



HAL
open science

Time-varying habitat selection analysis: A model and applications for studying diel, seasonal, and post-release changes

Romain Dejeante, Marion Valeix, Simon Chamaillé-Jammes

► To cite this version:

Romain Dejeante, Marion Valeix, Simon Chamaillé-Jammes. Time-varying habitat selection analysis: A model and applications for studying diel, seasonal, and post-release changes. *Ecology*, 2024, 105 (2), pp.e4233. 10.1002/ecy.4233 . hal-04749325

HAL Id: hal-04749325

<https://hal.science/hal-04749325v1>

Submitted on 23 Oct 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Journal name: Ecology

2 Manuscript type: Statistical report

3

4 **Time-varying habitat selection analysis: A model and applications for studying diel,**
5 **seasonal, and post-release changes**

6

7 Romain Dejeante^{1*} ; Marion Valeix^{1,2} ; Simon Chamaillé-Jammes^{1,3}

8 1. CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

9 2. CNRS, Université de Lyon, Université Lyon1, Laboratoire de Biométrie et Biologie

10 Evolutive UMR 5558, 69622 Villeurbanne, France

11 3. Mammal Research Institute, Department of Zoology and Entomology, University of

12 Pretoria, Pretoria, South Africa

13 * Corresponding author: romain.dejeante@cefe.cnrs.fr

14

15 Open Research: Data and code are archived on a figshare depository (Dejeante, Valeix, and

16 Chamaillé-Jammes 2023)

17

18 Keywords: habitat selection; migration; post-release; resource selection function; seasonality;

19 space use; temporal variation; time-varying effects

20 **Abstract**

21 Resource selection functions are commonly employed to evaluate animals' habitat selection,
22 e.g., the disproportionate use of habitats relative to their availability. While environmental
23 conditions or animal motivations may vary over time, sometimes in an unknown manner,
24 studying changes in habitat selection usually requires an *a priori* segmentation of time in
25 distinct periods. This limits our ability to precisely answer the question 'when is an animal's
26 habitat selection changing?'. Here, we present a straightforward and flexible alternative
27 approach based on fitting dynamic logistic models to used/available data. First, using
28 simulated datasets, we demonstrate that dynamic logistic models perform well to recover
29 temporal variations in habitat selection. We then show real-world applications for studying
30 diel, seasonal, and post-release changes in habitat selection of blue wildebeest (*Connochaetes*
31 *taurinus*). Dynamic logistic models allow to study temporal changes in habitat selection in a
32 framework consistent with resource selection functions, but without the need to segment time
33 in distinct periods, which can be a difficult task when little is known about the process
34 studied, or may obscure inter-individual variability in timing of change. These models should
35 undoubtedly find their place in the movement ecology toolbox. We provide R scripts to
36 facilitate their adoption. We also encourage future research to focus on how to account for
37 temporal autocorrelation in location data, as this would allow statistical inference from
38 locations data collected at a high frequency, an increasingly common situation.

39

40 **Introduction**

41 Changes in environmental conditions consistently challenge animals in their lives, leading
42 them to regularly adjust their behavior. One of the important ways animals do so is by using
43 the landscape they live in differently, i.e., by relocating themselves or selecting habitats
44 differently. This is most clearly exemplified by migrations, which occur in response to

45 seasonal changes in weather and/or resource availability (Dingle 2014). Changes at smaller
46 time-scales also occur, such as when animals shift habitats in response to forage depletion or
47 day/night alternation in predation risk (Courbin et al. 2019). Naturally, discovering and
48 understanding such changes in space use and habitat selection is a key goal of ecologists.

49 Over time, habitat selection analysis (HSA) conducted using the resource selection
50 function (RSF) approach (Boyce et al. 2002) has become the standard framework to study
51 changes in animals' habitat selection. RSF analyses statistically compare the environmental
52 characteristics of used locations collected over a period of time with the characteristics of
53 locations available during that period. As such, a RSF estimates the average strength of
54 selection for the various habitats considered over the period of interest. How this period is
55 defined is up to the researcher, but strongly affects the results and the associated
56 interpretations (Mayor et al. 2009). As the within-period variability in selection is averaged,
57 finer-scale temporal dynamics (e.g., day/night changes when the period covers weeks or
58 months) in selection are overlooked, and the mean selection strength estimated might
59 represent an average that is not meaningful. This would be the case if, for instance, the study
60 period encompasses two different phases in an animal's habitat selection behavior without the
61 researcher being aware of it.

62 Segmenting time to define biologically relevant periods over which to conduct HSA
63 may be difficult, and often involves somewhat arbitrary decisions with unknown
64 consequences. This is true for even well studied periods like seasons (Basille et al. 2013) or
65 day-night periods (Richter et al. 2020). Starts and ends of seasons vary between years, and
66 can only be roughly defined without ancillary data. Some seasons like spring or fall are also
67 clearly periods of environmental changes during which patterns of habitat selection are
68 unlikely to be constant. Animal needs and motivations, and thus habitat selection (Roever et
69 al. 2014) may also change at unpredictable (for the researcher) times, such as when they

70 disperse (Delgado et al. 2009). This again makes segmentation of time into distinct periods
71 difficult, or even irrelevant if one is interested in the dynamics of the change itself. This issue
72 has been recognized before and various suggestions have been offered, from using a
73 combination of movement metrics and habitat use information to define periods (but without
74 estimating habitat selection) (Basille et al. 2013), to integrating time as one of the predictors
75 in habitat-selection models (but with a constraint on the shape of the time-dependence)
76 (Picardi et al. 2021), or using continuous-time movement models (but with a complex
77 implementation) (Hooten et al. 2014). There is currently no simple yet flexible approach to
78 describe the temporal dynamics of habitat selection that underlie the long-term, averaged,
79 pattern revealed by RSF analyses.

80 Recent developments of multi-state step-selection functions (SSF) (Nicosia et al.
81 2017; Prima et al. 2022) now allow one to segment a movement trajectory, without *a priori*,
82 in periods differing by the way the animal moves and selects habitats. Each period represents
83 times when the animal is in one of a generally limited number of possible behavioral states.
84 Being SSF models, they do not estimate habitat selection at the same scale than RSF models:
85 they focus on establishing whether habitats can explain that some ‘steps’ (generally over
86 minutes or hours) are more likely than others. Thus, while useful (see examples in Prima et
87 al. 2022), multi-state SSFs cannot answer the question as to whether the selection revealed by
88 a RSF analysis represents a selection constant over time, an average measure of a fluctuating
89 pattern of selection, or even whether contrasted selection patterns during a period of interest
90 cancel out in the RSF estimation.

91 Here, we present how dynamic logistic regression models allow one to easily estimate
92 the temporal dynamics of habitat selection that underlie the long-term, averaged, pattern
93 revealed by RSF analyses, without *a priori* segmentation of time into distinct periods.
94 Dynamic logistic regression models are commonly used to analyze binary time series in

95 survival analysis (Martinussen and Scheike 2006), but can be applied to other data sources
96 (Fahrmeir 1992). First, we use simulated movement data to demonstrate that dynamic logistic
97 regression models can adequately recover time-varying habitat selection coefficients. We also
98 highlight the influence of parameters, whose values are under the researcher’s control, on the
99 estimation process. Second, we illustrate the usefulness of the approach by applying time-
100 varying HSA on blue wildebeest (*Connochaetes taurinus*) tracking data, showing how one
101 can describe temporal variations of animal habitat selection such as diel, seasonal, and post-
102 release changes. The relevant R scripts are provided to facilitate the adoption of the method
103 by ecologists.

104 **Methods**

105 *Dynamic logistic models for time-varying HSA*

106 *General principles of dynamic logistic models*

107 Here, we briefly describe the discrete-time state space model developed by Fahrmeir (1992)
108 to estimate time-varying coefficients from generalized linear models, and especially logistic
109 models. Generally, discrete-time state space models relate observations over time to hidden
110 parameters, with hidden parameters following a Markovian transition model (Auger-Méthé et
111 al. 2021). Applied to dynamic logistic regressions in the context of time-varying HSA, such a
112 model can be formulated using the following equations:

113 (equation 1) $\text{logit}(p_t) = \beta_{t,0} + \beta_{t,1}x_{t,1} + \dots + \beta_{t,n}x_{t,n}$

114 (equation 2) $\beta_t = \beta_{t-1} + v_t$, with $v_t \sim N(0, \mathbf{Q})$

115 with $p_t = \text{Pr}(y_t = 1)$ the probability of the binary response variable y_t being one (i.e., used
116 versus available), $(\beta_{t,0}, \dots, \beta_{t,n})$ the hidden parameter vectors (i.e., time-varying selection
117 coefficients), $(x_{t,1}, \dots, x_{t,n})$ the covariates (i.e., environmental layers), v_t the error process
118 (i.e., sequence of independent random variables), \mathbf{Q} the covariance matrix of the Markov
119 chain that contains values that will affect the smoothness of the estimated time-series of

120 habitat selection coefficients. Here, following Fahrmeir (1992) and Christoffersen (2021;
121 2022), we used a simple first order random walk model for the state equation (equation 2).
122 See Christoffersen (2021) for details on second-order random walk model formulation. The
123 covariance matrix \mathbf{Q} is a symmetric matrix of $n+1$ dimension, with initial values chosen by
124 the experimenter (see the “Implementation in the context of HSA” section to determine initial
125 values) and then estimated during the fitting process (see below).

126 The model coefficients and the values of the covariance matrix over time are
127 estimated from the EM algorithm described by Fahrmeir (1992). First, the E-step procedure
128 recursively iterates prediction, correction, and smoothing steps to approximate and maximize
129 posterior mode estimations of model coefficients, using the generalized extended Kalman
130 filter and smoother algorithm described by Fahrmeir and Kaufmann (1991). Second, the M-
131 step procedure automatically updates over time the covariance matrix. A more comprehensive
132 description of the EM algorithm is provided by Christoffersen (2021).

133 *Implementation in the context of HSA*

134 To conduct time-varying HSA using dynamic logistic models, the following steps are
135 required. First, as in RSF analyses, a sample of locations that could be considered ‘available’
136 is drawn. This can be, for instance, locations sampled randomly within the animal home
137 range. Each used location ($y_t = 1$) obtained at time t is paired with N random locations
138 ($y_t = 0$). Each used and available location is then characterized using environmental
139 variables or any other variable of interest ($x_{t,1}, \dots, x_{t,n}$). Finally, the time-varying parameters
140 ($\beta_{t,1}, \dots, \beta_{t,n}$) are estimated by fitting a dynamic logistic model, with type of location (used
141 vs. available) as response variable y_t and the time series $x_{t,n}$ as predictors (cf. equation 1).

142 Note that caution is required when estimating time-varying habitat selection
143 coefficients from location data collected at relatively high frequency. Classical RSF and the
144 model presented here do not account for temporal autocorrelation in location data. In

145 particular, it is assumed that, within the time interval between two locations, the animal could
146 relocate anywhere in the area in which random locations are drawn. When this is not the case,
147 estimates of habitat selection coefficients are unbiased but their standard errors are biased
148 downward, i.e., are too small. In this situation, one may either subsample data to a lower
149 frequency to obtain a valid statistical inference, or remain within the framework of a
150 descriptive analysis aiming at exploring data, for instance for gaining insights on the possible
151 existence of frequent habitat selection changes.

152 Here we fit the dynamic logistic model using the “ddhazard” function from the
153 *dynamichazard* R package by Christoffersen (2021), which implements the method described
154 by Fahrmeir (1992). We provide in “online appendix” the script needed to run a time-varying
155 HSA on a simulated trajectory (Dejeante, Valeix, and Chamaillé-Jammes 2023); the model
156 fitting takes about 3s on this dataset, on PC with an Intel(R) Xeon(R) CPU E5-1650 0 @
157 3.20GHz.

158 *General guidelines to initialize the wiggleness parameter (Q)*

159 To fit a dynamic logistic model, one needs to first provide initial values to fill in the
160 covariance matrix, diagonal at initialization, and initiate the estimation process. Here, we
161 provided the same initial values for all diagonal elements (referred to as Q hereafter). As this
162 initial value can greatly affect the wiggleness of the model (see Results), we also refer to Q as
163 the wiggleness parameter. While using caution is thus required when choosing the initial
164 value of Q , our results show that this value can be increased until (1) the estimates of Q after
165 fitting converge towards a similar value (Appendix S1: Figure S1) and (2) the estimated
166 coefficients of habitat selection converge to a similar value too (Appendix S1: Figure S2).
167 Hence, we encourage users of the model to test several initial values for Q . One way to select
168 among them is by looking at the correlations between the estimated values of Q after fitting

169 and/or the correlations between the time series of the estimated time-varying coefficients
170 (Appendix S1).

171 *Evaluation of the accuracy of dynamic logistic models for time-varying HSA*

172 To assess the ability of our approach to detect shifts in habitat selection patterns, we (1)
173 simulated animal trajectories emerging from time-varying selection for one environmental
174 variable, and (2) fitted dynamic logistic models on the simulated data to compare the
175 estimated coefficients with the theoretical values used in the simulations.

176 *Landscape and movement simulation*

177 For simplicity, animal trajectories were simulated on one habitat layer (500×500 cells), with
178 values that did not vary over time. To mimic patchy landscapes, we used spatially correlated
179 Gaussian random fields, which attribute a continuous value ranging from 0 to 1 to each cell,
180 using the *localGibbs* R package (Michelot, Blackwell, and Matthiopoulos 2019). Following
181 Michelot, Blackwell, and Matthiopoulos (2019), we then simulated animal trajectories over
182 500 time steps using a local Gibbs movement model. For each time t , 1000 potential locations
183 were uniformly generated within a 2×100 -pixel radius around the current location, and the
184 location at time $t+1$ was sampled among them with probabilities proportional to the strength
185 of selection for potential locations. This strength of selection was determined by the value of
186 the habitat layer at these locations, and by the model coefficient describing how the strength
187 of selection changes with values of the habitat variable. An important benefit of using a local
188 Gibbs model is that the coefficient of habitat selection used in the simulation model is
189 theoretically equal to the one that should be estimated by a RSF fitted on the data (Michelot,
190 Blackwell, and Matthiopoulos 2019). The local Gibbs model, however, does not allow one to
191 directly simulate animal trajectories with time-varying habitat selection coefficients. Hence,
192 at each time t , we changed the value of the coefficient of the local Gibbs model to generate
193 the location at time $t+1$, based on the location and on the coefficient at time t .

194 *Scenarios of temporally-changing habitat selection*

195 To be able to test whether changes in habitat selection strength could be robustly recovered
196 by dynamic logistic models, we built scenarios that differed in terms of how often the
197 model's coefficient of habitat selection changed over time. We did so by randomly sampling,
198 in the $[-5, 5]$ range, and either changing every 20 steps (referred as "frequent change"
199 scenario) or every 250 steps (referred as "rare change" scenario), the model's habitat
200 selection coefficient. To avoid having sudden, step-like, changes in habitat selection, we then
201 used spline regressions to smooth the variations of habitat selection over time. For each
202 scenario, we generated 100 trajectories per simulated landscape, and replicated this on 100
203 different landscapes. We then tested our ability to recover the temporal changes in the
204 model's habitat selection coefficient by fitting a dynamic logistic regression model to each
205 trajectory as presented above, drawing 100 available locations at each time-step within the
206 99% utilization distribution location-based kernel of each simulated trajectory. We also
207 assessed to what extent the model's estimation was affected by the value of the wiggleness
208 parameter Q . We did so by fitting, for each dataset of each scenario, a set of models with
209 different values of Q , ranging from 0.01 (i.e., low wiggleness) to 2 (i.e., high wiggleness). For
210 each value of Q , we then averaged the estimated coefficients over each set of 100 simulated
211 trajectories per landscape, and fitted a linear regression with the mean estimated coefficient
212 as response and theoretical coefficients, which were used in the simulations, as predictors,
213 adding a random intercept with replication number. A slope near 1 would indicate that a
214 dynamic logistic model is able to estimate the temporal changes in the habitat selection
215 coefficient correctly, and an intercept near 0 would indicate that the estimations are not
216 biased.

217 In addition, to demonstrate that the time-varying HSA approach reveals the temporal
218 dynamics of the selection process that is commonly studied using RSF analyses, we averaged

219 the time-varying coefficients estimated from 5000 trajectories (of 500 time-steps each)
220 covering a broad range of selection patterns and landscape composition, and compare these
221 values with the coefficients estimated by a conventional RSF analysis on the same
222 trajectories.

223 *Time-varying HSA: applications*

224 To illustrate some applications of time-varying HSA, we analyzed wildebeest movement
225 datasets collected in Hluhluwe-iMfolozi Park (South Africa). There, surface-water
226 availability, which is high during the wet season (October-March) as temporary waterholes
227 are filled up by the rains, becomes low in the dry season (April to September), with water
228 remaining available only in a few rivers. Since wildebeests are water-dependent grazers that
229 preferentially forage in open grasslands, we used the distance to the closest main river and the
230 habitat openness as relevant habitat variables to demonstrate the use of dynamic logistic
231 models. For each study below, we fitted the models with a relatively high value for Q ($Q=2$),
232 as simulations showed that high wiggleness in the estimates lead to better results (see Results
233 section). We used the *amt* R package to generate random points and extract the values of
234 predictors at used and available locations (Signer, Fieberg, and Avgar 2019).

235 *Short-term temporal variations: diel changes in habitat selection*

236 We used tracking data collected on one wildebeest over one month in the dry season, at a fix
237 rate of one location every 15 minutes. In the context of the model presented here, such data
238 are highly autocorrelated and estimated standard errors and confidence intervals are likely
239 biased downward. Interpretation of results should therefore be done with caution. Habitat
240 selection coefficients remain however estimated without bias, and we included the analysis
241 here to show how it allows exploring changes in habitat selection at short time scales. Other
242 analyses, more statistically robust, are presented below.

243 Following the practical implementation of time-varying HSA described above, we
244 estimated the habitat selection of this wildebeest by (1) generating, for each time t , 100
245 random locations within its home range (99% utilization distribution location-based kernel),
246 (2) extracting the environmental characteristics of used and random locations, and (3) fitting
247 a dynamic logistic regression to compare the habitat openness and the distance to the closest
248 main river between the used and available locations over time. A preliminary visual
249 inspection of the GPS tracking data suggested day/night relocations of the wildebeest
250 (Appendix S2: Figure S1). To check whether these changes were associated with changes in
251 habitat selection, we estimated the temporal autocorrelation of the time-varying habitat
252 selection coefficients.

253 *Long-term temporal variations: seasonal changes in habitat selection*

254 We used tracking data collected on one wildebeest over one year at a fix rate of one location
255 every 15 minutes. To avoid issues related to the temporal autocorrelation in location data, and
256 because the temporal scale of the analysis does not require locations to be collected at such a
257 high frequency, we subsampled our dataset to one location per day and one location per night.
258 A preliminary visual inspection of the spatial data showed that the individual moved mostly
259 westward and then eastward during the period (Appendix S2: Figure S2). Hence, in addition
260 to habitat openness and distance to the closest river, we added longitude to the model's
261 predictors. We generated 10 random locations per time t within its home range to fit the time-
262 varying HSA. To provide an example of how one can subsequently delineate temporal
263 periods that are homogeneous in terms of habitat selection, we further segmented the time
264 series of each model's coefficients separately, using the segmentation method described, and
265 implemented in the *segclust2d* R package, by Patin et al. (2020).

266 *Event-based variations: post-release changes in habitat selection*

267 We used the tracking data of three wildebeest simultaneously introduced in the park in
268 October 2020. Data were collected over the 100 days following the release date, at a fix rate
269 of one location every hour. As in the previous analysis on the long-term temporal variations
270 of wildebeest's habitat selection, we subsampled the dataset to one location per night and one
271 location per day to avoid issues with the temporal autocorrelation in location data. We then
272 estimated wildebeest's habitat selection drawing 100 random locations, for each time t ,
273 within their individual home ranges. To incorporate the dispersal of the released individuals
274 into HSA, we added longitude and latitude to model's predictors. Hence, we fitted a dynamic
275 logistic model for each individual, using habitat openness, distance to the closest river,
276 longitude, and latitude as predictors.

277 **Results**

278 *Theoretical evaluation*

279 In general, we found that dynamic logistic models allowed us to adequately recover the
280 temporal changes in the coefficients of habitat selection used in the simulations. When the
281 true coefficients did not change often ('rare change' scenarios), the wiggleness parameter had
282 little impact and estimations were always good (Figure 1a-b; Appendix S1: Figure S3). When
283 the true coefficients did change often ('frequent change' scenarios), it became critical to use
284 high values of the wiggleness parameter to obtain estimates matching the theoretical
285 coefficients (Figure 1c-d; Appendix S1: Figure S3). Importantly, the effect of the wiggleness
286 parameter tend to stabilize at large values of Q (Appendix S1: Figure S4), making it safe to
287 use large values when investigating large and frequent changes in habitat selection.

288 The average of the time-varying coefficients was nearly equal to the coefficient
289 estimated by a conventional RSF (Figure 2a), demonstrating that the time-varying HSA
290 approach addresses the same selection process as the one studied by conventional RSF
291 analyses, while providing more information as it describes the temporal dynamics of

292 selection. Also, it can reveal whether the coefficients of a RSF are biologically relevant -
293 when time-varying selection coefficients have uni-modal distributions (Figure 2b) - or not -
294 when time-varying selection coefficients have multi-modal distributions (Figure 2c), and RSF
295 coefficients represent a statistical average that never represents the true selection process.

296 ***Short-term temporal variations: diel changes in habitat selection***

297 A time-varying HSA conducted with a dynamic logistic model suggested that the wildebeest's
298 selection for open habitats and rivers varied greatly over the month of the study (Figure 3). In
299 particular, the wildebeest's selection for open habitats apparently changed across the
300 day/night cycle, as the auto-correlation period of the coefficient was approximately 24h
301 (Appendix S2: Figure S3). Open habitats seemed to be strongly selected during night-time,
302 but not selected, and sometimes even avoided, during daytime (Figure 3a). Such day/night
303 shifts were not noticeable for the selection of areas close to rivers (Figure 3b), but there
304 seemed to be variations over periods of 3 or 4 days. Contrary to the diel variations in the
305 selection of open habitats, such variations would be hard to detect using the common HSA
306 approach based on a segmentation of time into distinct periods.

307 ***Long-term temporal variations: seasonal changes in habitat selection***

308 The time-varying HSA showed clear seasonal changes in the wildebeest's habitat selection,
309 which could then be separated in several periods according to the segmented time-series
310 (Figure 4). The existence and timing of some these periods were unpredictable *a priori*. For
311 example, this wildebeest maintained the same overall strength of selection for open habitats
312 from November to August, whereas this period covers months from both the dry and wet
313 seasons (Figure 4a). Also, we note that during the dry season (April to June) this wildebeest
314 did not preferentially use areas close to rivers, but selected areas close to rivers consistently
315 from July to mid-August (green segment) and likely did back-and-forth trips to and away
316 from the rivers from mid-August to October (yellow segment) (Figure 4b).

317 ***Event-based variations: post-release changes in habitat selection***

318 After their release, the three wildebeest generally selected open habitats, but their level of
319 selection differed between individuals (Appendix S2: Figure S4), particularly towards the end
320 of the study period (Figure 5a). Differences in the selection for areas close to rivers (Figure
321 5b) or in the longitude (Figure 5c) and latitude (Figure 5d) of the park also became apparent
322 at the end of the first month after release. Then, although the three wildebeest established in
323 different areas (see difference in selection for longitude and latitude), the selection of areas
324 close to rivers remained and was similar for two wildebeests (colored in green and yellow),
325 whereas the third one avoided the areas close to rivers (colored in purple).

326 **Discussion**

327 There is clear evidence that animals' habitat selection changes regularly and at different time-
328 scales, from diel to seasonal shifts, or during key life-history events such as dispersal.
329 Unfortunately, ecologists have had limited and often unsatisfactory options to study these
330 changes. Most commonly, an *a priori* segmentation of time into distinct periods of apparent
331 biological relevance is made, although this segmentation can sometimes be difficult to justify,
332 let alone to validate. The alternative approach of simply integrating time as predictor in a
333 RSF has limitations (see discussion in Picardi et al. 2021), and more statistically complex
334 approaches (Hooten et al. 2014) are unlikely to be broadly used. In this work, we propose a
335 novel approach based on dynamic logistic models (Fahrmeir 1992) to easily estimate
336 temporal changes in habitat selection, in a framework consistent with RSF. We demonstrate,
337 using simulations, its general validity, while highlighting a point of attention (parameter Q).
338 We also showcase its use for the study of diel, seasonal, and post-release changes in habitat
339 selection.

340 With this time-varying HSA approach, one can simultaneously estimate both the
341 timing and the amplitude of habitat selection changes. Estimation of the timing of change

342 from the data is what makes this approach novel and attractive. Many times, *a priori*
343 segmentation of time into distinct periods requires expert knowledge or is based on ancillary
344 data (e.g., climate data) whose relevance for a particular dataset is not warranted. ‘Letting the
345 data speak’ allows revealing the actual pattern of change. This may be of particular
346 importance, for instance, in the study of inter-individual variability, as the timing of change
347 can be one of the differencing variables, as evidenced in our post-release study case. As
348 recognized by Picardi et al. (2021), time-varying HSA opens a new avenue to broaden the
349 scope of the studies of inter-individual differences in space use, which has so far focused on
350 movement characteristics or habitat selection strength. More generally, even when the
351 relevance of an *a priori* segmentation of time into distinct periods is easier to ascertain, such
352 as when comparing daytime to night-time habitat selection, time-varying HSA allows one to
353 immediately identify unusual periods (e.g., night of the 27th of August, when the wildebeest
354 did not increase its selection for open habitat). These unusual periods may either be of
355 interest (in such case, one would have to conduct one standard HSA per night to have
356 discovered this), or be ‘noise’ that should not affect the estimation of habitat selection
357 strength during more ‘usual’ periods (conversely to what occurs in a standard HSA).

358 Importantly, data-driven estimation of the timing of change in habitat selection makes
359 it possible to derive ‘segments’ of homogeneous habitat selection, and opens the way to
360 estimate specific habitat selection ‘modes’ of animals defined by the strength of habitat
361 selection. Behavioral modes relevant to space use are commonly defined by movement
362 characteristics such as speed and turning angles (Patin et al. 2020; McClintock and Michelot
363 2018), but do not integrate information about habitat selection. The use of segmentation-
364 clustering algorithm such as *segclust2d* or hidden-Markov models on the time-series
365 coefficients obtained by time-varying HSA will allow one to extract habitat selection modes,
366 and to estimate the duration and frequencies of such modes. This could complement very

367 recent works developing behavioral-mode detection approaches based on SSF (Prima et al.
368 2022; Nicosia et al. 2017; Klappstein, Thomas, and Michelot 2022), although by definition
369 the temporal scale of selection considered is much different.

370 Despite that, rigorously, conventional RSF models are not time-series models, our
371 approach is closer to the RSF than to the SSF framework. Indeed, by generating random
372 points within the whole animal's home range, the estimated time-varying coefficients
373 measure when an animal is spending time in a "rare" habitat relatively to its large-scale
374 availability. The selection process measured here is the fact that animals move and stay in
375 rare habitats over time, and not the 'step' selection resulting from animal's choice within the
376 steps allowed by the sampling rate. Hence, we make the biological and statistical assumption
377 that animal's habitat selection at time t depends on the history of animal's habitat selection up
378 to t (Fahrmeir 1994). An example of why such an assumption makes sense is animal
379 migration: once established in a new range, coefficients from a SSF (i.e., fine scale) would
380 not show a selection for this new range, while coefficient from a RSF (i.e., large scale) would
381 show a selection for such areas when considering the whole study area as available.

382 One common use of habitat selection modelling is to predict and map population
383 distribution within landscapes (Morris, Proffitt, and Blackburn 2016). How to best map
384 predicted space use from a time-varying habitat selection analysis is not obvious as
385 coefficients are, by definition, time-varying. However, one can perform a time-varying
386 habitat selection analysis to detect temporal periods of homogeneous habitat selection (as
387 done in this work), and use the average of coefficients to predict the distribution of space use
388 within the periods of interest, which for instance could be seasons. When habitat selection is
389 continuously changing, it does not make sense to predict a static distribution, either from a
390 conventional RSF or from a time-varying HSA. A time-varying analysis, however, allows one
391 to actually verify whether habitat selection is changing or not over the period of interest.

392 Results from the time-varying approach proposed here are to some extent sensitive to
393 the model's wiggleness. In particular, but without surprise, model allowing for little
394 wiggleness (small values of Q) can provide a poor fit to the data when habitat selection often
395 changes. Models allowing for high wiggleness generally perform much better, especially if
396 habitat selection often changes. There was no obvious evidence of an optimum value of Q to
397 look for, as correlations between the estimates of habitat selection plateaued when increasing
398 Q values. Therefore, running a time-varying HSA with a high value for Q appears a safe way
399 to conduct robust analyses. Note however that dynamic logistic models do not account for the
400 temporal autocorrelation that could characterize the used locations if these were collected at a
401 high frequency, relatively to the movement of the animal. In such case, the estimated standard
402 errors of the models' coefficients would be biased downward (i.e., be too small), which could
403 lead to overconfident interpretations. Some movement modelling frameworks such as
404 integrated-SSF (Avgar et al. 2016), MCMC movement models (Michelot et al. 2020) or
405 continuous-time models (Michelot et al. 2019) naturally account for autocorrelation. These
406 models however estimate average habitat selection at the temporal scale of data collection
407 (SSF and MCMC models) or at a near-instantaneous scale (continuous-time models), which
408 may not be what ecologists are interested in when they focus on large-scale behavioral
409 decisions. Continuous-time models could have time-varying formulations (Michelot et al.
410 2021), but unfortunately fitting these models is computationally heavy and thus slow. The
411 RSF framework and dynamic logistic models remain therefore attractive. How to best
412 account for temporal autocorrelation in location data in RSF models is currently being
413 studied (see Alston et al. 2023), and we encourage future research to focus on how to account
414 for temporal autocorrelation in dynamic logistic models. As the estimation of the coefficients
415 themselves is not biased in presence of autocorrelation, the analysis of high-frequency data

416 with dynamic logistic models could still be useful to obtain a visual description of the
417 temporal trend in habitat selection, if interpreted with caution.

418 In conclusion, we think dynamic logistic models offer an easy yet powerful approach
419 to conduct time-varying HSA, for both exploratory and inferential studies. Our work, in
420 which we show real-world applications and provide R scripts, aims to facilitate the
421 appropriation of the method by ecologists and enriches their statistical toolbox. Novel
422 questions about how animals time their response to environmental changes can now be
423 addressed.

424 **Acknowledgements**

425 We are grateful to Ezemvelo for providing the authorization to conduct this research, and to
426 its ecologist D.J. Druce for his continuous administrative and field support, as well as for a
427 review of the manuscript. We acknowledge the field efforts of B. Gehr and R. Leeming and
428 anyone involved in the wildebeest captures. G. Fradin created the layer for habitat openness.
429 This work was partially funded by the French National Research Agency (program ANR-16-
430 IDEX-0006) through the i-Site MUSE (project REPOS). We thank editor B. McClintock and
431 two anonymous reviewers for their comments that greatly improved the manuscript.

432 **Conflict of interest statement**

433 The authors declare no competing interests.

434 **References**

435 Alston, Jesse M., Christen H. Fleming, Roland Kays, Jarryd P. Streicher, Colleen T. Downs,
436 Tharmalingam Ramesh, Björn Reineking, and Justin M. Calabrese. 2023. “Mitigating
437 Pseudoreplication and Bias in Resource Selection Functions with Autocorrelation-informed
438 Weighting.” *Methods in Ecology and Evolution* 14 (2): 643–54. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.14025)
439 210X.14025.

440 Auger-Méthé, Marie, Ken Newman, Diana Cole, Fanny Empacher, Rowenna Gryba, Aaron
441 A. King, Vianey Leos-Barajas, et al. 2021. “A Guide to State–Space Modeling of Ecological
442 Time Series.” *Ecological Monographs* 91 (4). <https://doi.org/10.1002/ecm.1470>.

443 Avgar, Tal, Jonathan R. Potts, Mark A. Lewis, and Mark S. Boyce. 2016. “Integrated Step
444 Selection Analysis: Bridging the Gap between Resource Selection and Animal Movement.”
445 *Methods in Ecology and Evolution* 7 (5): 619–30. <https://doi.org/10.1111/2041-210X.12528>.

446 Basille, Mathieu, Daniel Fortin, Christian Dussault, Jean-Pierre Ouellet, and Réhaume
447 Courtois. 2013. “Ecologically Based Definition of Seasons Clarifies Predator–Prey
448 Interactions.” *Ecography* 36 (2): 220–29. <https://doi.org/10.1111/j.1600-0587.2011.07367.x>.

449 Boyce, Mark S, Pierre R Vernier, Scott E Nielsen, and Fiona K. A Schmiegelow. 2002.
450 “Evaluating Resource Selection Functions.” *Ecological Modelling* 157 (2): 281–300.
451 [https://doi.org/10.1016/S0304-3800\(02\)00200-4](https://doi.org/10.1016/S0304-3800(02)00200-4).

452 Christoffersen, Benjamin. 2021. “Dynamichazard: Dynamic Hazard Models Using State
453 Space Models.” *Journal of Statistical Software* 99 (September): 1–38.
454 <https://doi.org/10.18637/jss.v099.i07>.

455 ———. 2022. “Ddhazard.” [https://cran.r-](https://cran.r-project.org/web/packages/dynamichazard/vignettes/ddhazard.pdf)
456 [project.org/web/packages/dynamichazard/vignettes/ddhazard.pdf](https://cran.r-project.org/web/packages/dynamichazard/vignettes/ddhazard.pdf).

457 Courbin, Nicolas, Andrew J. Loveridge, Hervé Fritz, David W. Macdonald, Rémi Patin,
458 Marion Valeix, and Simon Chamaillé-Jammes. 2019. “Zebra Diel Migrations Reduce
459 Encounter Risk with Lions at Night.” *Journal of Animal Ecology* 88 (1): 92–101.
460 <https://doi.org/10.1111/1365-2656.12910>.

461 Dejeante, Romain, Marion Valeix, and Simon Chamaillé-Jammes. 2023. “Time-Varying
462 Habitat Selection Analysis.” figshare. Collection.
463 <https://doi.org/10.6084/m9.figshare.c.6365415.v5>.

464 Delgado, María del Mar, Vincenzo Penteriani, Vilis O. Nams, and Letizia Campioni. 2009.
465 “Changes of Movement Patterns from Early Dispersal to Settlement.” *Behavioral Ecology*
466 *and Sociobiology* 64 (1): 35–43. <https://doi.org/10.1007/s00265-009-0815-5>.

467 Dingle, Hugh. 2014. “Migration: Definition and Scope.” In *Migration: The Biology of Life on*
468 *the Move*, edited by Hugh Dingle, 0. Oxford University Press.
469 <https://doi.org/10.1093/acprof:oso/9780199640386.003.0002>.

470 Fahrmeir, Ludwig. 1992. “Posterior Mode Estimation by Extended Kalman Filtering for
471 Multivariate Dynamic Generalized Linear Models.” *Journal of the American Statistical*
472 *Association* 87 (418): 501–9. <https://doi.org/10.1080/01621459.1992.10475232>.

473 ———. 1994. “Dynamic Modelling and Penalized Likelihood Estimation for Discrete Time
474 Survival Data.” *Biometrika* 81 (2): 317–30. <https://doi.org/10.2307/2336962>.

475 Fahrmeir, Ludwig, and Heinz Kaufmann. 1991. “On Kalman Filtering, Posterior Mode
476 Estimation and Fisher Scoring in Dynamic Exponential Family Regression.” *Metrika* 38 (1):
477 37–60. <https://doi.org/10.1007/BF02613597>.

478 Hooten, M.B., E.M. Hanks, D.S. Johnson, and M.W. Alldredge. 2014. “Temporal Variation
479 and Scale in Movement-Based Resource Selection Functions.” *Statistical Methodology* 17
480 (March): 82–98. <https://doi.org/10.1016/j.stamet.2012.12.001>.

481 Klappstein, Nj, L Thomas, and T Michelot. 2022. “Flexible Hidden Markov Models for
482 Behaviour-Dependent Habitat Selection.” Preprint. Ecology.
483 <https://doi.org/10.1101/2022.11.30.518554>.

484 Martinussen, Torben, and Thomas H. Scheike. 2006. *Dynamic Regression Models for*
485 *Survival Data*. Statistics for Biology and Health. New York, N.Y: Springer.

486 Mayor, Stephen J., David C. Schneider, James A. Schaefer, and Shane P. Mahoney. 2009.
487 “Habitat Selection at Multiple Scales.” *Écoscience* 16 (2): 238–47.
488 <https://doi.org/10.2980/16-2-3238>.

489 McClintock, Brett T., and Théo Michelot. 2018. “MomentuHMM: R Package for Generalized
490 Hidden Markov Models of Animal Movement.” *Methods in Ecology and Evolution* 9 (6):
491 1518–30. <https://doi.org/10.1111/2041-210X.12995>.

492 Michelot, Théo, Paul G. Blackwell, Simon Chamaille-Jammes, and Jason Matthiopoulos.
493 2020. “Inference in MCMC Step Selection Models.” *Biometrics* 76 (2): 438–47.
494 <https://doi.org/10.1111/biom.13170>.

495 Michelot, Théo, Paul G. Blackwell, and Jason Matthiopoulos. 2019. “Linking Resource
496 Selection and Step Selection Models for Habitat Preferences in Animals.” *Ecology* 100 (1):
497 e02452. <https://doi.org/10.1002/ecy.2452>.

498 Michelot, Théo, Richard Glennie, Catriona Harris, and Len Thomas. 2021. “Varying-
499 Coefficient Stochastic Differential Equations with Applications in Ecology.” *Journal of*
500 *Agricultural, Biological and Environmental Statistics* 26 (3): 446–63.
501 <https://doi.org/10.1007/s13253-021-00450-6>.

502 Michelot, Théo, Pierre Gloaguen, Paul G. Blackwell, and Marie-Pierre Étienne. 2019. “The
503 Langevin Diffusion as a Continuous-Time Model of Animal Movement and Habitat
504 Selection.” *Methods in Ecology and Evolution* 10 (11): 1894–1907.
505 <https://doi.org/10.1111/2041-210X.13275>.

506 Morris, Lillian R., Kelly M. Proffitt, and Jason K. Blackburn. 2016. “Mapping Resource
507 Selection Functions in Wildlife Studies: Concerns and Recommendations.” *Applied*
508 *Geography* 76 (November): 173–83. <https://doi.org/10.1016/j.apgeog.2016.09.025>.

509 Nicosia, Aurélien, Thierry Duchesne, Louis-Paul Rivest, and Daniel Fortin. 2017. “A Multi-
510 State Conditional Logistic Regression Model for the Analysis of Animal Movement.” *The*
511 *Annals of Applied Statistics* 11 (3). <https://doi.org/10.1214/17-AOAS1045>.

512 Patin, Rémi, Marie-Pierre Etienne, Emilie Lebarbier, Simon Chamaille-Jammes, and Simon
513 Benhamou. 2020. “Identifying Stationary Phases in Multivariate Time Series for Highlighting

514 Behavioural Modes and Home Range Settlements.” *Journal of Animal Ecology* 89 (1): 44–
515 56. <https://doi.org/10.1111/1365-2656.13105>.

516 Picardi, Simona, Nathan Ranc, Brian J. Smith, Peter S. Coates, Steven R. Mathews, and
517 David K. Dahlgren. 2021. “Individual Variation in Temporal Dynamics of Post-Release
518 Habitat Selection.” *Frontiers in Conservation Science* 2 (September): 703906.
519 <https://doi.org/10.3389/fcosc.2021.703906>.

520 Prima, Marie-Caroline, Thierry Duchesne, Jerod A. Merkle, Simon Chamaillé-Jammes, and
521 Daniel Fortin. 2022. “Multi-Mode Movement Decisions across Widely Ranging Behavioral
522 Processes.” *PLOS ONE* 17 (8): e0272538. <https://doi.org/10.1371/journal.pone.0272538>.

523 Richter, Laura, Niko Balkenhol, Christoph Raab, Horst Reinecke, Marcus Meißner, Sven
524 Herzog, Johannes Isselstein, and Johannes Signer. 2020. “So Close and yet so Different: The
525 Importance of Considering Temporal Dynamics to Understand Habitat Selection.” *Basic and
526 Applied Ecology* 43 (March): 99–109. <https://doi.org/10.1016/j.baae.2020.02.002>.

527 Roever, C. L., H. L. Beyer, M. J. Chase, and R. J. van Aarde. 2014. “The Pitfalls of Ignoring
528 Behaviour When Quantifying Habitat Selection.” *Diversity and Distributions* 20 (3): 322–33.
529 <https://doi.org/10.1111/ddi.12164>.

530 Signer, Johannes, John Fieberg, and Tal Avgar. 2019. “Animal Movement Tools (Amt): R
531 Package for Managing Tracking Data and Conducting Habitat Selection Analyses.” *Ecology
532 and Evolution* 9 (2): 880–90. <https://doi.org/10.1002/ece3.4823>.

533

534

535 **Figure**

536 **Figure 1.** Estimated coefficient of habitat selection (purple) according to the frequency of
537 change of the expected coefficient (yellow) and to the value of the model wigginess
538 parameter Q . The estimated coefficient is averaged on 100 simulations. Lighter ribbons show
539 standard deviation, and darker ribbons show 95% confidence intervals.

540 **Figure 2.** Comparison between time-varying HSA and conventional RSF. (a) Relationship
541 between the coefficients of habitat selection estimated from time-varying HSA and averaged
542 over the time-series, to the RSF coefficient. Each dot shows the coefficients estimated from
543 the trajectory of one individual simulated over 500 time steps. (b-c) Examples of the
544 distribution of the time-varying coefficients. The vertical line shows the average value of the
545 time-varying coefficients, whereas the point and range above the distribution shows the RSF
546 coefficient and its 95% confidence interval.

547 **Figure 3.** Estimations of short-term temporal variations of wildebeest's selection for open
548 habitats (a) and areas close to rivers (b). Positive coefficients indicate selection for open
549 habitats or areas far from rivers. Ribbons show 95% confidence interval. Note, however, that
550 location data used in this analysis were collected every 15-minutes, likely leading to
551 confidence intervals biased downward (i.e., too small) because of autocorrelation. The
552 selection coefficients are however unbiased. The night phases are shown by dark colors in the
553 background.

554 **Figure 4.** Estimations of long-term temporal variations of wildebeest's selection for open
555 habitats (a) and areas close to rivers (b). Positive coefficients indicate selection for open
556 habitats or areas far from rivers. Ribbons show 95% confidence interval. Data used in this
557 analysis were subsampled to one location per night and one location per day to avoid issues
558 with autocorrelation. Common definitions of wet (blue) and dry (red) seasons are shown in
559 the background in panels (c-d). Lines and ribbons are colored on a purple-to-yellow gradient,

560 with colors corresponding to segments of homogeneous habitat selection, as obtained with
561 the *segclust2d* approach.

562 **Figure 5.** Estimations of post-release variation of wildebeest's selection for open habitats,
563 areas close to rivers, longitude, and latitude. Positive coefficients indicate selection for open
564 habitats, areas far from rivers, or areas at greater longitude and latitude. Estimated
565 coefficients (line) and 95% confidence intervals (ribbons) are colored per individuals. Data
566 used in this analysis were subsampled to one location per night and one location per day to
567 reduce the autocorrelation between the used locations.
568

569 **Time-varying habitat selection analysis: A model and applications for studying diel,**
570 **seasonal, and post-release changes**

571 Romain Dejeante; Marion Valeix; Simon Chamaillé-Jammes

572 Journal name: Ecology

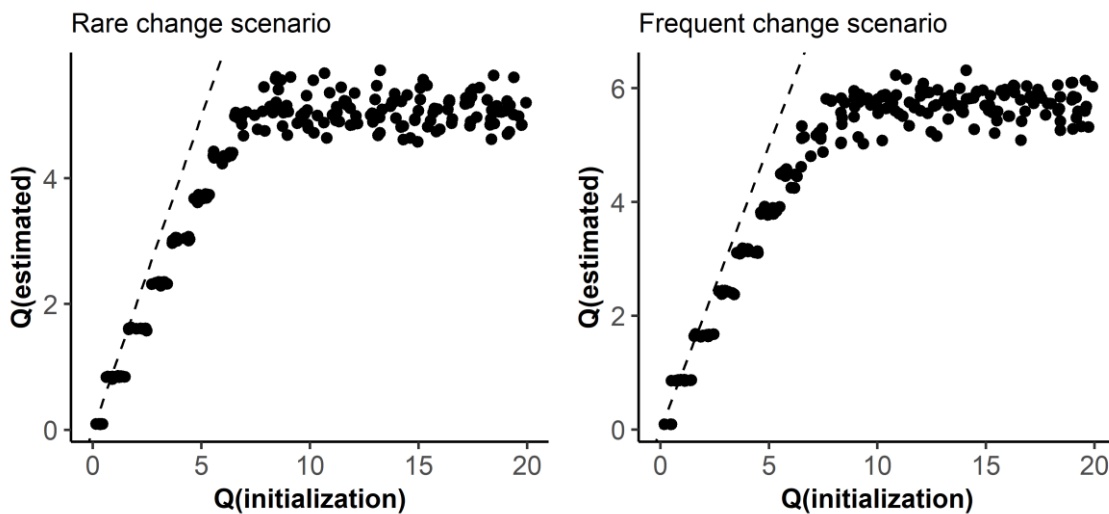
573 Manuscript type: Statistical report

574 **Appendix S1: Insights into Q , the wiggleness, and its initialization from computer**
575 **simulations**

576 S1.1. General guidelines to initialize the wiggleness parameter Q

577 First, our results show that the value of Q can be increased until the estimated value of Q at
578 the end of the fitting process converge towards a similar value (Appendix S1: Figure S1).
579 Hence, we encourage users of the model to test several values of Q until the estimated value
580 has converged.

581



582

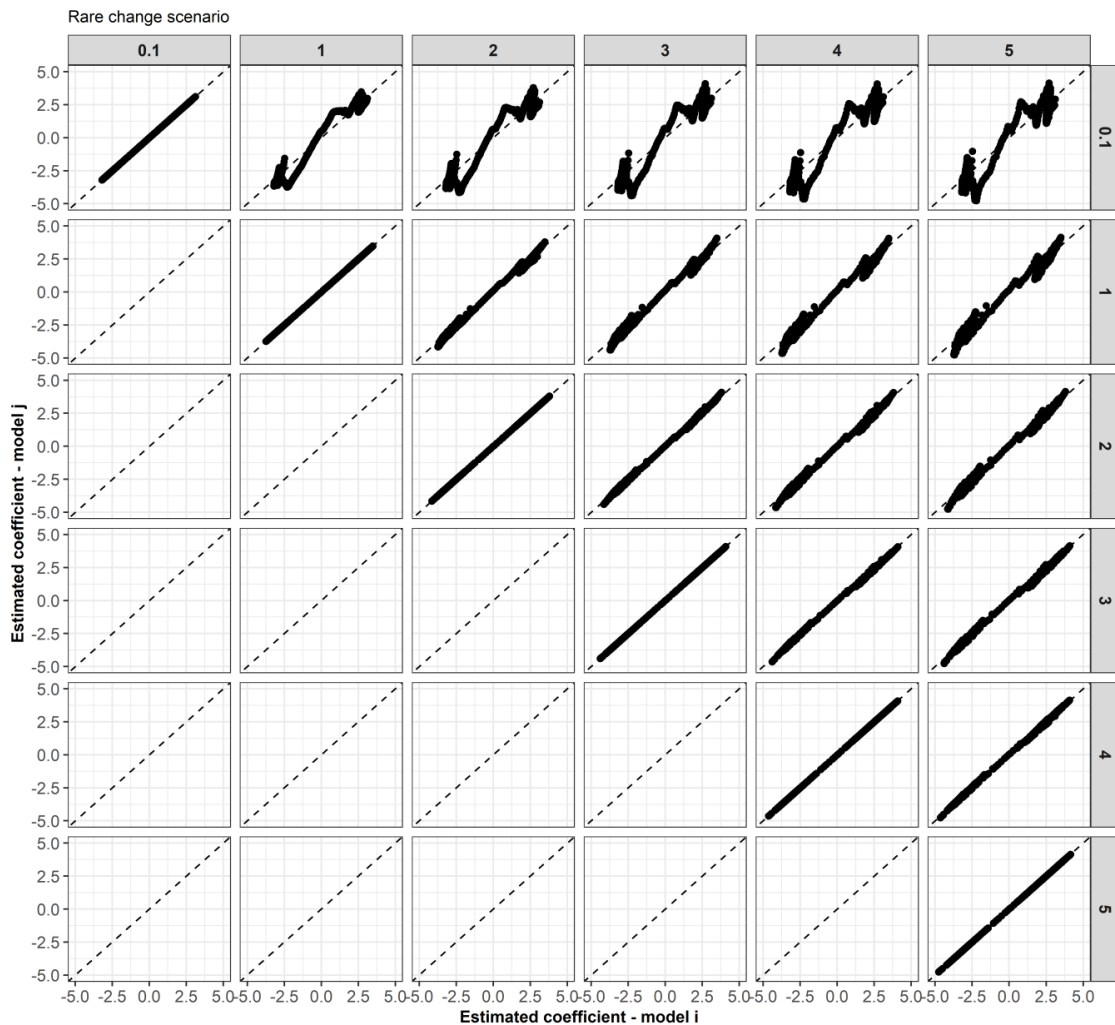
583 Figure S1. Influence of the initial value used to fill in the covariance matrix Q (initialization)
584 on the estimated value of the value of Q relevant for the variance of beta (here referred to as
585 $Q(\text{estimated})$). Each point is the result of one time-varying HSA fitted to one trajectory
586 simulated over 500 time steps.

587

588

589 Second, our results show that the value of Q can be increased until the estimated coefficients
590 of habitat selection converge towards a similar value (Appendix S1: Figure S2). Another way

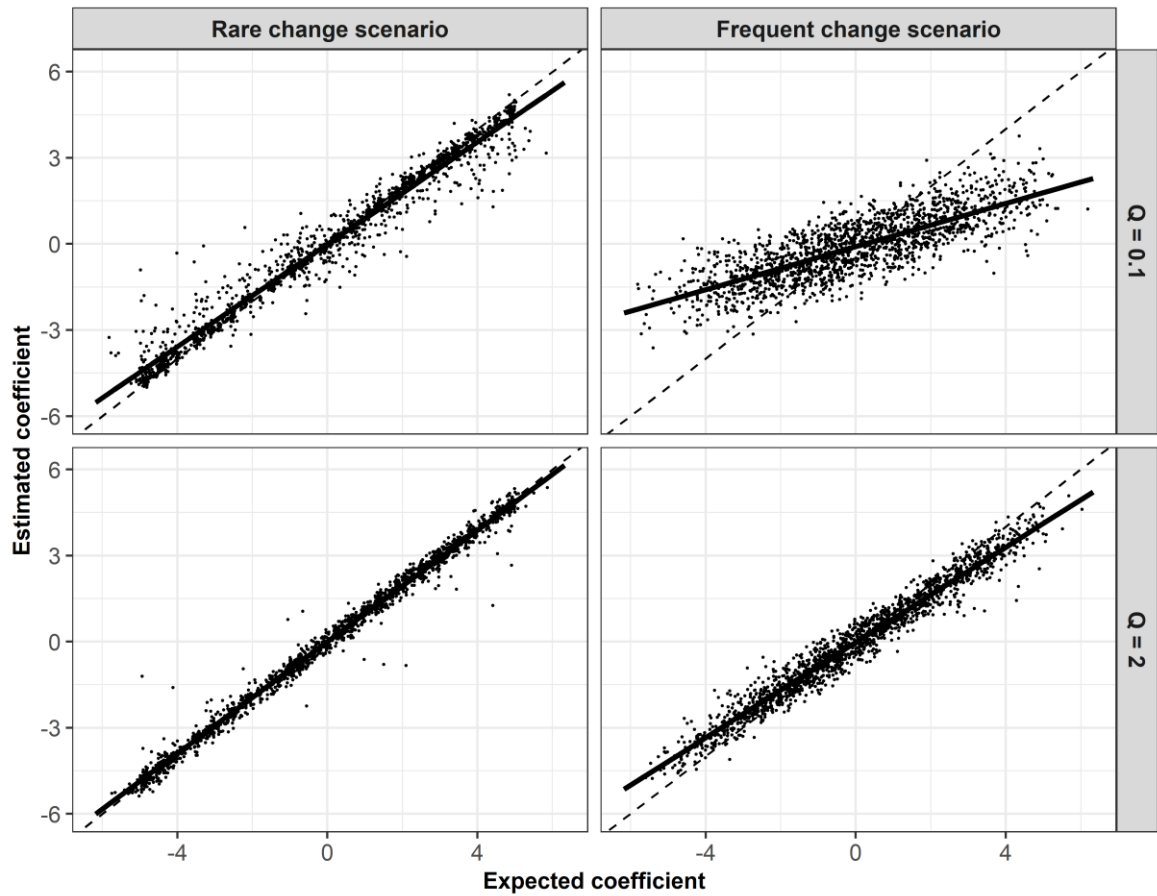
591 to select among several initial values of Q is therefore to look at the correlations between the
 592 time series of the estimated time-varying coefficients.



593
 594 Figure S2. Relationship between the coefficients of habitat selection estimated from models
 595 “i” and “j” implemented with different initial values used to fill in the covariance matrix (Q).
 596 These initial values are shown in the grey panels (0.1; 1; 2; 3; 4; 5). In this example, one
 597 should choose initial values of the covariance matrix larger than 1, since below 1 the
 598 estimated coefficients varied greatly from one model to another. When the estimated
 599 coefficients are greatly correlated together, the choice of the initial value to fill in Q is ‘good
 600 enough’ as it shows that the models have converged towards the same estimated coefficients.

601

602 S1.2. Evaluation of dynamic logistic models initialized with several values of Q



603

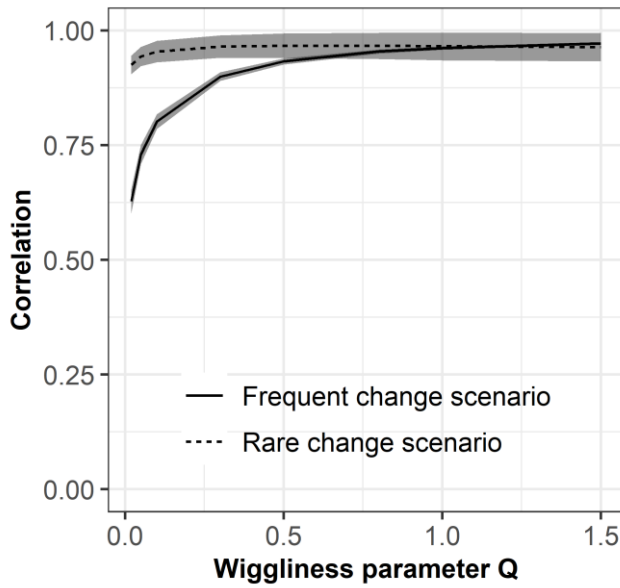
604 Figure S3. Comparison between the estimated and expected coefficients of habitat selection,

605 according to the value of the wiggleness parameter Q used in the dynamic logistic model.

606 High-wiggleness models performed better than low-wiggleness models to accurately estimate

607 time-varying coefficients of habitat selection, both when habitat selection changes rarely and

608 frequently over time.



609

610 Figure S4. Relationship between the value of the model wigginess parameter Q and the
 611 correlation between the expected time-varying selection strength and the average time-
 612 varying selection strength estimated on 100 replicates on 40 different landscapes, according
 613 to the frequency of change in habitat selection. Time-varying HSA was not sensitive to the
 614 choice of model wigginess to estimate rare changes of habitat selection. On the contrary,
 615 high-wigginess models performed better than low-wigginess models to estimate frequent
 616 changes of habitat selection.

617

618

619 **Time-varying habitat selection analysis: A model and applications for studying diel,**
620 **seasonal, and post-release changes**

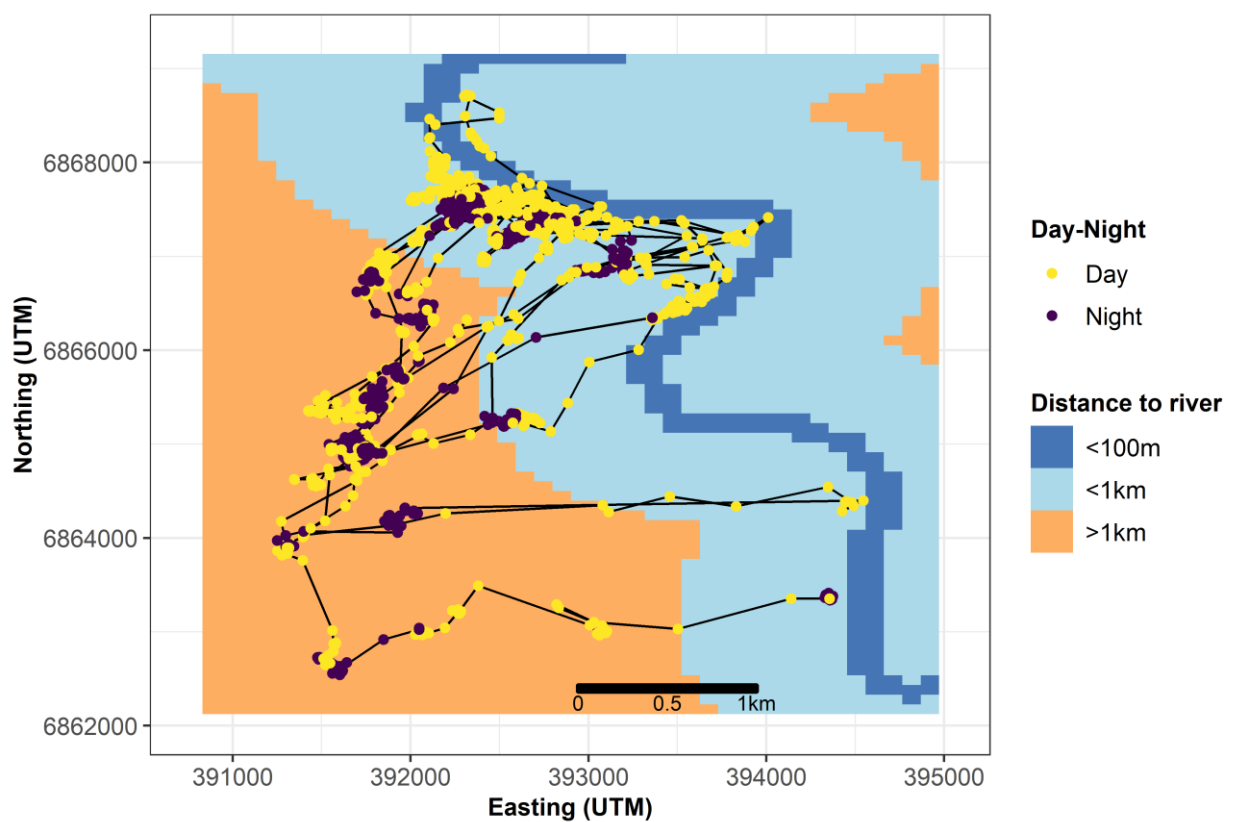
621 Romain Dejeante; Marion Valeix; Simon Chamaille-Jammes

622 Journal name: Ecology

623 Manuscript type: Statistical report

624 **Appendix S2: Applications of time-varying HSA on wildebeest examples**

625



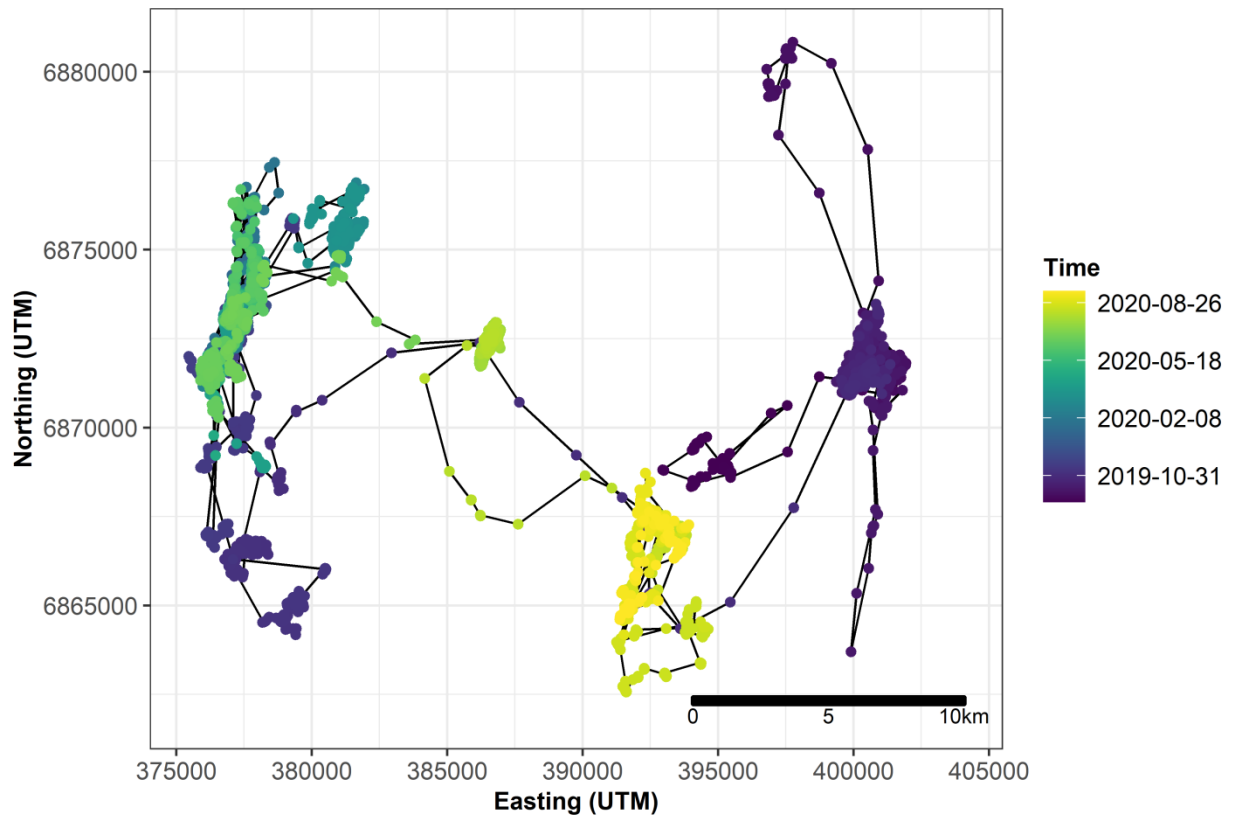
626

627 Figure S1. Illustration of the wildebeest's locations recorded during one month in the dry

628 season, at a fix rate of one location every 15 minutes. Background shows the distance to the

629 closest river. Locations collected during the night are colored in purple, whereas those

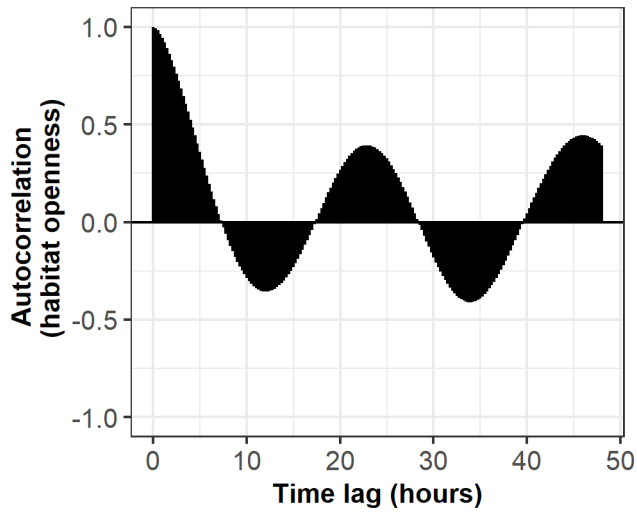
630 collected during the day are in yellow.



631

632 Figure S2. Illustration of the wildebeest's locations recorded during one year, at a fix rate of
633 one location every 15 minutes and subsampled to one location per hour. Locations are
634 colored based on their collection time.

635



636

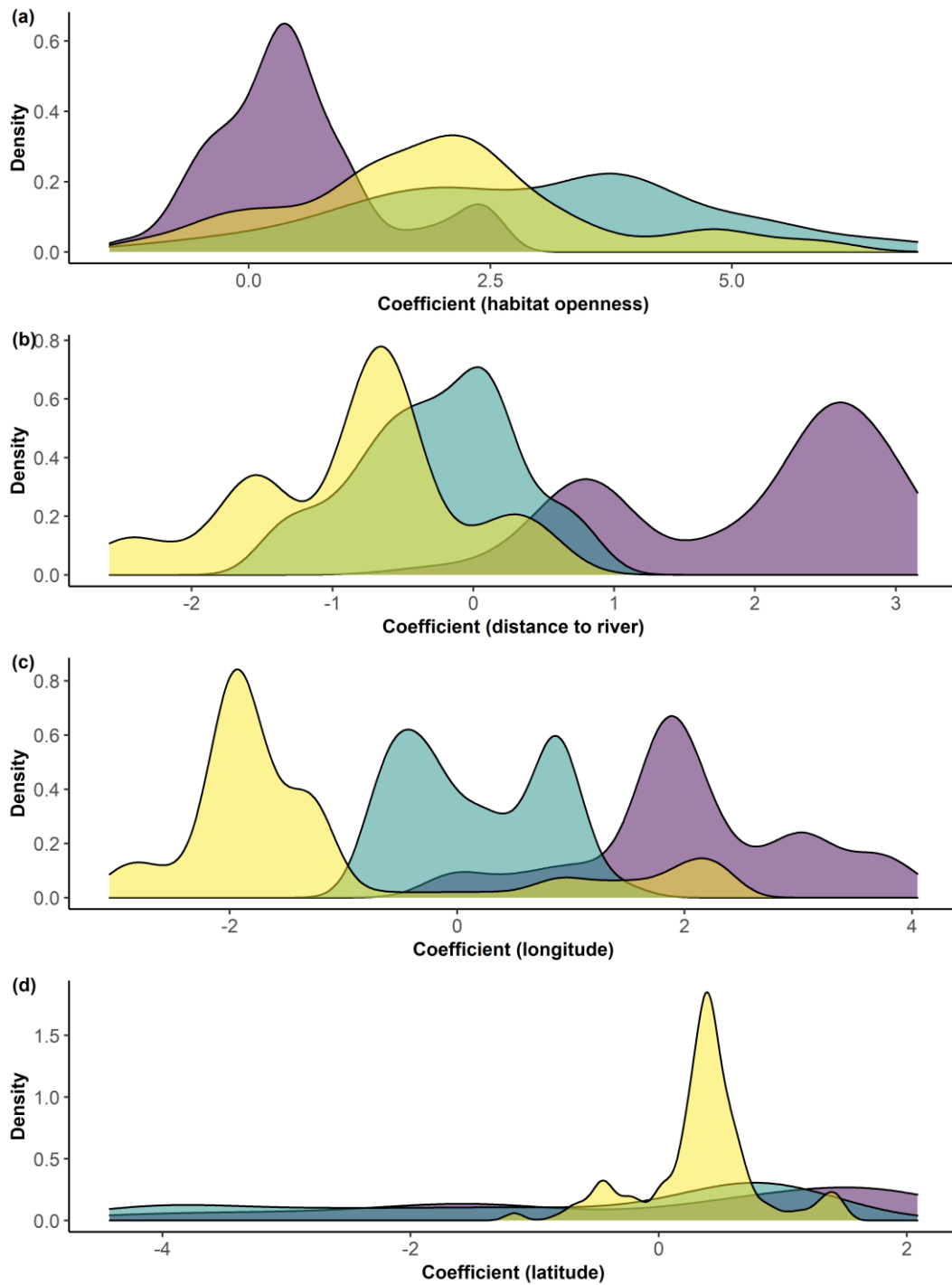
637 Figure S3. Temporal autocorrelation of the selection coefficient for open habitat $\beta(t)\beta(t +$

638 $lag)$. Values close to 1 (resp. -1) indicate high auto-correlation, with similar selection

639 strength (resp. opposite selection strengths), while values close to 0 indicate low auto-

640 correlation.

641



642

643 Figure S4. Distribution of the habitat selection coefficients for (a) habitat openness, (b)
 644 distance to the closest river, (c) longitude and (d) latitude. Each color shows the distribution
 645 of the selection coefficients for one individual.

646