatial

163 domain of interest (Cressie, 1992; Aarts et al., 2012). If we plug $\lambda(s_i) = \exp(\beta_0 + X_1(s_i)\beta_1 +$

164 $\ldots X_p(s_i)\beta_p)$ into eqn. (3), β_0 will cancel from the numerator and denominator, leaving us with:

$$L(\beta; s_1, \ldots, s_n) = \prod_{i=1}^{n} \frac{\exp(X_1(s_i)\beta_1 + \ldots X_p(s_i)\beta_p)}{\int_{s \in G} \exp(X_1(s_i)\beta_1 + \ldots X_p(s_i)\beta_p) ds} = \prod_{i=1}^{n} \frac{w(x(s_i); \beta)}{\int_{s \in G} w(x(s); \beta) ds} \tag{4}$$

165 where $w(x(s); \beta) = \exp(\beta_1 x_1(s) + \ldots \beta_p x_p(s))$ is our resource-selection function.

166 The binomial likelihood associated with logistic regression differs from eqn. (4), but Warton &

167 Shepherd (2010) showed that logistic regression estimators of slope coefficients converge to the those

168 of the IPP model as the number of available points increases toward infinity. Thus, the connection

169 to the IPP model addresses a common question that arises when estimating resource-selection

170 functions, namely, "how many available points do I need?" The exact answer depends on how

171 difficult it is to estimate the integral in the denominator of eqn. (4); the recommendation we offer

172 is to increase the number of available points until the estimated slope coefficients no longer change

173 much. Fithian & Hastie (2013) later showed that the convergence results of Warton & Shepherd

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174 (2010) hold only if the model is correctly specified, but assigning "infinite weights" to available points

175 ensures the results hold more generally. Therefore, when fitting logistic regression or other binary

176 response models (e.g., boosted regression trees) to use-availability data, we also suggest assigning a

177 large weight (say 1000 or more) to each available location and a weight of 1 to all observed locations

178 (larger values can be used to verify that results are robust to this choice). For a coded example in R

179 (R Core Team, 2019), see section **Interpreting Parameters in Resource-Selection Functions**

180 and Supplementary Appendix A.

Weighted Distributions

182 Weighted distribution theory provides another way to interpret parameters in resource-selection

183 functions (Lele & Keim, 2006; Johnson, Thomas, Ver Hoef, & Christ, 2008). Let:

184 • $u(x)$ = the frequency distribution of habitat covariates, x, at locations used by our study

185 animals.

186 • $a(x)$ = the frequency distribution of habitat covariates, x, at locations assumed to be available

187 to our study animals.

188 We can think of the *resource-selection* function, $w(x; \beta)$, as providing a set of weights that takes us

189 from the distribution of available habitat to the distribution of used habitat:

$$u(x) = \frac{w(x, \beta)a(x)}{\int_{z \in E} w(z, \beta)a(z)dz} \tag{5}$$

190 The denominator of eqn. (5) ensures that the left hand side integrates to 1 and thus, $u(x)$ is a proper

191 probability distribution; the variable z here is just a dummy variable used to allow integration

192 over the frequency distribution of our environmental covariates. Because these distributions are

193 written in terms of the habitat covariates, x, instead of geographical locations, we say that model is

194 parameterized in *environmental space* (E) (Hirzel & Le Lay, 2008; Elith & Leathwick, 2009).

195 To show that weighted distribution theory is consistent with the IPP formulation discussed above,

196 we can rewrite eqn. (5) in *geographic space* (G):

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$$u(s) = \frac{w(x(s), \beta)a(s)}{\int_{g \in G} w(x(g), \beta)a(g)dg}, \tag{6}$$

where the denominator integrates over a geographic area, G, that is assumed to be available to the animal and g is a dummy variable for integration. Here $u(s)$ is equivalent to the utilization distribution encountered in the literature on probabilistic estimators of animal home ranges (Van Winkle, 1975; Worton, 1989; Signer & Fieberg, 2020) and tells us how likely we are to find an individual at location s in geographic space. The utilization distribution, $u(s)$, depends on the environmental covariates associated with location s, through $w(x(s); \beta)$, and the distribution of available locations in geographic space, $a(s)$. Typically, $a(s)$ is assumed to be a uniform distribution within the geographical domain of availability, G (e.g., the individual's home range, the population's range, or the species range depending on the hierarchical level of habitat selection of interest; Johnson, 1980), and all areas within G are assumed to be equally available to the organism. Hence, $a(s)$ is typically a constant, $1/|G|$, that cancels from the numerator and denominator. Then, if we let $w(x(s); \beta) = \exp(x\beta)$, we end up with the conditional likelihood of the Inhomogeneous Poisson process model (eqn. (4)) (Aarts et al., 2012).

Interpreting Parameters in Resource-Selection Functions

To demonstrate how the IPP and weighted distribution theory frameworks help with interpreting parameters in fitted resource-selection functions, we now consider a simple example using 3,004 locations of a fisher named Lupe tracked as part of a larger telemetry study (LaPoint et al., 2013a, 2013b). These data are publicly available and have been featured in a workshop highlighting Movebank's *Env-DATA* system for annotating locations with environmental covariates (Dodge et al., 2013; Fieberg et al., 2018). The location data were combined with available points sampled randomly from within a minimum convex polygon (MCP) formed using Lupe's locations. The used and available locations were then transformed to a projected coordinate reference system (NAD83 / Conus Albers) and annotated with environmental variables measuring population density (University & CIAT, 2005), elevation (U. S. / Japan ASTER Science Team, 2009), and landcover class (Defourny et al., 2009). The original landcover data were grouped to form a variable named `landuseC` with the following categories: `forest`, `grass` and `wet` (Fig. 1). We created centered

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223 (mean $= 0$) and scaled (SD $= 1$) variables labeled `elevation` and `popden` from the original elevation

224 and population density variables. We also created an indicator variable, `case_`, taking on a value of

225 1 for all used points and 0 for all available points (later, we discuss how to choose the number of

226 available points).

227 For ease of interpretation, we will begin by assuming the effects of elevation, population density, and

228 landcover class are additive and linear on the log scale (eqn. (2)). Later, we will discuss how we can

229 relax these assumptions using interactions to allow the effect of covariates to depend on the value

230 of other habitat covariates and polynomials or splines to to relax the assumption of linearity. We

231 assign a weight of 5000 to the available locations and a weight of 1 to all observed locations (Fithian

232 & Hastie, 2013). We can then fit a weighted logistic regression model using the `glm` function in R:

```
Lupe.dat$w <- ifelse(Lupe.dat$case_==1, 1, 5000)
```

```
RSF.Lupe <- glm(case_ ~ elevation + popden + landuseC,
                data = Lupe.dat,
                weight = w,
                family = binomial)
```

233 Before interpreting the coefficients, it is important to make sure we have included a sufficient number

234 of available points to allow parameter estimates to converge to stable values. To evaluate parameter

235 stability, we fit logistic regression models to data sets with increasing numbers of available points

236 (from 1 available point per used point to 100 available points per used point; see Supplementary

237 Appendix A for the code). The intercept decreased as we increased the number of available points

238 (as it is roughly proportional to the log difference between the numbers of used and available

239 points), but the slope parameter estimates, on average, did not change much once we included at

240 least 10 available points per used point (Fig. 2). Further, as expected, estimates varied less from

241 sample to sample as we increased the number of available points. Thus, we conclude that, in this

242 particular case, having 10 available points per used point is sufficient for interpreting the slope

243 coefficients. Using more available points reduces Monte Carlo error, however, so we will proceed

244 with 100 available points per used point.

245 Let's consider the interpretation of the continuous covariates reflecting elevation and population

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246 density (Table 1, *Model 1*). Qualitatively, we might infer from the positive coefficient for `elevation`

247 and negative coefficient for `popden` that, all other things being equal, Lupe is likely to select

248 locations at higher elevations and in areas of lower population density. But, how do we interpret

249 these coefficients quantitatively? Consider the following two locations, both in the same landcover

250 class and with the same associated population density, but differing by 1 unit in `elevation` (since

251 we have scaled this variable, a difference of 1 implies that the two observations differ by 1 SD in the

252 original units of elevation):

- location s_1: `elevation` $= 3$, `popden`=1.5, `landuseC` = `wet`
- location s_2: `elevation` $= 2$, `popden`=1.5, `landuseC` = `wet`

255 Using eqn. (6), we can calculate the relative risk of Lupe using location 1 relative to location 2:

$$\frac{u(s_1)}{u(s_2)} = \frac{\exp(3\beta_{elevation} + 1.5\beta_{pop\_den} + 0\beta_{grass} + 1\beta_{wet})a(s_1)}{\exp(2\beta_{elevation} + 1.5\beta_{pop\_den} + 0\beta_{grass} + 1\beta_{wet})a(s_2)} \tag{7}$$

256 where we have dropped the integral from eqn. (6) because it appears in both the numerator and

257 denominator (and thus, cancels out). Now, if both locations are *equally available*, then $a(s_1) = a(s_2)$,

258 and we have:

$$\frac{u(s_1)}{u(s_2)} = \frac{\exp(3\beta_{elevation})\exp(1.5\beta_{pop\_den} + \beta_{wet})}{\exp(2\beta_{elevation})\exp(1.5\beta_{pop\_den} + \beta_{wet})} = \exp(\beta_{elevation}) = \exp(0.303) = 1.35 \tag{8}$$

259 In epidemiology, $\exp(\beta)$ is referred to as a *risk* or *hazard ratio.* In the context of habitat-selection

260 analyses, Avgar et al. (2017) refer to it as quantifying *relative selection strength* (RSS).

261 Note that we would arrive at the exact same expression if we chose *any* two locations that differed

262 by 1 unit of `elevation` and had the same values for `popden` and `landuseC`. Thus, $\exp(\beta_{elevation})$

263 quantifies the risk (or hazard) ratio of two locations that differ by 1 SD unit of `elevation` but

264 are otherwise equivalent (i.e., they are equally available and have the same values of all other

265 habitat covariates). If Lupe were to be presented with two such hypothetical locations, the model

266 suggests she would be 1.35 times more likely to choose the one with the higher elevation. A similar

267 interpretation can be ascribed to `popden`. Given two observations that differ by 1 SD unit of `popden`

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268 but are otherwise equal, Lupe would be $\exp(-0.183) = 0.833$ times as likely to choose the location

269 with higher population density (or, equivalently, $\exp(0.183) = 1.20$ times more likely to choose the

270 location with the lower population density).

271 What about the coefficients for the landcover categories? Looking again at the regression output

272 (Table 1, *Model 1*), we see that `grass` has a negative coefficient and `wet` has a positive coefficient.

273 It is tempting to infer that Lupe spends most of her time in wet areas and rarely spends time in

274 grassy habitats. As Figure 1 makes it clear, however, these inferences are not exactly correct. First,

275 it is important to understand how categorical predictors are encoded in regression models. There

276 are a number of different ways to parameterize the effect of categorical variables and unfamiliar

277 readers may want to work through an introductory regression text (e.g., Chapter 6 of Kéry (2010)).

278 The default coding in R is to treat one of the levels (whichever comes first alphabetically) as a

279 reference level and then to create a set of dummy variables that contrast the remaining levels of

280 the categorical variable with this reference level. In our case, `forest` is the reference level. The

281 coefficients associated with `grass` and `wet` represent contrasts between these land cover classes and

282 the `forest` class.

283 Let's again consider 2 locations, this time assuming they have the same elevation and population

284 densities, but with one location in `wet` and the other location in `forest`:

285 • location s_1: `elevation` $= 2$, `popden`$=1.5$, `landuseC` $=$ `wet`

286 • location s_2: `elevation` $= 2$, `popden`$=1.5$, `landuseC` $=$ `forest`

287 The relative risk of an animal using location 1 relative to location 2 is given by (eqn. (6)):

$$\frac{u(s_1)}{u(s_2)} = \frac{\exp(2\beta_{elevation} + 1.5\beta_{pop\_den} + 0\beta_{grass} + 1\beta_{wet})a(s_1)}{\exp(2\beta_{elevation} + 1.5\beta_{pop\_den} + 0\beta_{grass} + 0\beta_{wet})a(s_2)} = \exp(\beta_{wet})\frac{a(s_1)}{a(s_2)} \tag{9}$$

288 Thus, *assuming the two locations are equally available*, we might infer that Lupe would be

289 $\exp(0.250) = 1.28$ times more likely to choose the `wet` location than the location in `forest`.

290 Of course, we know from Figure 1 that `forest` and `wet` are not equally available on the landscape.

291 The higher availability of `forest` habitat implies that Lupe is more likely to be in `forest` than

292 `wet`. We could attempt to correct for differences in availability within the MCP surrounding Lupe's

293 locations by multiplying our result by the ratio of habitat availability for `wet` relative to `forest`

294 habitats (2.3% versus 95.7%; Fig. 1), giving us $\exp(0.250)(0.023)/(0.957) = 0.03$. This calculation

295 suggests we are ($1/0.03 = 33$) times more likely to find Lupe in `forest` than `wet` habitat. With

296 this calcualtion we had to assume, perhaps naively, that the availability distributions for `popden`

297 and `elevation` were the same in both `wet` and `forest` cover classes. In reality, if Lupe decides to

298 move from `forest` to `wet`, it is likely that she will experience a change in `elevation` and `popden`

299 too (i.e., these factors will not be held constant). To quantify the relative risk of finding Lupe in

300 `forest` versus `wet` habitat, while also accounting for the effects other environmental characteristics

301 that are associated with these habitat types, we can use integrated hazards – i.e., we can integrate

302 the spatial utilization distribution, $u(s)$, over all `forest` and `wet` habitats:

$$\frac{u(s, s \in forest)}{u(s, s \in wet)} = \frac{\int_G u(s)I(s \in forest)ds}{\int_G u(s)I(s \in wet)ds} \tag{10}$$

303 where $I(s \in forest)$ and $I(s \in wet)$ are indicator functions equal to 1 when location s is in `forest`

304 or `wet`, respectively (and 0 otherwise). We can estimate this ratio using:

$$\frac{\hat{u}(s, s \in forest)}{\hat{u}(s, s \in wet)} = \frac{\sum_{i=1}^{n_a} \hat{w}(x(s_i); \hat{\beta})I(s_i \in forest)}{\sum_{i=1}^{n_a} \hat{w}(x(s_i); \hat{\beta}))I(s_i \in wet)}. \tag{11}$$

305 where the sum is over the distribution of available locations.

306 This ratio is also equal to 33, which agrees with the observed data; Lupe was found in `forest` habitat

307 33 times more often than in `wet` habitat (see Supplementary Appendix A for code demonstrating

308 how to calculate these quantities in R). Thus, we conclude Lupe is 33 times more likely to be found

309 in `forest` than `wet` habitat, assuming she restricts her movements to the MCP surrounding her

310 observed locations and all of this MCP is equally available to her.

311 Before moving on, it is important to note that naively-adjusted (multiplying by availability of `wet`

312 and `forest` habitats) and integrated-hazards (i.e., adjusted) risk ratios will not always agree. In

313 fact, we find that they differ when comparing the risk of finding Lupe in `wet` versus `grass` habitat,

314 with the integrated-hazards risk ratio better agreeing with the observed data (see Supplementary

315 Appendix A). Somewhat related, Avgar et al. (2017) suggested calculating *average effects* for

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316 continuous predictors, X, by comparing the change in relative risk from increasing X by 1 unit

317 (to $X = x + 1$) to the average value of $w(x(s); \beta)$ for all locations s with $x(s) = x$. These average

318 effects will also be influenced by cross-correlations among predictor variables included in the model.

319 Instead of integrating $u(s)$ over discrete cover types, we could integrate over a specific geographic

320 area. In addition, we could choose to change the area of interest (and thus, area of integration)

321 from G to $\tilde{G}$. This approach makes it possible to use the same integrated hazards approach (i.e.,

322 eqn. (11)) to project how Lupe would spend her time in a novel environment (referred to as an

323 "out-of-sample" prediction). Out-of-sample predictions often suffer from poor accuracy, especially

324 when compared to "in sample" predictions, i.e., predictions for the same area and time frame from

325 which the original data were collected (Torres et al., 2015; Yates et al., 2018). We return to this

326 important point in the discussion section.

327 Let's next consider what happens if we change the reference level of the land cover variable from

328 `forest` to `wet` (Table 1, *Model 2*).

```
Lupe.dat <- within(Lupe.dat,

                   landuseC1 <- relevel(landuseC, ref = "other"))
RSF.Lupe2 <- glm(case_ ~ elevation + popden + landuseC1,

                 data = Lupe.dat,

                 weight = w,

                 family = binomial)
```

329 The coefficients for `elevation` and `popden` do not change. Note, however, that the coefficient for

330 `forest` is negative despite Lupe using `forest` more than its availability (i.e., $u(s, s \in forest) >$

331 $a(s, s \in forest)$) and Lupe spending more than 95% of her time in the forest! What is going on?

332 Remember, the coefficients for categorical predictors reflect use:availability ratios for each level of

333 the predictor relative to the use:availability ratio for the reference class. The coefficient for `forest`

334 is negative because the use:availability ratio for `forest` is less than the use:availability ratio for

335 the reference class, `wet` (see Fig. 1). Depending on the reference level, it is possible to have a

336 positive (negative) coefficient even when that landcover class is used more (less) than its availability.

337 Furthermore, it is possible for landcover class to be used frequently but have a negative coefficient.

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338 We have seen many ecologists, including some that are very quantitatively skilled and familiar with

339 habitat-selection models, make mistakes when interpreting coefficients associated with categorical

340 predictors! This example also highlights the importance of plotting your data (e.g., Fig. 1) and

341 considering habitat availability when interpreting regression coefficients. Plotting distributions

342 of covariates for both used and available locations is one of the best ways to understand fitted

343 habitat-selection models, and is a good strategy to use for both continuous and categorical predictors

344 (Merow, Smith, & Silander, 2013; Fieberg, Forester, et al., 2018).

Interactions Between Environmental Predictors

346 Consider the distribution of `elevation` at used and available locations across the different habitat

347 classes (Fig. 3). We see that there is a wider range of `elevation` in `forest` and `wet` habitat

348 compared to `grass` habitat, and there is a clear association between `elevation` and `landuseC`, with

349 higher median `elevation` at used locations in `forest` and `grass` habitat relative to `wet` habitat.

350 Perhaps more importantly, we also see that values of `elevation` are higher, on average for used

351 locations (compared to available locations) in `forest` and `grass`, whereas the opposite is true in

352 `wet` habitat. Although we should be skeptical of interactions that we discover while exploring our

353 data (i.e., interactions that were not specified *a priori*), an analyst may be tempted to include an

354 interaction between `elevation` and `landuseC`. In *Model 3* (Table 1), we revert to having `forest`

355 as the reference level and include the interaction between `elevation` and `landuseC`.

```
Lupe.dat <- within(Lupe.dat , landuseC <- relevel(landuseC, ref = "forest"))
RSF.Lupe3 <- glm(case_ ~ elevation + popden + landuseC + elevation:landuseC,
                 data = Lupe.dat,
                 weight = w,
                 family = binomial)
```

356 Using this syntax, R creates two new variables `elevation:landuseCgrass` equal to `elevation`

357 when `landuseC` is `grass` and is 0 otherwise and `elevation:landuseCwet` equal to `elevation` when

358 `landuseC` is `wet` and is 0 otherwise. The coefficients associated with these predictors quantify

359 the change in slope (i.e., change in the effect of `elevation`) when the locations fall in `grass` or

360 `wet` relative to the slope when the locations fall in `forest`. Starting from eqn. (6) and using the

15

361 estimates for *Model 3* in Table 1, we can easily derive that the relative risk of choosing between two

362 equally available locations that differ by 1 SD unit of `elevation` is equal to $\exp(0.313) = 1.37$ when

363 the two locations are in `forest`, $\exp(0.313 + 0.112) = 1.53$ when the locations are in `grass`, and

364 $\exp(0.313 - 0.499) = 0.83$ when the locations are in `wet` habitat. Thus, we might conclude that Lupe

365 would select for higher elevations when in `forest` or `grass`, but avoid higher elevations when in

366 `wet`. Alternatively, we can consider how `elevation` changes Lupe's view of the different landcover

367 categories, noting that $\beta_{grass} = -1.471 + 0.112\texttt{elevation}$ and $\beta_{wet} = 0.183 - 0.499\texttt{elevation}$.

368 Thus, we see that Lupe's relative avoidance of `grass` (relative to `forest`) and selection for `wet`

369 (relative to `forest`) both decline with `elevation`, and Lupe's inherent ranking of these 3 habitat

370 types will change as `elevation` increases.

Non-Linear Effects and Other Considerations

372 When building models, it is important to consider the functional relationships between different

373 environmental characteristics and habitat use. For example, we may classify available predictors

374 based on whether they represent resources (higher values are generally preferable), risks (lower

375 values are generally preferable) or conditions (values that are not too high or too low are preferable)

376 (e.g., Matthiopoulos et al., 2015). It is often useful to allow for non-linear effects of conditions

377 by including quadratic terms or using a set of spline basis functions. In either case, we end up

378 requiring multiple coefficients to capture how relative risk changes with the environmental predictor.

379 Consider, for example, that we could include a quadratic term to model the effect of `elevation`.

380 Estimating the relative risk for two locations, s_1 and s_2, that differ in their values of `elevation` but

381 are otherwise equivalent would be straightforward using eqn. (6) - we would just need to calculate

382 hazard ratios using coefficients for `elevation` and `elevation`^{2}:

$$\frac{u(s_1)}{u(s_2)} = \frac{\exp(elevation(s_1)\beta_{elevation} + elevation(s_1)^2\beta_{elevation^2})}{\exp(elevation(s_2)\beta_{elevation} + elevation(s_2)^2\beta_{elevation^2})} \tag{12}$$

383 Lastly, we note that Avgar et al. (2017) provide simple formulas for calculating risk or hazard ratios

384 under a number of different scenarios (e.g., models with quadratic polynomials, log-transformed

385 covariates, and models with interactions). The `log_rss` function in the `amt` package (Signer et al.,

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386 2019) relies on R's generic `predict` function to aid the user in calculating the log of these hazard

387 ratios for any combination of model structure and two alternative locations; its use is illustrated in

388 Supplementary Appendix B. Understanding how these formulas are derived, however, helps build

389 intuition and frees the user to construct estimators and estimation targets that capture relevant

390 quantities of specific interest.

Statistical Independence

392 An important assumption of the IPP model, and hence, resource-selection functions, is that any

393 clustering of spatial locations can be explained solely by spatial covariates. Strictly speaking, this

394 assumption will almost never be met, particularly with modern-day telemetry studies that allow

395 several locations to be collected on the same day. Telemetry observations close in time tend to

396 also be close in space - i.e., telemetry observations exhibit serial dependence (Fleming et al., 2014).

397 This serial dependence is likely to manifest itself in residual spatial autocorrelation that could be

398 modeled using a spatial random effect or a spatial predictor constructed to account for the effects

399 of movement constraints on habitat availability (Johnson, Hooten, & Kuhn, 2013). Models with

400 spatial random effects are, however, more complicated and difficult to fit.

401 Alternatively, if telemetry observations are collected at regular time intervals, then the locations

402 may be argued to provide a representative sample of habitat use from a specific observation window

403 (Otis & White, 1999; Fieberg, 2007). In these cases, it may be helpful to view our estimates of

404 the parameters in our resource-selection function, $\hat{\beta}$, as useful summaries of habitat use for tagged

405 individuals during these fixed time periods. Nevertheless, the assumption of independence of our

406 locations is clearly problematic and will lead to estimates of uncertainty that are on average too

407 small. If we are primarily interested in population-level inferences, then we may choose to ignore

408 within-individual autocorrelation when estimating individual-specific coefficients but use a robust

409 form of SE that treats individuals as independent when describing uncertainty in population-level

410 parameters (e.g., using a bootstrap; Fieberg, Vitense, & Johnson, 2020) or generalized estimating

411 equations approach (e.g., Fieberg, Rieger, Zicus, & Schildcrout, 2009; Koper & Manseau, 2009;

412 Fieberg, Matthiopoulos, Hebblewhite, Boyce, & Frair, 2010).

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Step-Selection Functions

Step-selection functions were developed to deal with serial dependence as well as temporally varying availability distributions resulting from movement constraints (Fortin et al., 2005; Thurfjell et al., 2014). Rather than treat locations as independent and identically distributed (with availability that does not depend on time), step-selection analyses model transitions or "steps" connecting sequential locations (Δt units apart) in geographical space:

$$u(s, t + \Delta t)|u(s', t) = \frac{w(x(s); \beta(\Delta t))\phi(s, s'; \gamma(\Delta t))}{\int_{\tilde{s} \in G} w(x(\tilde{s}, s'); \beta(\Delta t))\phi(\tilde{s}, s'; \gamma(\Delta t))d\tilde{s}} \tag{13}$$

where $u(s, t + \Delta t)|u(s', t)$ gives the conditional probability of finding the individual at location s at time $t + \Delta t$ given it was at location s' at time t, $w(x(s); \beta(\Delta t))$ is referred to as a step-selection function, and $\phi(s, s'; \gamma(\Delta t))$ is a selection-independent movement kernel that describes how the animal would move in homogeneous habitat or in the absence of habitat selection (i.e., when $w(x(s); \beta(\Delta t)) = $ a constant for all s). Note that we represent the parameter vectors (β and γ) as functions of the step duration (Δt). This notation reflects the fact that step-selection parameters are scale dependent (i.e., different Δt's will result in different estimates of β and γ; see Avgar et al. (2016) for more details). Thus, we generally require observations to be equally spaced in time, and care must be taken when comparing inference from models fitted at different temporal resolution (but see Munden et al., 2020).

As with resource-selection analyses, it is typical to model $w(x(s); \beta(\Delta t))$ as a log-linear function of spatial covariates and regression parameters, $w(x(s); \beta(\Delta t)) = \exp(X_1(s)\beta_1 + \ldots X_p(s)\beta_p)$. A key difference between resource-selection and step-selection analyses, however, is that the latter allow the available distribution to be time-dependent and equal to $a(s, t + \Delta t) = \phi(s, s', \gamma(\Delta t))$. Consequently, step-selection analyses allow explicit consideration of temporally dynamic environmental covariates, $x(s', t)$ and $x(s, t + \Delta t)$ (and, possibly, environmental covariates measured along the path between these two locations). One option that often performs well and enhances interpretability is to include habitat covariates at the start of the movement step in the model for ϕ and habitat covariates at the end of the movement step in the model for w, resulting in a more general formulation: $w(x(s, t + \Delta t); \beta(\Delta t))\phi(s, s'; \gamma(\Delta t, x(s', t)))$; we provide an example in Supplentary Appendix B.

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Models for $\phi(s, s'; \gamma(\Delta t))$

Step-selection approaches build on an early idea by Arthur, Manly, McDonald, & Garner (1996) to model time-dependent availability via a circular buffer with radius R centered on the previous location. Rhodes et al. (2015) showed that this model is equivalent to assuming:

$$\phi(s, s'; \gamma(\Delta t)) = \begin{cases} \frac{1}{\pi R^2}, & \text{if } ||s - s'|| \leq R \\ 0, & \text{otherwise} \end{cases} \tag{14}$$

where $||s - s'||$ is the Euclidean distance between locations s and s', referred to as the *step length*. Rhodes et al. (2015) also demonstrated that circular buffers imply that individuals are more likely to move large distances than short distances since there is more area, and thus probability, associated with outer rings of the circle. Instead, they suggested using an exponential distribution to accommodate right-skewed step-length distributions and a tendency for animals to make shorter rather than longer movements:

$$\phi(s, s'; \gamma(\Delta t)) = \frac{\lambda \exp(-\lambda ||s - s'||)}{2\pi ||s - s'||} \tag{15}$$

Rather than specify a model directly in terms of $\phi(s, s'; \gamma(\Delta t))$, it is more common to see movement kernels specified in terms of the distribution of step lengths, $d = ||s - s'||$, and turn angles (changes in direction from the previous bearing), θ. In the sections that follow, we will let $g(d; \gamma_d(\Delta t))$ and $f(\theta; \gamma_\theta(\Delta t))$ represent step-length and turn-angle distributions, respectively. Step-selection analyses frequently use either an exponential or gamma distribution for $g(d; \gamma_d(\Delta t))$. Turn angles may be assumed to be uniformly distributed as in Arthur et al. (1996) and Rhodes et al. (2015). Alternatively, circular distributions, such as the von Mises distribution or wrapped Cauchy or Weibull distributions, allow for a mode at 0 and can thus accommodate correlated movements (i.e., sequential steps are assumed, on average, to follow in the same direction as the previous step).

Although step-length and turn-angle distributions are typically assumed to be independent, animals commonly exhibit a mix of of temporally persistent movement behaviors, ranging between high-displacement movements (e.g., when traveling between habitat patches, migrating, or dispersing)

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461 and low-displacement movements (e.g., during foraging or resting bouts). If positional data are

462 collected more frequently than the occurrence of behavioral switches, we might expect a negative cross-

463 correlation between step lengths and turn angles (moving far is likely to coincide with moving straight)

464 and a positive auto-correlation between the current and previous step lengths and turn angles.

465 Moreover, as implied by the more flexible formulation, $w(x(s, t + \Delta T); \beta(\Delta t))\phi(s, s'; \gamma(\Delta t, x(s', t)))$,

466 both step-length and turn-angle distribution may shift as a function of spatial and/or temporal

467 covariates such as habitat permeability (e.g., elevation ruggedness, snow depth, or vegetation

468 density), time of day, season, and predation risk (Avgar, Mosser, Brown, & Fryxell, 2013; Avgar et

469 al., 2016). Thus, although ϕ is a "selection-independent" movement kernel, it may still depend on

470 environmental or temporal covariates, and hence, may vary through space and time, resulting in

471 both auto and cross correlations in step attributes.

472 Cross-correlation between step lengths and turn angles is difficult to model with common statistical

473 distributions, but could be accommodated using copulae (Durante & Sempi, 2010). Alternatively,

474 one could resample (i.e., bootstrap) step length and turn angle pairs, (d_t, θ_t), to preserve any

475 correlation that is present in the data (Fortin et al., 2005). Although we generally find the bootstrap

476 appealing (Fieberg et al., 2020), it has limitations in this context. In particular, the observed

477 distribution of step lengths and turn angles will reflect both inherent movement characteristics of

478 the species (captured by ϕ) as well as habitat selection (captured by w). Using the observed steps as

479 a non-parametric model for ϕ without adjustment for the effect of w can result in biased estimates

480 of β (Forester, Im, & Rathouz, 2009). We will return to this point in the next section. As mentioned

481 previously (see **Statistical Independence**), and regardless of the source of correlation, it may

482 be preferable to calculate robust SEs by treating individuals as the relevant sampling unit when

483 performing population-level inference (e.g., Prima, Duchesne, & Fortin, 2017). Lastly, cross- and

484 auto-correlations in step lengths and turn angles, as well as their dependencies on various temporal

485 or environmental characteristics, could be modeled parametrically using an integrated step-selection

486 function (Avgar et al., 2016). To do so, we need to include appropriate statistical interactions (e.g.,

487 between concurrent and previous step lengths/turn angles and between these step-attributes and

488 environmental or temporal covariates). We discuss this process further below, and provide examples

489 in the Supplementary Appendix B. See also Prokopenko, Boyce, & Avgar (2017), Scrafford, Avgar,

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Heeres, & Boyce (2018), and Dickie, McNay, Sutherland, Cody, & Avgar (2020).

Estimation of Movement and Habitat-Selection Parameters

Although it is possible to simultaneously estimate movement (γ) and habitat selection (β) parameters using maximum likelihood (e.g., Rhodes et al., 2015) or Bayesian methods (e.g., Johnson et al., 2008), this is rarely done in practice as it would require custom-written code. Instead, it is common to use the following approach:

1. Estimate or approximate $\phi(s, s'; \gamma(\Delta t))$ using observed step lengths and turn angles, giving $\hat{\phi}(s, s'; \hat{\gamma}(\Delta t))$.

2. Generate time-dependent available locations by simulating potential movements from the previously observed location, $u(t, s')$. Similar to applications of RSFs, it is up to the user to decide how many available locations to sample for each used location, and, due to similar considerations (properly approximating the availability domain: $a(s, t + \Delta t) = \phi(s, s'; \gamma(\Delta t))$, the more points the merrier.

3. Estimate β using conditional logistic regression, with strata formed by combining time-dependent used and available locations.

If we knew $\phi(s, s', \gamma(\Delta t))$ and could simulate directly from it (skipping step 1), then this approach would provide unbiased estimates of β (Forester et al., 2009). However, as mentioned in the previous section, estimating $\phi(s, s'; \gamma(\Delta t))$ from observed steps without adjusting for $w(x(s); \beta(\Delta t))$ can lead to biased estimates of γ and β.

Forester et al. (2009) considered the case where the step-length distribution, $g(d, \gamma_d)$, is given by an exponential distribution with unknown parameter, λ. They showed that estimating λ directly from the observed distribution of step lengths (without adjusting for the effect of $w(x(s); \beta)$), and then proceeding with steps 2 and 3 results in a biased estimators of β, but that the bias (if $g(d, \gamma_d)$ is given by an exponential distribution) is eliminated if $\log(d_t)$ is included as a predictor in the model. Avgar et al. (2016) further showed that the coefficient associated with $\log(d_t)$ could be used to modify $\hat{\lambda}$, leading to an unbiased estimator of λ and thus, $g(d, \gamma_d)$. In addition, they showed how similar adjustments could be used to obtain unbiased estimators of step-length (γ_d) and habitat-selection (β) parameters when the distribution of step lengths is given by a gamma,

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⁵¹⁸ half-normal, or log-normal distribution. Similarly, Duchesne, Fortin, & Rivest (2015) showed that

⁵¹⁹ including $\cos(\theta)$ as a predictor can lead to unbiased estimators of turn angle parameters (γ_θ) when

⁵²⁰ the distribution of turn angles follows a von Mises distribution. These adjustments are available

⁵²¹ in the `amt` package for the exponential, gamma, and von Mises distributions (Signer et al., 2019).

⁵²² Avgar et al. (2016) coined the term *integrated* step-selection analysis to emphasize that these

⁵²³ results provide new opportunities to model both movement and habitat selection via tried and true

⁵²⁴ statistical software for fitting conditional logistic regression models.

⁵²⁵ In Supplementary Appendix B, we provide a "How to" guide for implementing an integrated

⁵²⁶ step-selection analysis using the `amt` package in R (R Core Team, 2019; Signer et al., 2019).

⁵²⁷ Conducting an integrated step-selection analysis requires, in addition to the 3 steps outlined in

⁵²⁸ this section, that we add a fourth step that re-estimates the movement parameters in $\phi(s, s'; \gamma(\Delta t))$

⁵²⁹ using regression coefficients associated with movement characteristics (e.g., $\log(d_t)$, $cos(\theta)$). This

⁵³⁰ last step adjusts the parameters in $\phi(s, s'; \gamma(\Delta t))$ to account for the effect of habitat selection

⁵³¹ when estimating the movement kernel (Avgar et al., 2016); this step is unnecessary if no inference

⁵³² about movement is being made. Importantly, interactions may be included between movement

⁵³³ characteristics (e.g., $\log(d_t)$, $cos(\theta)$) and environmental covariates, $x(s', t)$, to allow the movement

⁵³⁴ kernel to depend on the environment. When interactions are included, step 4 results in a movement

⁵³⁵ kernel, $\phi(s, s'; \gamma(\Delta t, x(s', t)))$, that depends on the habitat the animal is in at the start of the

⁵³⁶ movement step (Fig. 4).

⁵³⁷ **Interpretation of Parameters in an Integrated Step-Selection Analysis**

⁵³⁸ The habitat-selection parameters can be interpreted in the same way as parameters in resource-

⁵³⁹ selection functions (i.e., as spatial hazards, assuming locations are equally available and differing

⁵⁴⁰ in terms of a single habitat covariate). Hence, the $ln(RSS)$ expressions in Avgar et al. (2017),

⁵⁴¹ and the `log_rss` function in `amt`, are suitable for calculating and interpreting the effects of the

⁵⁴² various habitat covariates. However, it is important to recognize that the used and available

⁵⁴³ distributions in step-selection analyses are dynamic and non-uniform in space. In particular, they

⁵⁴⁴ depend an individual's current location and movement tendencies (as well as the observed time scale

⁵⁴⁵ determined by Δt; Barnett & Moorcroft, 2008; Signer, Fieberg, & Avgar, 2017). Thus, questions

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546 that require integrating hazards over space (e.g., eqn. (10)) are more difficult to address, but may be

547 computed using simulation modeling (Signer et al., 2017), by solving the master equation (formed by

548 multiplying the right hand side of eqn. (13) by $u(s', t)$ and then integrating over G with respect to s')

549 for its steady state (Potts et al., 2014a, 2014b), or in some cases, by translating the fitted model into a

550 partial differential equation model with analytical steady-state distribution (Potts & Schlägel, 2020).

551 We also note that alternative modeling frameworks exist with parameters that directly describe

552 long-term relative risk (e.g., Michelot et al., 2019b, 2019a; Michelot, Blackwell, Chamaillé-Jammes,

553 & Matthiopoulos, 2020), but these methods are more computationally challenging to implement,

554 and therefore, less likely to be widely used in applied settings. The `amt` package has a basic capacity

555 to simulate the utilization distribution based on a parameterized integrated step-selection function

556 (Signer et al., 2017), and we expect this approach to become more flexible in the near future.

557 Using an integrated step-selection approach (e.g., as in Fig. (**???**)(fig:movekern)), it is also possible

558 to draw ecological inference using the selection-free movement kernel. For example, the fitted

559 step-length and turn-angle distributions can tell us how much more likely an animal is to take large

560 versus small steps or to turn left or right relative to moving straight. We can also calculate moments

561 of these distributions under different environmental conditions, which can be informative when our

562 models include interactions between movement characteristics and environmental predictors. For

563 example, we could calculate the expected selection-free displacement rates (and/or directionality)

564 as function of local snow depth (that is, if snow depth was included in our model as an interaction

565 with step length). To calculate these expected values we must first adjust the 'tentative' parameters

566 used to sample available steps (e.g., if we use a gamma distribution, the tentative shape and scale

567 parameters) using the coefficient estimates obtained for step length (and/or its transformation) and

568 cos(turn angle). The details of how to carry on these adjustments are provided in Supplementary

569 Appendix C and in Avgar et al. (2016). Once the selection-free movement parameters are obtained,

570 one can use them to calculate various aspects of the (theoretical) distributions of step lengths and

571 turn angles, such as the mean, the median, or the 95% confidence bounds (see Supplementary

572 Appendix B for examples).

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Discussion

We have highlighted how connecting resource-selection functions to IPP models and weighted distribution theory helps with interpreting parameters in resource-selection functions using simple examples. We have also reviewed step-selection analyses and demonstrated how to estimate movement and habitat-selection parameters when conducting an integrated step-selection analysis using the `amt` package. So far, we have focused on interpreting results when analyzing data from a single individual. We end with a brief discussion addressing statistical dependencies, particularly when analyzing data from multiple individuals, along with issues related to model transferability and parameter sensitivity to changes in habitat availability and species population density.

Statistical Dependencies

Earlier, we highlighted the importance of statistical independence as it applies to individual locations when estimating resource-selection functions. We also noted that step-selection analyses typically assume step lengths and turn angles are independent of each other and also over time, though it is possible to account for these correlations using appropriate interactions (e.g., between step length at time t and time $t-1$, step length and turn angle both at time t). It would be nice to have multivariate distributions available that are capable of describing correlated step lengths and turn angles and any inherent autocorrelation. It is plausible, however, that models that allow movement parameters to vary by habitat type, using interactions between step length, turn angle, and habitat covariates, will be able to account for much of the autocorrelation and cross-correlation (between step lengths and turn angles) present in the data. Similarly, autocorrelation and cross-correlations may be accommodated by models that include a (possibly latent) behavioral state, with movement and habitat-selection parameters that are state-dependent (Nicosia, Duchesne, Rivest, Fortin, & others, 2017; Suraci et al., 2019).

In addition to cross-correlation between step lengths and turn angles and serial dependencies, individuals living in different environments may exhibit different habitat-selection patterns and thus, repeated observations on the same set of individuals will induce further statistical dependencies. A simple strategy for dealing with repeated measures when individuals can be assumed to be independent is to fit models to individual animals and then treat the resulting coefficients as data

when inferring population-level patterns (Murtaugh, 2007; Fieberg et al., 2010). For example, sample means of the regression coefficients can be used to characterize average habitat-selection parameters. Estimating among-animal variability is trickier due to sampling error; naively ignoring sampling error will lead to a positive bias in estimates of among-animal variability, but more formal two-step methods can address this issue (Craiu, Duchesne, Fortin, & Baillargeon, 2011, 2016; Dickie et al., 2020). Alternatively, generalized linear mixed models with random coefficients can be used to quantify among-animal variability in resource-selection and step-selection analyses (Muff, Signer, & Fieberg, 2020).

Although it is possible to conduct integrated step-selection analyses with hierarchical models containing random effects, we have much to learn about how these approaches perform in practice. For example, Muff et al. (2020) found that parameters describing among-animal variability in habitat-selection parameters were biased low when movement characteristics were included in the model. Mixed-effect models with random coefficients are also "parameter hungry", requiring $p(p+1)/2$ variance and covariance parameters to be estimated, where p is the number of random coefficients. Models that allow all coefficients to be animal-specific and to covary are thus likely to be computationally challenging to fit and problematic for small data sets containing only a few individuals. For this reason, Muff et al. (2020) assumed coefficients did not covary in their applied examples. In the context of our fisher analysis, this equates to assuming that knowing an individual's coefficient for `popden` tells us nothing about that animal's parameters for `elevation` or `landuseC` variables. For categorical variables, it is natural to expect parameters to have a negative covariance (since, for example, spending more time in `forest` must come at the expense of spending less time in other landuse categories). Research evaluating the performance of mixed-effect step-selection analyses under various data-generating scenarios would be helpful for evaluating robustness to assumption violations (e.g., those regarding the distribution of random parameters).

Sensitivity of Selection Coefficients to Species Population Density and Habitat Availability

Before concluding, we feel it is important to briefly discuss the oft observed pattern of density and availability dependence in habitat-selection inference (Mysterud & Ims, 1998; Matthiopoulos,

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629 Hebblewhite, Aarts, & Fieberg, 2011; Matthiopoulos et al., 2015). Density-dependent inference
630 may be observed when the same analysis is applied to individuals or populations of the same
631 species, under similar environmental conditions, but at different population densities. Availability
632 dependence (also referred to as a "functional response") may be observed when the same analysis is
633 applied to individuals or populations of the same species, which experience different landscape-scale
634 resource or habitat availabilities. For example, van Beest, McLoughlin, Mysterud, & Brook (2016),
635 found that individual elk display availability-dependent resource-selection patterns (switching from
636 selection to avoidance of certain habitats as function of the availability of these habitats within
637 their home range), but that the strength of this functional response depended on elk population
638 density. Such context dependencies are in fact so common that we do not know of a single instance
639 where researchers were looking for them and failed to find them. Recently, Avgar, Betini, & Fryxell
640 (2020) showed that such context dependencies in habitat-selection patterns are expected to emerge
641 even under the simplest theoretical model of an Ideal Free Distribution (Fretwell, 1969). Thus,
642 habitat-selection models often have poor predictive capacity when transferred across different study
643 areas, or even within the same area over time (e.g., Torres et al., 2015). Yet, these differences may
644 also be exploited; modeling frameworks that leverage data from multiple environments and across a
645 range of population densities can potentially increase predictive capabilities (Matthiopoulos, Field,
646 & MacLeod, 2019). As with any other attempt to model complex ecological data, critical evaluation
647 of model performance for both within and out-of-sample data is essential (Fieberg, Forester, et al.,
648 2018).

Authors' Contributions

650 JF developed the idea for the review, led the writing of the manuscript, and drafted the initial
651 version of Supplementary Appendix A; B.S. and J.S. drafted the initial version of Supplementary
652 Appendix B; B.S. and T.A. drafted the initial version of Supplementary Appendix C. All authors
653 contributed critically to the manuscript text and Additional Files, and gave final approval for
654 publication.

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Data Availability

All of the data used in this paper are available from within the `amt` package (Signer et al., 2019).

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Tables

Table 1: Regression coefficients (SE) in fitted resource-selection functions fit to data from Lupe the fisher. Models 1 and 3 use forest as the reference level, Model 2 uses wet as the reference level. Model 3 includes interactions between elevation and landcover classes.

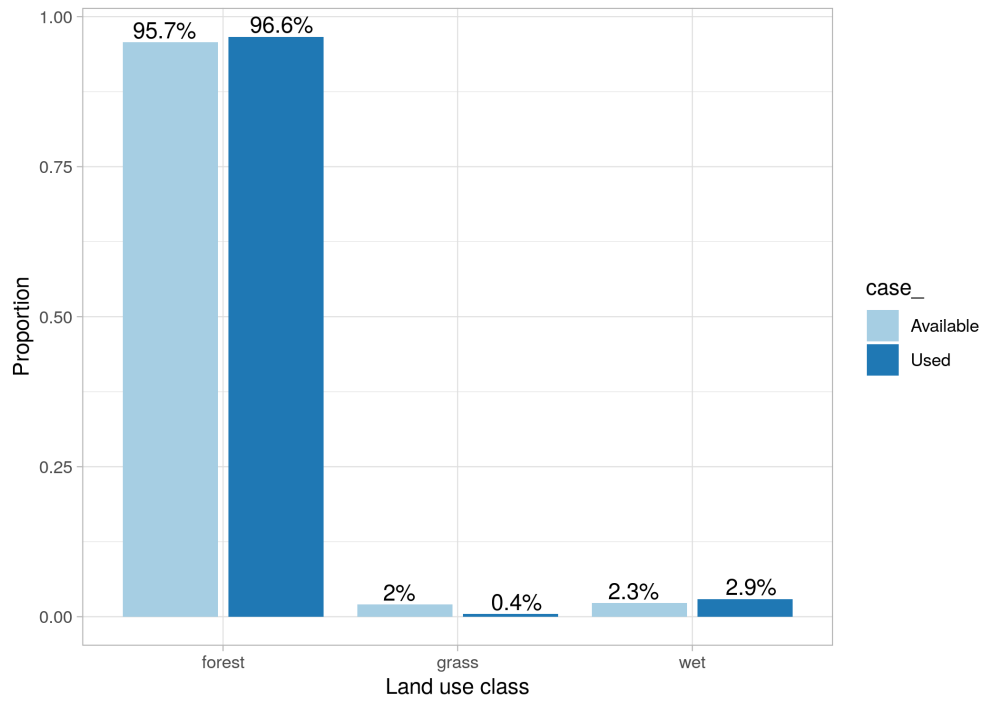|	Model 1	Model 2	Model 3
(Intercept)	-13.168	-12.918	-13.171
	(0.019)	(0.107)	(0.020)
elevation	0.303	0.303	0.313
	(0.017)	(0.017)	(0.017)
popden	-0.183	-0.183	-0.186
	(0.021)	(0.021)	(0.021)
landuseCgrass	-1.477		-1.471
	(0.278)		(0.278)
landuseCwet	0.250		0.183
	(0.108)		(0.116)
landuseC1forest		-0.250	
		(0.108)	
landuseC1grass		-1.727	
		(0.297)	
elevation:landuseCgrass			0.112
			(0.380)
elevation:landuseCwet			-0.498
			(0.127)

874 # Figures

Figure 1: Distribution of used and available locations among different landscape cover classes for a fisher in upstate New York (LaPoint et al., 2013a, 2013b).
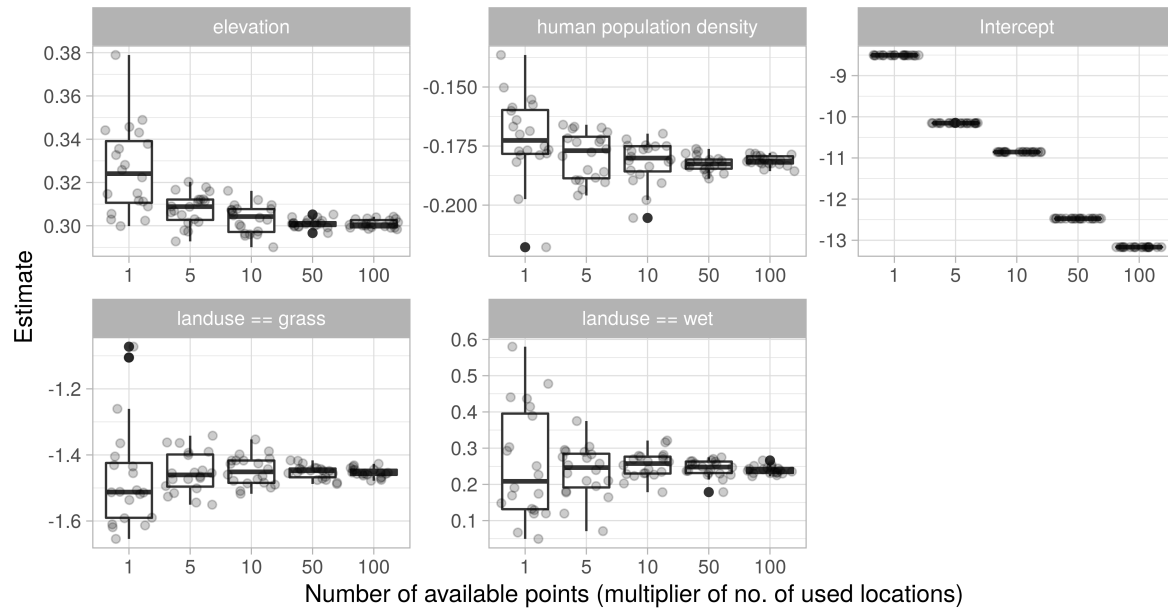
Figure 2: Estimated parameters in fitted resource-selection functions using increasing numbers of available points. Each dot represents an estimate from fitting a logistic regression model to 3004 GPS telemetry locations combined with a random sample of available points, with sample size given by the x-axis (where 1 means 3004 available points and 100 means 300,400 available points).
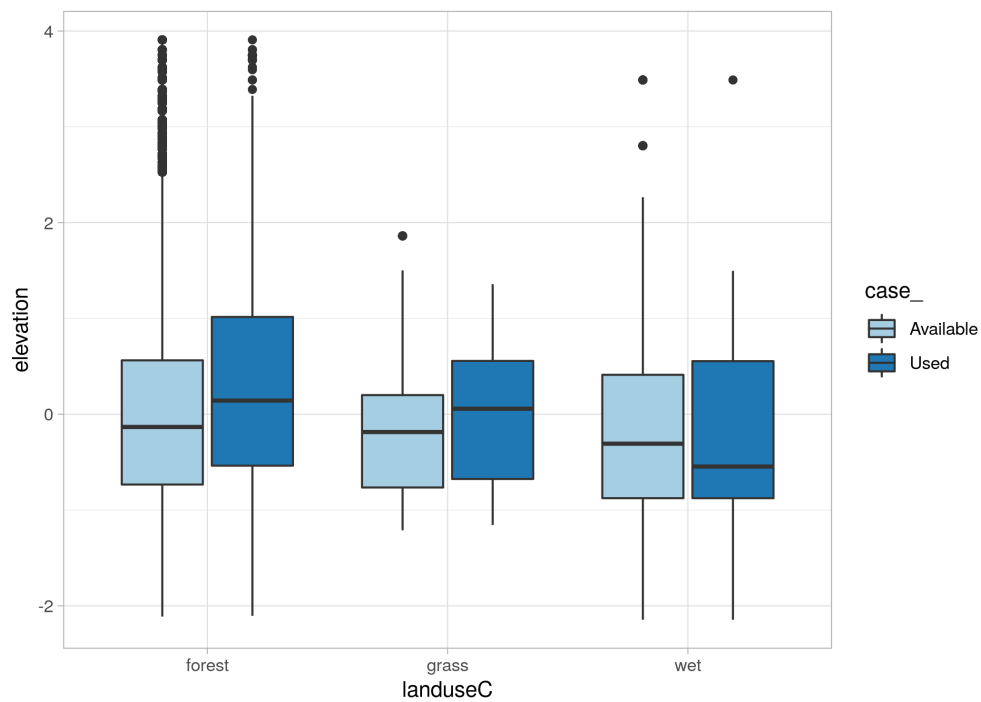
Figure 3: Distribution of elevation at used and available locations within each of 3 landcover types.
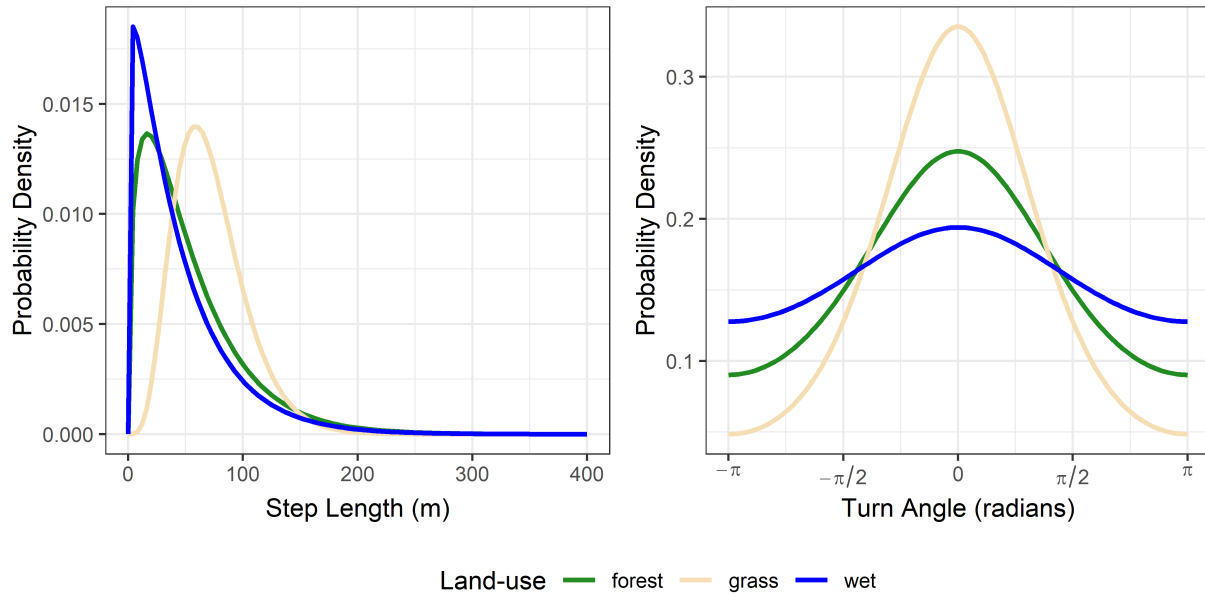
Figure 4: Step-length and turn-angle distributions from an integrated step-selection analysis applied to Lupe's location data (see Supplementary Appendix B). The conditional logistic regression model included interactions between movement characteristics (step length, log step length, and cosine of of the turn angle) and the landuse category Lupe was in at the start of the movement step. We see that Lupe tends to take larger, more directed steps when in `grass` and slower and more tortuous steps in `wet` habitat.

Supporting Information

Supplementary Appendix A: `AppA_RSF_examples.html`, a tutorial demonstrating how to fit and interpret parameters in resource-selection functions.

Supplementary Appendix B: `AppB_SSF_examples.html`, a tutorial demonstrating how to fit and interpret parameters and output when conducting an integrated step-selection analysis.

Supplementary Appendix C: `AppC_iSSA_movement.html`, a description of methods used to adjust 'tentative' parameters in step-length and turn-angle distributions for the effects of habitat selection.