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1 **Time-varying habitat selection analysis: a model and applications for studying diel,**
2 **seasonal and post-release changes**

3

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14 Code and Appendix S1 are available in the figshare digital repository:

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16 **Abstract**

17 Resource selection functions are commonly employed to evaluate animals' habitat selection, e.g.
18 the disproportionate use of habitats relative to their availability. While environmental conditions
19 or animal motivations may vary over time, sometimes in an unknown manner, studying changes
20 in habitat selection usually requires *a priori* time discretization. This limits our ability to
21 precisely answer the question 'when is an animal's habitat selection changing?'. Here, we
22 present a straightforward and flexible alternative approach based on fitting dynamic logistic
23 models to used/available data. First, using simulated dataset, we demonstrate that dynamic
24 logistic models performed well to recover temporal variations in habitat selection. We then show
25 real-world applications for studying diel, seasonal, and post-release changes in habitat selection
26 of blue wildebeest (*Connochaetes taurinus*). Finally, we provide the relevant R scripts to
27 facilitate the adoption of the method by ecologists. Dynamic logistic models allow to study
28 temporal changes in habitat selection in a framework consistent with resource selection
29 functions, but without the need to discretize time, which can be a difficult task when little is
30 known about the process studied, or may obscure inter-individual variability in timing of change.
31 These models should undoubtedly find their place in the movement ecology toolbox.

32

33 **Keywords:** habitat selection; migration; post-release; resource selection function; seasonality;
34 space use; temporal variation; time-varying effects

35 **1. Introduction**

36 Changes in environmental conditions consistently challenge animals in their lives, leading them
37 to regularly adjust their behavior. One of the important way animals do so is by using the
38 landscape they live in differently, i.e. by relocating themselves or selecting habitats differently.
39 This may be most clearly exemplified by migrations, which occur in response to seasonal
40 changes in weather and/or resource availability (Dingle 2014). Changes at smaller time-scales
41 also occur, such as when animals shift habitats in response to forage depletion or day/night
42 alternation in predation risk (Courbin et al. 2019). Naturally, discovering and understanding such
43 changes in space use and habitat selection is a key goal of ecologists.

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

56 Discretizing time to define biologically relevant periods over which to conduct HSA
57 may be difficult, and often involves somewhat arbitrary decisions with unknown consequences.

58 This is true for even apparently obvious periods like seasons (Basille et al. 2013) or day-night
59 periods (Richter et al. 2020). Starts and ends of seasons vary between years, and can only be
60 roughly defined without ancillary data. Some seasons like spring or fall are also clearly periods
61 of environmental changes during which patterns of habitat selection are unlikely to be constant.
62 Animal needs and motivations, and thus habitat selection (Roever et al. 2014) may also change at
63 unpredictable (for the researcher) times, such as when they disperse (Delgado et al. 2009). This
64 again makes discretization of time difficult, or even irrelevant if one is interested in the dynamics
65 of the change itself. This issue has been recognized before and various suggestions have been
66 offered, from using a combination of movement metrics and habitat use information to define
67 periods (but without estimating habitat selection) (Basille et al. 2013), to integrating time directly
68 into the RSF predictor (but with a constraint on the shape of the time-dependence) (Picardi et al.
69 2021) or using continuous-time movement models (but with a complex implementation) (Hooten
70 et al. 2014). Generally, we feel that ecologists are still lacking an easy and flexible tool to answer
71 the question ‘when is an animal’s habitat selection changing?’, learning from the data with no
72 assumption about when changes should happen.

73 Here, we present how dynamic logistic regression models allow one to easily estimate
74 the temporal dynamics of habitat selection without *a priori* discretization of time. Dynamic
75 logistic regression models are commonly used to analyze binary time series in survival analysis
76 (Martinussen and Scheike 2006), but can be applied to other data sources (Fahrmeir 1992). First,
77 we use simulated movement data to demonstrate that dynamic logistic regression models can
78 adequately recover time-varying habitat selection coefficients. We also highlight the influence of
79 parameters, whose values are under the researcher’s control, on the estimation process. Second,
80 we illustrate the usefulness of the approach by applying time-varying HSA on blue wildebeest

81 (*Connochaetes taurinus*) tracking data, showing how one can describe temporal variations of
82 animal habitat selection such as diel, seasonal and post-release changes. The relevant R scripts
83 are provided to facilitate the adoption of the method by ecologists.

84 **2. Methods**

85 **2.1. Dynamic logistic models for time-varying HSA**

86 2.1.1. General principles of dynamic logistic models

87 Here, we briefly describe the discrete-time state space model developed by Fahrmeir (1992) to
88 estimate time-varying coefficients from generalized linear models, and especially logistic
89 models. Generally, discrete-time state space models relate observations over time to hidden
90 parameters, with hidden parameters following a Markovian transition model (Auger-Méthé et al.
91 2021). Once applied to dynamic logistic regressions in the context of time-varying HSA, such
92 relationships can be simplified as (1) and (2):

$$93 \quad (1) \text{logit}(y_t) = \beta_{t,0} + \beta_{t,1}x_{t,1} + \dots + \beta_{t,n}x_{t,n}$$

$$94 \quad (2) \beta_t = T_t\beta_{t-1} + v_t$$

95 with y_t a binary response variable (i.e. used/available), $(\beta_{t,1}, \dots, \beta_{t,n})$ the hidden parameters (i.e.
96 time-varying selection coefficient), $(x_{t,1}, \dots, x_{t,n})$ the covariates (i.e. environmental layers), v_t
97 the error process with $v_t \sim N(0, Q_t)$, Q_t and T_t the covariance and transition matrices of the
98 Markov chain at time t . The transition matrix T_t is estimated by the model. The covariance
99 matrix Q_t is a diagonal matrix with initial values (at t_0) chosen by the researcher, and then
100 automatically updated over time during the fitting process. Hereafter, for simplicity, we call Q
101 the initial value used by the researcher to fill in the Q_t diagonal matrix, and as it can greatly
102 affect the wiggleness of the model (see Results), we also refer to Q as the wiggleness parameter.
103 Time-varying coefficients $(\beta_{t,1}, \dots, \beta_{t,n})$ are estimated by maximization of the posterior

104 densities, following a partial Bayesian approach. Basically, the generalized extended Kalman
105 filter and smoother algorithm described by Fahrmeir and Kaufmann (1991) recursively iterates
106 prediction, correction and smoothing steps to approximate posterior mode estimation in dynamic
107 generalized linear models.

108 2.1.2. Implementation in the context of HSA

109 To conduct time-varying HSA using dynamic logistic models, the following steps are required:
110 first, as in RSF analyses, a sample of locations that could be considered ‘available’ is drawn. This
111 can be, for instance, locations sampled randomly within the animal home range. Each used
112 location ($y_t = 1$) obtained at time t is paired with N random locations ($y_t = 0$). Each used and
113 available location is then characterized using environmental variables or any other variable of
114 interest ($x_{t,1}, \dots, x_{t,n}$). Finally, the time-varying parameters ($\beta_{t,1}, \dots, \beta_{t,n}$) are estimated by
115 fitting a dynamic logistic model, with type of location (used vs. available) as response variable
116 y_t and the covariate time series $x_{t,n}$ as predictors. Here, to fit the dynamic logistic model, we
117 used the “ddhazard” function from the *dynamichazard* R package by (Christoffersen 2021),
118 which implements the method described by (Fahrmeir 1992). We provide the R script needed to
119 run a time-varying HSA on a simulated trajectory (Appendix S1).

120 **2.2. Evaluation of the accuracy of dynamic logistic models for time-varying HSA**

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

125

126

127 2.2.1. Landscape and movement simulation

128 For simplicity, animal trajectories were simulated on one habitat layer (500×500 cells), with
129 values that did not vary over time. To mimic patchy landscapes, we used spatially correlated
130 Gaussian random fields, which attribute a continuous value ranging from 0 to 1 to each cell,
131 using the *localGibbs* R package (Michelot, Blackwell, and Matthiopoulos 2019). Following
132 Michelot, Blackwell, and Matthiopoulos (2019), we then simulated animal trajectories over 500
133 time steps using a local Gibbs movement model. For each time t , 1000 potential locations were
134 uniformly generated within a 100-pixel radius around the current location, and the location at
135 time $t+1$ was sampled among them with probabilities proportional to the strength of selection for
136 potential locations. This strength of selection was determined by the value of the habitat layer at
137 these locations, and by the model coefficient describing how the strength of selection changes
138 with values of the habitat variable. An important benefit of using a local Gibbs model is that the
139 coefficient of habitat selection used in the simulation model is theoretically equal to the one that
140 should be estimated by a RSF fitted on the data (Michelot, Blackwell, and Matthiopoulos 2019).

141 2.2.2. Scenarios of temporally-changing habitat selection

142 To be able to test whether changes in habitat selection strength could be robustly recovered by
143 dynamic logistic models, we built scenarios that differed in terms of how often the model's
144 coefficient of habitat selection changed over time. We did so by randomly sampling, in the $[-5, 5]$
145 range, and either every 20 steps (referred as "frequent change" scenario) or every 250 steps
146 (referred as "rare change" scenario), the model's habitat selection coefficient. To avoid having
147 sudden, step-like, changes in habitat selection, we then used spline regressions to smooth the
148 variations of habitat selection over time. For each scenario, we generated 100 trajectories per
149 simulated landscape, and replicated this on 100 different landscapes. We then tested our ability to

150 recover the temporal changes in the model's habitat selection coefficient by fitting a dynamic
151 logistic regression model to each trajectory as presented above, drawing 100 available locations,
152 at each time-step, within the 99% utilization distribution location-based kernel of each simulated
153 trajectory. We also assessed to what extent the model's estimation was affected by the value of
154 the wiggleness parameter Q . We did so by fitting, for each dataset of each scenario, a set of
155 models with different values of Q , ranging from 0.01 (i.e. low wiggleness) to 2 (i.e. high
156 wiggleness). For each value of Q , we then averaged the estimated coefficients over each set of
157 100 simulated trajectories per landscape, and fitted a linear regression with the mean estimated
158 coefficient as response and theoretical coefficients which were used in the simulations as
159 predictors, adding a random intercept with replication number. A slope near 1 would indicate that
160 a dynamic logistic model is able to estimate the temporal changes in the habitat selection
161 coefficient correctly, and an intercept near 0 would indicate that the estimations are not biased.

162 **2.3. Time-varying HSA: applications**

163 To illustrate some applications of time-varying HSA, we analyzed wildebeest movement datasets
164 collected in Hluhluwe-iMfolozi Park (South Africa). There, surface-water availability, which is
165 high during the wet season (October-March) as temporary waterholes are filled up by the rains,
166 becomes low in the dry season (April to September), with water remaining available only in a
167 few rivers. Since wildebeests are water-dependent grazers that preferentially forage in open
168 grasslands, we used the distance to the closest main river and the habitat openness as relevant
169 habitat variables to demonstrate the use of dynamic logistic models. For each study below, we
170 fitted the models with a high-value for Q ($Q=2$), as simulations showed that high wiggleness in
171 the estimates lead to better results (see Results section, or Appendix S2).

172

173 2.3.1. Short-term temporal variations: diel changes in habitat selection

174 We used tracking data collected on one wildebeest over one month in the dry season, at a fix rate
175 of one location every 15 minutes. Following the practical implementation of time-varying HSA
176 described above, we estimated the habitat selection of this wildebeest by (1) generating, for each
177 time t , 100 random locations within its home range, (2) extracting the environmental
178 characteristics of used and random locations, and (3) fitting a dynamic logistic regression to
179 compare the habitat openness and the distance to the closest main river between the used and
180 available locations over time. A preliminary visual inspection of the spatial data suggested that
181 day/night and longer, few-days, changes in locations occurred (Appendix S3: Figure S1). To
182 check whether these changes were associated with changes in habitat selection, we estimated the
183 temporal auto-correlation of the time-varying habitat selection coefficients.

184 2.3.2. Long-term temporal variations: seasonal changes in habitat selection

185 We used tracking data collected on one wildebeest over one year, at a fix rate of one location
186 every 15 minutes, and subsampled to one location per hour. A preliminary visual inspection of
187 the spatial data showed that the individual moved mostly westward and then eastward during the
188 period (Appendix S3: Figure S2). Hence, in addition to habitat openness and distance to the
189 closest river, we added longitude to the model's predictors. We generated 10 random locations,
190 per time t , within its home range to fit the time-varying HSA. To provide an example of how one
191 can subsequently delineate temporal periods that are homogeneous in terms of habitat selection,
192 we further segmented the time series of each model's coefficients, using the segmentation
193 method described by (Patin et al. 2020) and implemented in the *segclust2d* R package.

194

195

196 2.3.3. Event-based variations: post-release changes in habitat selection

197 We used the tracking data of three wildebeest simultaneously introduced in the park in October
198 2020. Data were collected over the 100 days following the release date, at a fix rate of one
199 location every hour. Similarly to previous applications, we estimated wildebeest's habitat
200 selection drawing 100 random locations, for each time t , within their individual home ranges. To
201 incorporate the dispersal of the released individuals into HSA, we added longitude and latitude to
202 model's predictors. Hence, we fitted a dynamic logistic model for each individual, using habitat
203 openness, distance to the closest river, longitude and latitude as predictors.

204 **3. Results**

205 **3.1. Theoretical evaluation**

206 In general, we found that dynamic logistic models allowed us to adequately recover the temporal
207 changes in the coefficients of habitat selection used in the simulations. When the true coefficients
208 did not change often ('rare change' scenarios), the wiggleness parameter had little impact and
209 estimations were always good (Fig. 1a-b; Appendix S2: Figure S1). When the true coefficients
210 did change often ('frequent change' scenarios), it became critical to use high values of the
211 wiggleness parameter to obtain estimates matching the theoretical coefficients (Fig. 1c-d;
212 Appendix S2: Figure S1). Importantly, the effect of the wiggleness parameter tend to stabilize at
213 large values of Q (Appendix S2: Figure S2), making it safe to use large values when
214 investigating large and frequent changes in habitat selection.

215 **3.2. Short-term temporal variations: diel changes in habitat selection**

216 A time-varying HSA conducted with a dynamic logistic model very clearly revealed that the
217 wildebeest's selection for open habitats and rivers varied greatly over the month of the study
218 (Fig. 2a-b). In particular, the wildebeest's selection for open habitats clearly changed across the

219 day/night cycle, as the auto-correlation period of the coefficient was approximately 24h
220 (Appendix S3: Figure S3). Open habitats were strongly selected during nighttime, but were not
221 selected, and sometimes even avoided, during daytime (Fig. 2a). We did not find such a pattern
222 for the selection of areas close to rivers (Fig. 2b), but there were variations over periods of 3 or 4
223 days. Contrary to the diel variations in the selection of open habitats, such variations would be
224 hard to detect using the common HSA approach based on time discretization.

225 **3.3. Long-term temporal variations: seasonal changes in habitat selection**

226 The time-varying HSA showed clear seasonal changes in the wildebeest' habitat selection, which
227 could then be separated in several periods according to the segmented time-series (Fig. 2c-d).
228 The existence and timing of some these periods were unpredictable *a priori*. For example, this
229 wildebeest maintained the same overall strength of selection for open habitats from November to
230 August, whereas this period covers months from both the dry and wet seasons (Fig. 2c). Also, we
231 note that during the dry season (April to June) this wildebeest did not preferentially use areas
232 close to rivers, but selected areas close to rivers consistently from July to mid-August (green
233 segment) and likely did back-and-forth trips to and away from the rivers from mid-August to
234 October (yellow segment) (Fig. 2d).

235 **3.4. Event-based variations: post-release changes in habitat selection**

236 After their release, the three wildebeest generally selected open habitats, but their level of
237 selection differed between individuals (Appendix S3: Figure S4), particularly towards the end of
238 the study period (Fig. 3a). Differences in the selection for areas close to rivers (Fig. 3b) or in the
239 longitude (Fig. 3c) and latitude (Fig. 3d) of the park also became apparent at the end of the first
240 month after release. Then, although the three wildebeest established in different areas (see
241 difference in selection for longitude and latitude), the selection of areas close to rivers remained

242 and was similar for two wildebeests (colored in green and yellow), whereas the third one avoided
243 the areas close to rivers (colored in purple).

244 **4. Discussion**

245 There is obvious evidence that animals' habitat selection changes regularly and at different time-
246 scales, from diel to seasonal shifts, or during key life-history events such as dispersal.

247 Unfortunately, ecologists have had limited and often unsatisfactory options to study these
248 changes. Most commonly, an *a priori* discretization of time periods of apparent biological
249 relevance is made, although this discretization can sometimes be difficult to justify, let alone to
250 validate. The alternative approach of simply integrating time as predictor in a RSF has
251 limitations (see discussion in Picardi et al. (2021)), and more statistically complex approaches
252 (Hooten et al. 2014) are unlikely to be broadly used. In this work, we propose a new approach
253 based on dynamic logistic models (Fahrmeir 1992) to easily estimate temporal changes in habitat
254 selection, in a framework consistent with RSF. We demonstrated, using simulations, its general
255 validity, while highlighting a point of attention (parameter Q). We also showcased its use for the
256 study of diel, seasonal and post-release changes in habitat selection. In addition, we provided the
257 necessary R scripts to make the use of time-varying HSA accessible to the ecologist community.

258 With this time-varying HSA approach, one can simultaneously estimate both the
259 timing and the amplitude of habitat selection changes. Estimation of the timing of change from
260 the data is what makes this approach novel and attractive. Many times, *a priori* discretization of
261 time is a guesstimate from expert knowledge or is based on ancillary data (e.g. climate data)
262 whose relevance for a particular dataset is not warranted. 'Letting the data speak' allows
263 revealing the actual pattern of change. This may be of particular importance, for instance, in the
264 study of inter-individual variability, as the timing of change can be one of the differencing

265 variables, as evidenced in our post-release study case. As recognized by Picardi et al. (2021),
266 time-varying HSA opens a new avenue to broaden the scope of the studies of inter-individual
267 differences in space use, which has so far focused on movement characteristics or habitat
268 selection strength. More generally, even when the relevance of an *a priori* discretization of time
269 is easier to ascertain, such as when comparing daytime to night-time habitat selection, time-
270 varying HSA allows one to immediately identify unusual periods (e.g. night of the 27th of
271 August, when the wildebeest did not increase its selection for open habitat). These unusual
272 periods may either be of interest (in such case, one would have to conduct one standard HSA per
273 night to have discovered this), or be ‘noise’ that should not affect the estimation of habitat
274 selection strength during more ‘usual’ periods (conversely to what occurs in a standard HSA).

275 Importantly, data-driven estimation of the timing of change in habitat selection makes
276 it possible to derive ‘segments’ of homogeneous habitat selection, and open the way to estimate
277 specific habitat selection ‘modes’ of animals defined by the strength of habitat selection. Until
278 now, behavioral modes in space use could be defined by movement characteristics such as speed
279 and turning angles (Patin et al. 2020; McClintock and Michelot 2018), but could not integrate
280 information about habitat selection, although it was likely to strongly contribute to define these
281 modes. The use of segmentation-clustering algorithm such as *segclust2d* or hidden-Markov
282 models on the time-series coefficients obtained by time-varying HSA will allow one to do this,
283 and to estimate the duration and frequencies of such modes. This could complement very recent
284 works developing behavioral-mode detection approaches based on step-selection functions
285 (Prima et al. 2022; Klappstein, Thomas, and Michelot 2022).

286 Results from the time-varying approach proposed here are to some extent sensitive to
287 the model’s wiggleness. In particular, but without surprise, model allowing for little wiggleness

288 (small values of Q) can provide a poor fit to the data when habitat selection often changes.
289 Models allowing for high wiggleness generally performed much better, especially if habitat
290 selection often changed. There was no obvious evidence of an optimum value of Q to look for, as
291 correlations plateaued when increasing Q values. Therefore, running a time-varying HSA with a
292 high value for Q appears a safe way to conduct robust analyses.

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

298

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306

307 **Conflict of interest statement**

308 The authors declare no competing interests.

309

310

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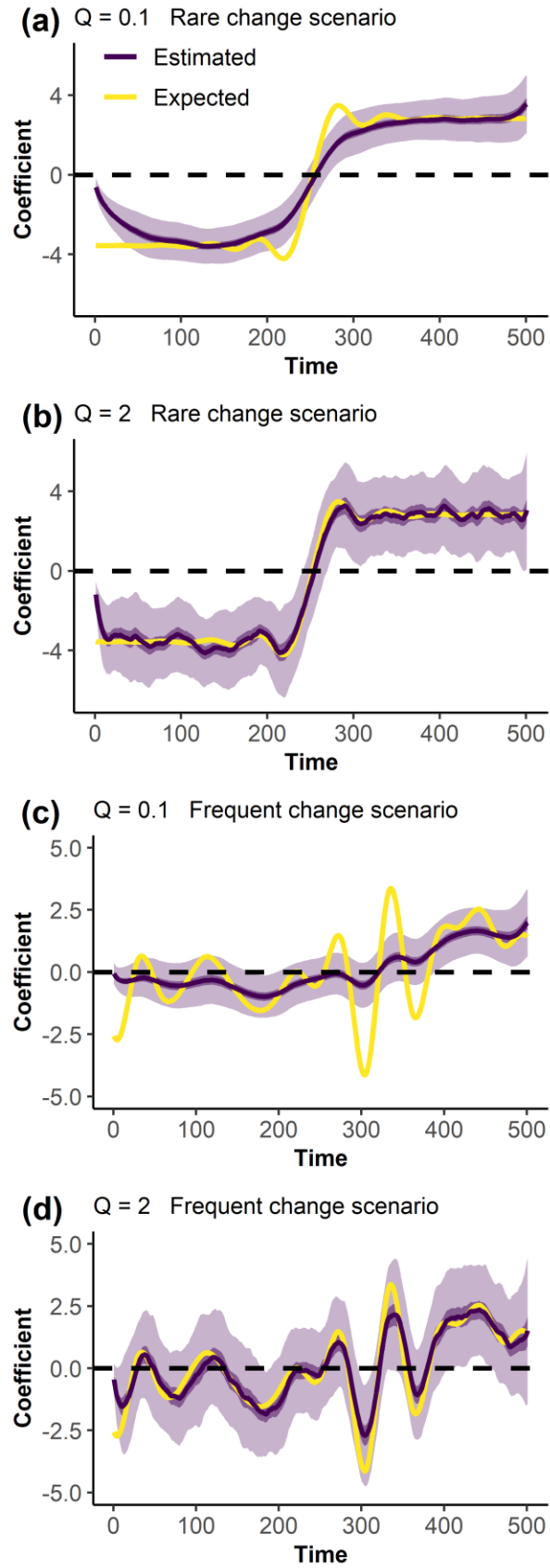
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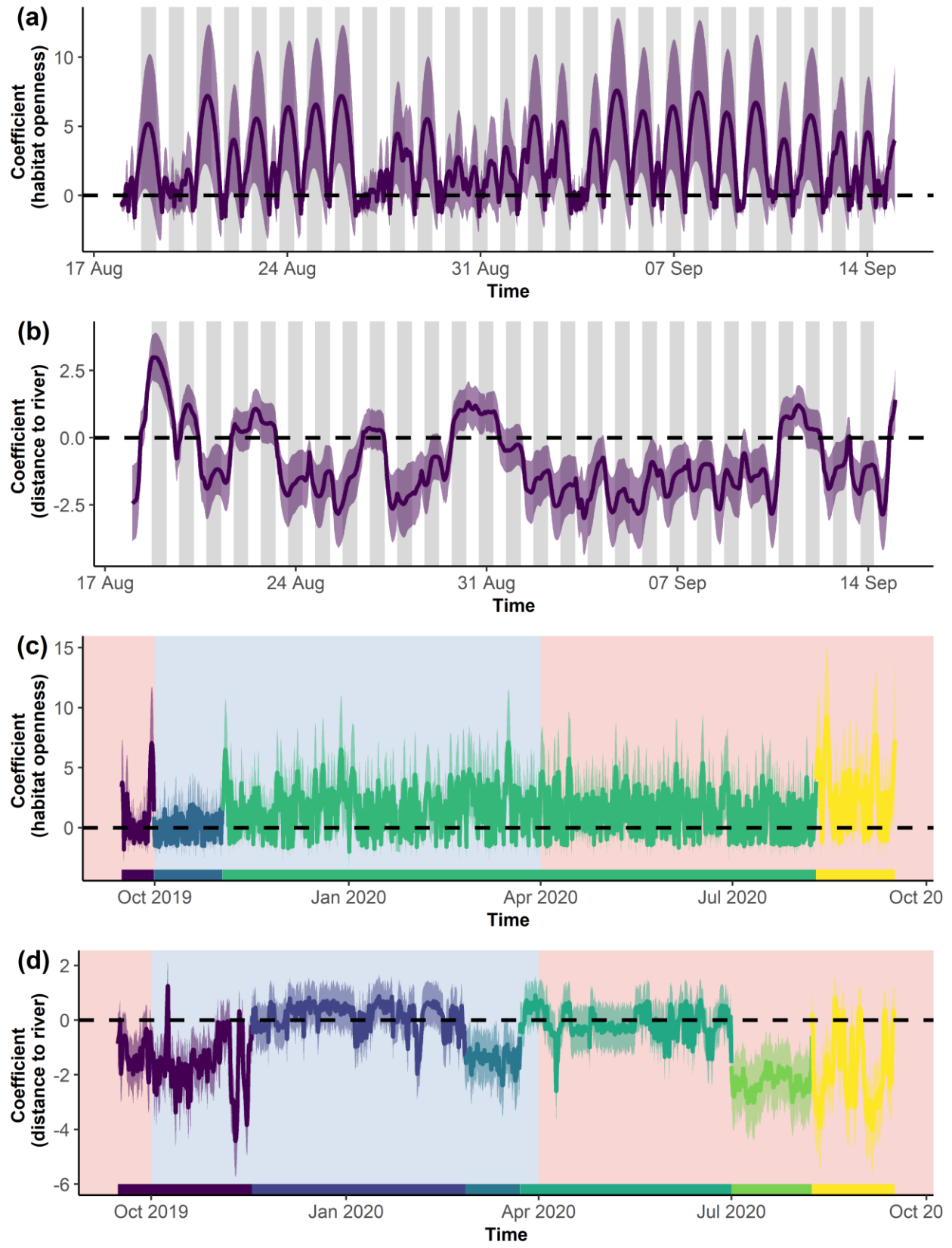
378 **Figure**

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

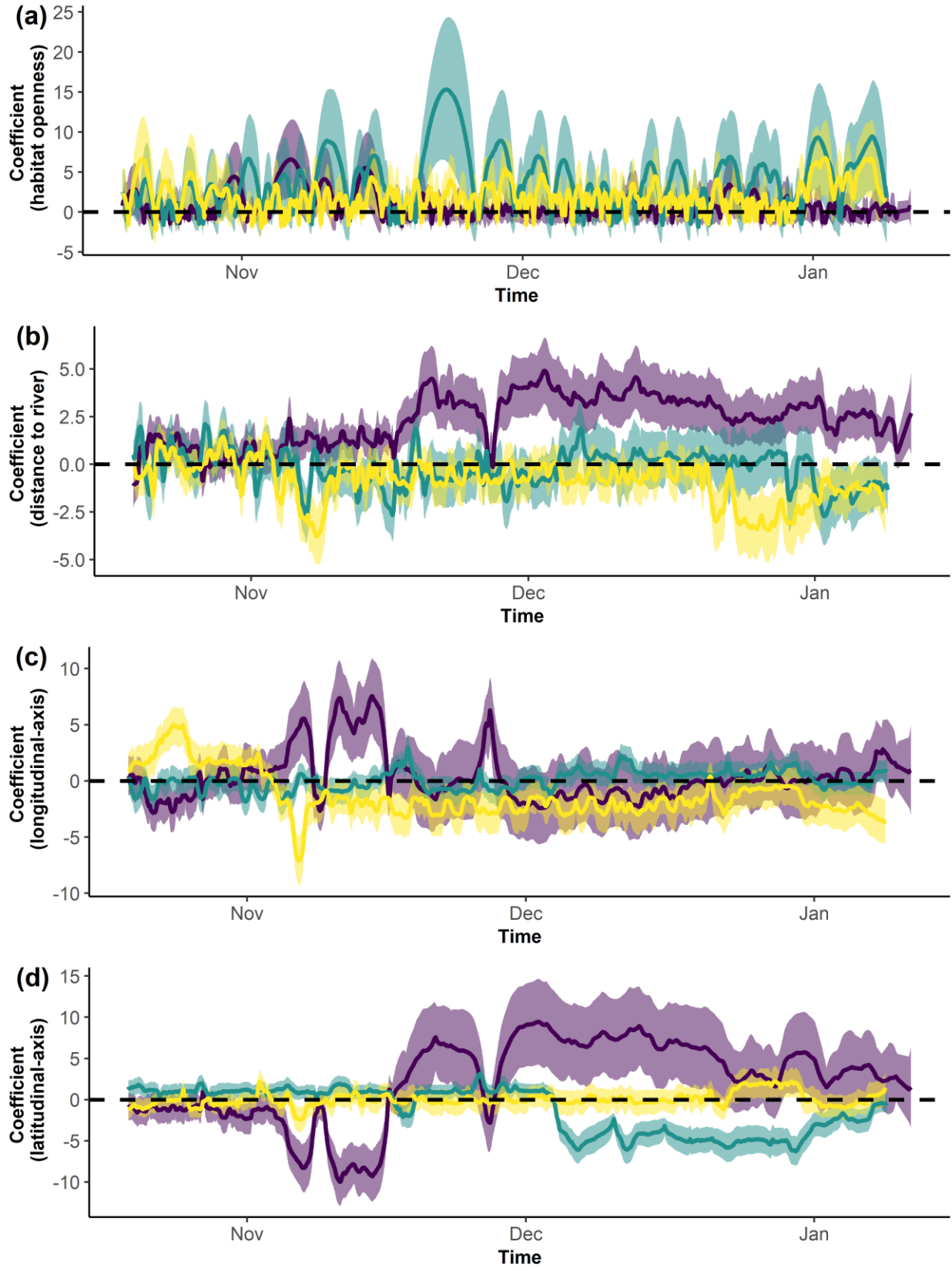
383 **Figure 2.** Estimations of short (a-b) and long-term (c-d) temporal variations of wildebeest's
384 selection for open habitats and areas close to rivers. Positive coefficients indicate selection for
385 open habitats or areas far from rivers. Ribbons show 95% confidence interval. The night phases
386 are shown by dark colors in panel (a-b). Common definitions of wet (blue) and dry (red) seasons
387 are shown in background in panel (c-d), whereas segments of homogeneous habitat selection are
388 colored on a purple-to-yellow gradient.

389 **Figure 3.** Estimations of post-release variation of wildebeest's selection for open habitats, areas
390 close to rivers, longitude and latitude. Positive coefficients indicate selection for open habitats,
391 areas far from rivers, or areas at greater longitude and latitude. Estimated coefficients (line) and
392 95% confidence intervals (ribbons) are colored per individuals.





394
395 Figure 2



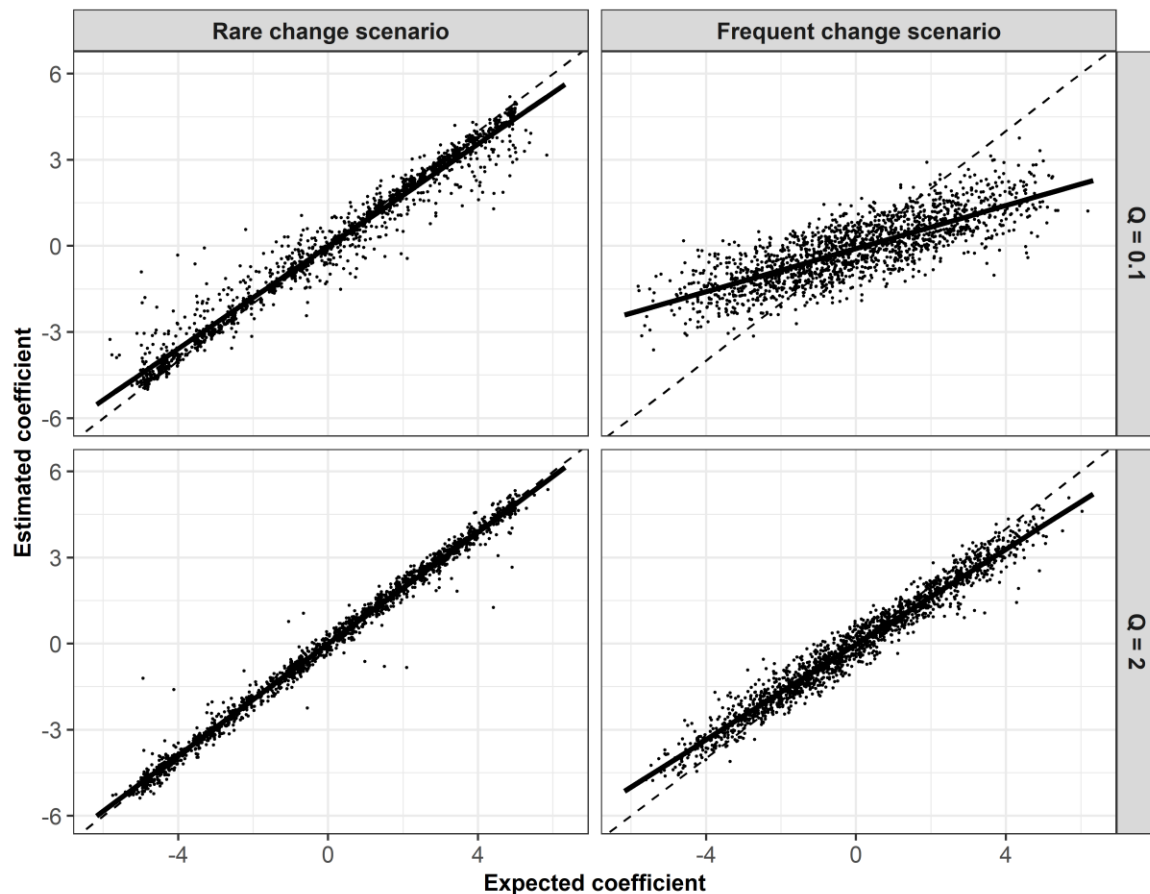
396
397 Figure 3

398 **Supplementary information**

399 **Appendix S1**

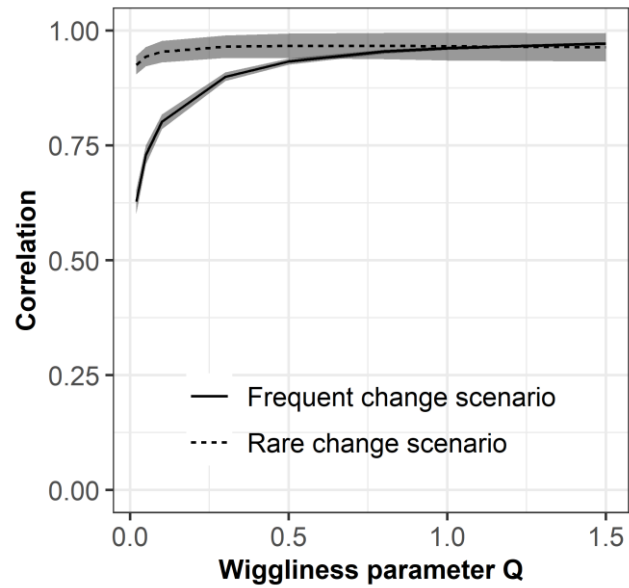
400 Available in the figshare digital repository: <https://doi.org/10.6084/m9.figshare.c.6365415.v3>

401 **Appendix S2: Computer simulations to evaluate time-varying HSA**



402

403 **Figure S1.** Comparison between the estimated and expected coefficients of habitat selection,
404 according to the value of the wigginess parameter Q used in the dynamic logistic model. High-
405 wigginess models performed better than low-wigginess models to accurately estimate time-
406 varying coefficients of habitat selection, both when habitat selection changes rarely and
407 frequently over time.

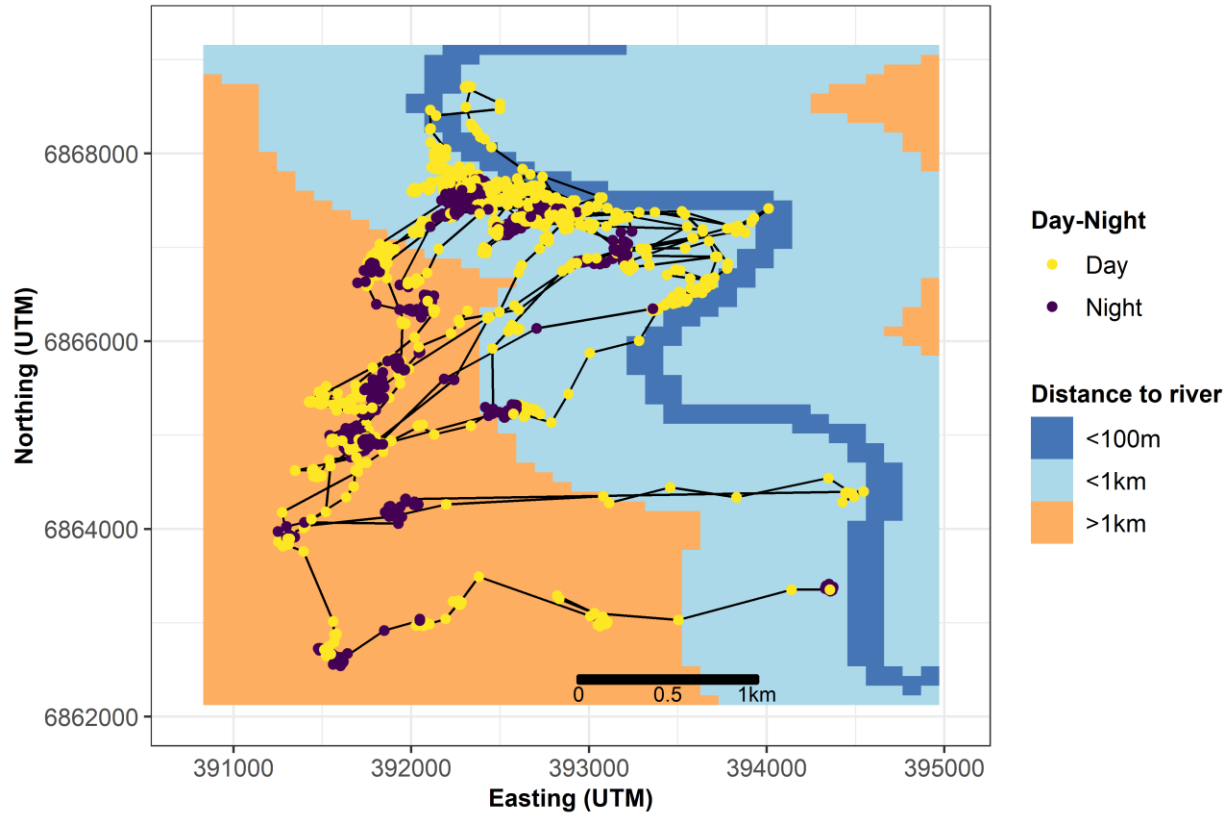


408

409 **Figure S2.** Relationship between the value of the model wigginess parameter Q and the
410 correlation between (1) the expected time-varying selection strength and (2) the average time-
411 varying selection strength estimated on 100 replicates on 40 different landscapes, according to
412 the frequency of change in habitat selection. Time-varying HSA was not sensitive to the choice
413 of model wigginess to estimate rare changes of habitat selection. On the contrary, high-
414 wigginess models performed better than low-wigginess models to estimate frequent changes of
415 habitat selection.

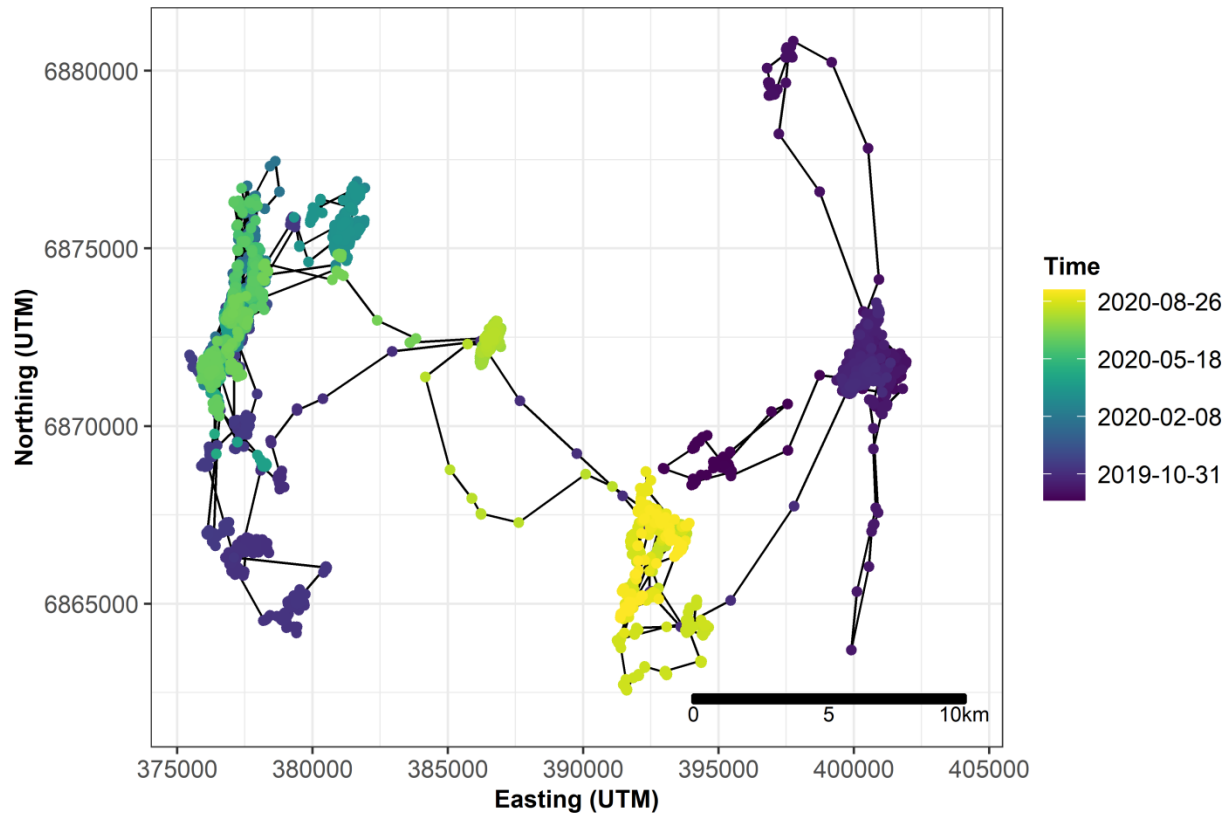
416 **Appendix S3: Applications of time-varying HSA on wildebeest examples**

417



418

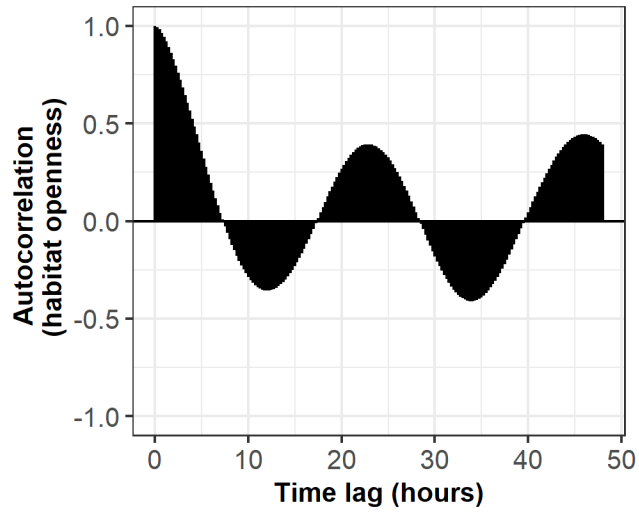
419 **Figure S1.** Illustration of the wildebeest's locations recorded during one month in the dry season,
420 at a fix rate of one location every 15 minutes. Background shows the distance to the closest river.
421 Locations collected during the night are colored in purple, whereas those collected during the
422 day are in yellow.



423

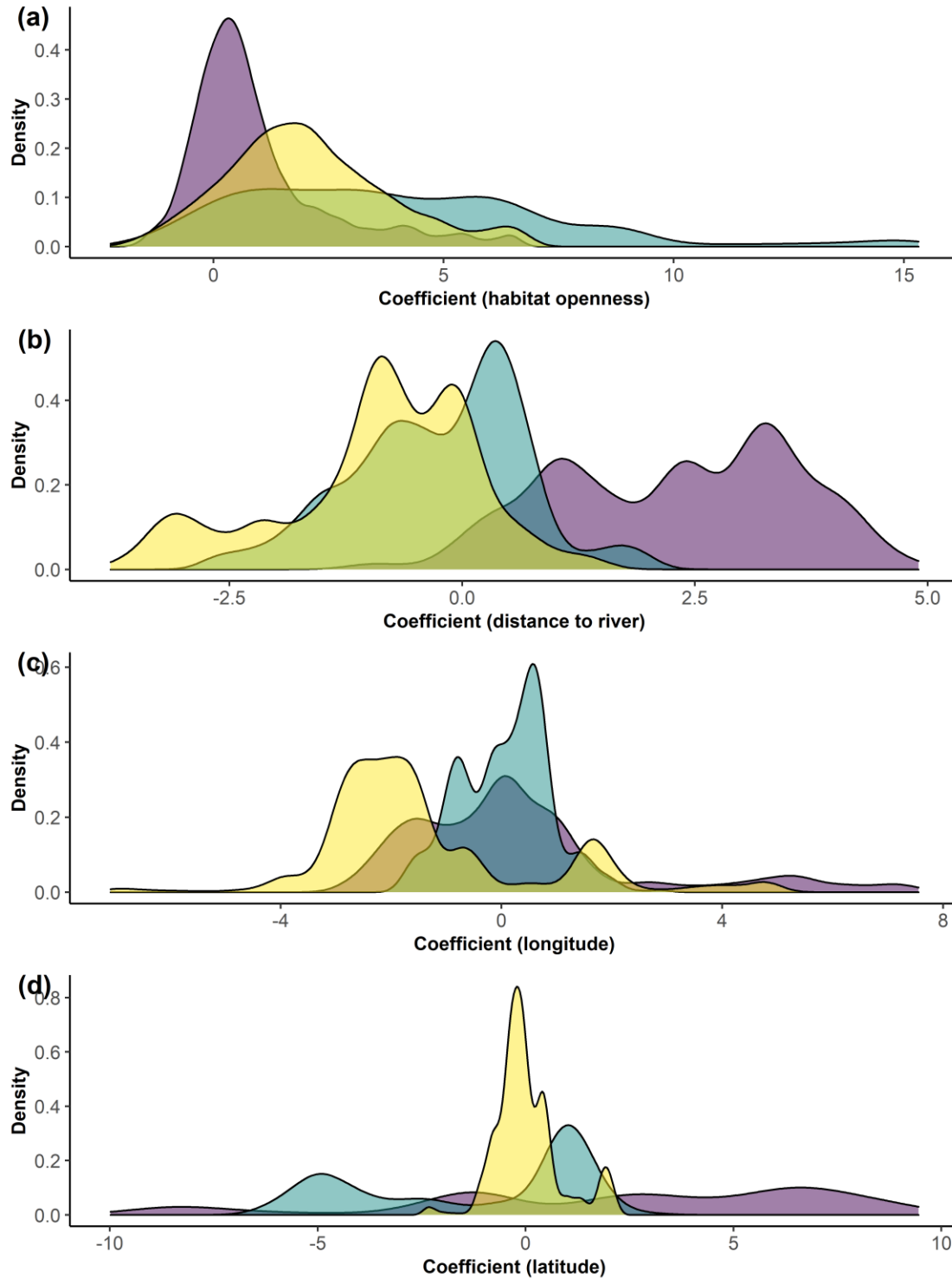
424 **Figure S2.** Illustration of the wildebeest's locations recorded during one year, at a fix rate of one
425 location every 15 minutes and subsampled to one location per hour. Locations are colored based
426 on their collection time.

427



428

429 **Figure S3.** Temporal autocorrelation of the selection coefficient for open habitat $\beta(t)\beta(t +$
430 $lag)$. Values close to 1 (resp. -1) indicate high auto-correlation, with similar selection strength
431 (resp. opposite selection strengths), while values close to 0 indicate low auto-correlation.



432

433 **Figure S4.** Distribution of the habitat selection coefficients for (a) habitat openness, (b) distance

434 to the closest river, (c) longitude and (d) latitude. Each color shows the distribution of the

435 selection coefficients for one individual.