

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

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Abstract

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

KEYWORDS

habitat selection, migration, post-release, resource selection function, seasonality, space use, temporal variation, time-varying effects

INTRODUCTION

Changes in environmental conditions consistently challenge animals in their lives, leading them to adjust their behavior regularly. One of the important ways

animals do so is using the landscape they live in differently, that is, by relocating themselves or selecting habitats differently. This is most clearly exemplified by migrations, which occur in response to seasonal changes in weather and/or resource availability (Dingle, 2014).

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

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

Segmenting time to define biologically relevant periods over which to conduct HSA may be difficult, and often involves somewhat arbitrary decisions with unknown consequences. This is true even for well studied periods like seasons (Basille et al., 2013) or day–night periods (Richter et al., 2020). Starts and ends of seasons vary between years, and can only be roughly defined without ancillary data. Some seasons like spring or fall are also clearly periods of environmental changes during which patterns of habitat selection are unlikely to be constant. Animal needs and motivations, and thus habitat selection (Roever et al., 2014) may also change at unpredictable (for the researcher) times, such as when they disperse (Delgado et al., 2009). This again makes segmentation of time into distinct periods difficult or even irrelevant if one is interested in the dynamics of the change itself. This issue has been recognized before and various suggestions have been offered, from using a combination of movement metrics and habitat use information to define periods (but without estimating habitat selection) (Basille et al., 2013), to integrating time as one of the predictors in habitat selection models (but with a constraint on the shape of the time dependence) (Picardi et al., 2021), or using continuous-time movement models (but with a complex implementation) (Hooten et al., 2014). There is currently no simple yet flexible approach

to describe the temporal dynamics of habitat selection that underlie the long-term, averaged, pattern revealed by RSF analyses.

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

Here, we present how dynamic logistic regression models allow one to easily estimate the temporal dynamics of habitat selection that underlie the long-term, averaged, pattern revealed by RSF analyses, without *a priori* segmentation of time into distinct periods. Dynamic logistic regression models are commonly used to analyze binary time series in survival analysis (Martinussen & Scheike, 2006), but can be applied to other data sources (Fahrmeir, 1992). First, we use simulated movement data to demonstrate that dynamic logistic regression models can adequately recover time-varying habitat selection coefficients. We also highlight the influence of parameters, whose values are under the researcher's control, on the estimation process. Second, we illustrate the usefulness of the approach by applying time-varying HSA on blue wildebeest (*Connochaetes taurinus*) tracking data, showing how one can describe temporal variations of animal habitat selection such as diel, seasonal, and post-release changes. The relevant R scripts are provided to facilitate the adoption of the method by ecologists.

METHODS

Dynamic logistic models for time-varying HSA

General principles of dynamic logistic models

Here, we briefly describe the discrete time state space model developed by Fahrmeir (1992) to estimate time-varying coefficients from generalized linear models,

especially logistic models. Generally, discrete time state space models relate observations over time to hidden parameters, with hidden parameters following a Markovian transition model (Auger-Méthé et al., 2021). Applied to dynamic logistic regressions in the context of time-varying HSA, such a model can be formulated using the following equations:

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

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

with $p_t = Pr(y_t = 1)$ the probability of the binary response variable y_t being one (i.e., used versus available), $(\beta_{t,0}, \dots, \beta_{t,n})$ the hidden parameter vectors (i.e., time-varying selection coefficients), $(x_{t,1}, \dots, x_{t,n})$ the covariates (i.e., environmental layers), v_t the error process (i.e., sequence of independent random variables), \mathbf{Q} the covariance matrix of the Markov chain that contains values that will affect the smoothness of the estimated time series of habitat selection coefficients. Here, following Fahrmeir (1992) and Christoffersen (2021, 2022), we used a simple first-order random walk model for the state equation (Equation 2). See Christoffersen (2021) for details on second-order random walk model formulation. The covariance matrix \mathbf{Q} is a symmetric matrix of $n + 1$ dimension, with initial values chosen by the experimenter (see the [Implementation in the context of HSA](#) section to determine initial values) and then estimated during the fitting process (see below).

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

Implementation in the context of HSA

The following steps are required to conduct time-varying HSA using dynamic logistic models. First, as in RSF analyses, a sample of locations that could be considered “available” is drawn. This can be, for instance, locations sampled randomly within the animal home range. Each used location ($y_t = 1$) obtained at time t is paired with N random locations ($y_t = 0$). Each used and available

location is then characterized using environmental variables or any other variable of interest $(x_{t,1}, \dots, x_{t,n})$. Finally, the time-varying parameters $(\beta_{t,1}, \dots, \beta_{t,n})$ are estimated by fitting a dynamic logistic model, with the type of location (used vs. available) as the response variable y_t and the time series $x_{t,n}$ as predictors (cf. Equation 1).

Note that caution is required when estimating time-varying habitat selection coefficients from location data collected at relatively high frequency. Classical RSF and the model presented here do not account for temporal autocorrelation in location data. In particular, it is assumed that, within the time interval between two locations, the animal could relocate anywhere in the area in which random locations are drawn. When this is not the case, estimates of habitat selection coefficients are unbiased but their standard errors are biased downward; that is, they are too small. In this situation, one may either subsample data to a lower frequency to obtain a valid statistical inference, or remain within the framework of a descriptive analysis aiming at exploring data, for instance for gaining insights on the possible existence of frequent habitat selection changes.

Here we fitted the dynamic logistic model using the “ddhazard” function from the *dynamichazard* R package by Christoffersen (2021), which implements the method described by Fahrmeir (1992). In Dejeante et al. (2023a), we provide the script needed to run a time-varying HSA on a simulated trajectory; the model fitting takes ~3 s on this dataset, on a PC with an Intel(R) Xeon(R) CPU E5-1650 0 @ 3.20GHz.

General guidelines to initialize the wiggleness parameter (Q)

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

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

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

Landscape and movement simulation

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

Scenarios of temporally changing habitat selection

To test whether changes in habitat selection strength could be robustly recovered by dynamic logistic models, we built scenarios that differed in terms of how often the model's coefficient of habitat selection changed over time. We did so by random sampling, in the $[-5, 5]$

range, and either changing every 20 steps (referred to as the “frequent change” scenario) or every 250 steps (referred to as the “rare change” scenario) the model's habitat selection coefficient. To avoid having sudden, step-like, changes in habitat selection, we then used spline regressions to smooth the variations of habitat selection over time. For each scenario, we generated 100 trajectories per simulated landscape, and replicated this on 100 different landscapes. We then tested our ability to recover the temporal changes in the model's habitat selection coefficient by fitting a dynamic logistic regression model to each trajectory as presented above, drawing 100 available locations at each time step within the 99% utilization distribution location-based kernel of each simulated trajectory. We also assessed to what extent the model's estimation was affected by the value of the wiggleness parameter Q . We did so by fitting, for each dataset of each scenario, a set of models with different values of Q , ranging from 0.01 (i.e., low wiggleness) to 2 (i.e., high wiggleness). For each value of Q , we then averaged the estimated coefficients over each set of 100 simulated trajectories per landscape, and fitted a linear regression with the mean estimated coefficient as response and theoretical coefficients, which were used in the simulations, as predictors, adding a random intercept with replication number. A slope near 1 would indicate that a dynamic logistic model is able to estimate the temporal changes in the habitat selection coefficient correctly, and an intercept near 0 would indicate that the estimations are not biased.

In addition, to demonstrate that the time-varying HSA approach reveals the temporal dynamics of the selection process that is commonly studied using RSF analyses, we averaged the time-varying coefficients estimated from 5000 trajectories (of 500 time steps each) covering a broad range of selection patterns and landscape composition, and compare these values with the coefficients estimated by a conventional RSF analysis on the same trajectories.

Time-varying HSA: Applications

To illustrate some applications of time-varying HSA, we analyzed wildebeest movement datasets collected in Hluhluwe-iMfolozi Park (South Africa). There, surface-water availability, which is high during the wet season (October to March) as temporary waterholes are filled up by the rains, becomes low in the dry season (April to September), with water remaining available only in a few rivers. Because wildebeests are water-dependent grazers that preferentially forage in open grasslands, we used the distance to the closest main

river and the habitat openness as relevant habitat variables to demonstrate the use of dynamic logistic models. For each study below, we fitted the models with a relatively high value for Q ($Q = 2$), as simulations showed that high wiggleness in the estimates led to better results (see *Results* section). We used the *amt* R package to generate random points and extract the values of predictors at used and available locations (Signer et al., 2019).

Short-term temporal variations: Diel changes in habitat selection

We used tracking data collected on one wildebeest over 1 month in the dry season, at a fixed rate of one location every 15 min. In the context of the model presented here, such data are highly autocorrelated and estimated standard errors and confidence intervals are likely to be biased downward. Interpretation of results should therefore be done with caution. Habitat selection coefficients remain however estimated without bias, and we included the analysis here to show how it allows exploring changes in habitat selection at short time scales. Other analyses, more statistically robust, are presented below.

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

Long-term temporal variations: Seasonal changes in habitat selection

We used tracking data collected on one wildebeest over 1 year at a fixed rate of one location every 15 min. To avoid issues related to the temporal autocorrelation in location data, and because the temporal scale of the analysis does not require locations to be collected at such a high frequency, we subsampled our dataset to one location per day and one location per night. A preliminary visual inspection of the spatial data showed that the individual moved mostly westward and then eastward during

the period (Appendix S2: Figure S2). Hence, in addition to habitat openness and distance to the closest river, we added longitude to the model's predictors. We generated 10 random locations per time t within its home range to fit the time-varying HSA. To provide an example of how one can subsequently delineate temporal periods that are homogeneous in terms of habitat selection, we further segmented the time series of each model's coefficients separately, using the segmentation method described, and implemented in the *segclust2d* R package, by Patin et al. (2020).

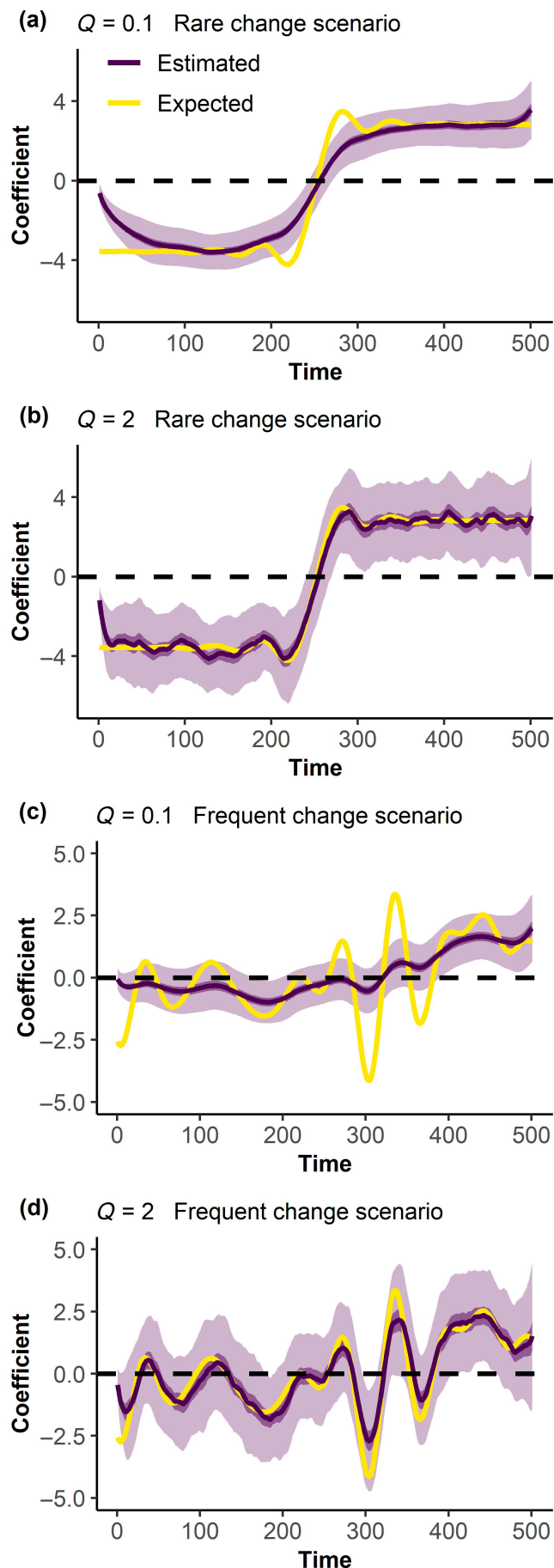
Event-based variations: Post-release changes in habitat selection

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

RESULTS

Theoretical evaluation

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



The average of the time-varying coefficients was nearly equal to the coefficient estimated by a conventional RSF (Figure 2a), demonstrating that the time-varying HSA approach addresses the same selection process as the one studied by conventional RSF analyses, while providing more information as it describes the temporal dynamics of selection. Also, it can reveal whether the coefficients of an RSF are biologically relevant (when time-varying selection coefficients have uni-modal distributions; Figure 2b) or not (when time-varying selection coefficients have multimodal distribution; Figure 2c), and RSF coefficients represent a statistical average that never represents the true selection process.

Short-term temporal variations: Diel changes in habitat selection

A time-varying HSA conducted with a dynamic logistic model suggested that the wildebeest's selection for open habitats and rivers varied greatly over the 1 month of the study (Figure 3). In particular, the wildebeest's selection for open habitats apparently changed across the day/night cycle, as the autocorrelation period of the coefficient was approximately 24 h (Appendix S2: Figure S3). Open habitats seemed to be strongly selected during night-time, but not selected, and sometimes even avoided, during daytime (Figure 3a). Such day/night shifts were not noticeable for the selection of areas close to rivers (Figure 3b), but there seemed to be variations over periods of 3 or 4 days. Contrary to the diel variations in the selection of open habitats, such variations would be hard to detect using the common HSA approach based on a segmentation of time into distinct periods.

Long-term temporal variations: Seasonal changes in habitat selection

The time-varying HSA showed clear seasonal changes in the wildebeest's habitat selection, which could then be separated into several periods according to the segmented time series (Figure 4). The existence and timing of some of these periods were unpredictable *a priori*. For example,

FIGURE 1 (a–d) Estimated coefficient of habitat selection (purple) according to the frequency of change of the expected coefficient (yellow) and to the value of the model wiggleness parameter Q . The estimated coefficient is averaged on 100 simulations. Lighter ribbons show standard deviation, and darker ribbons show 95% confidence intervals.

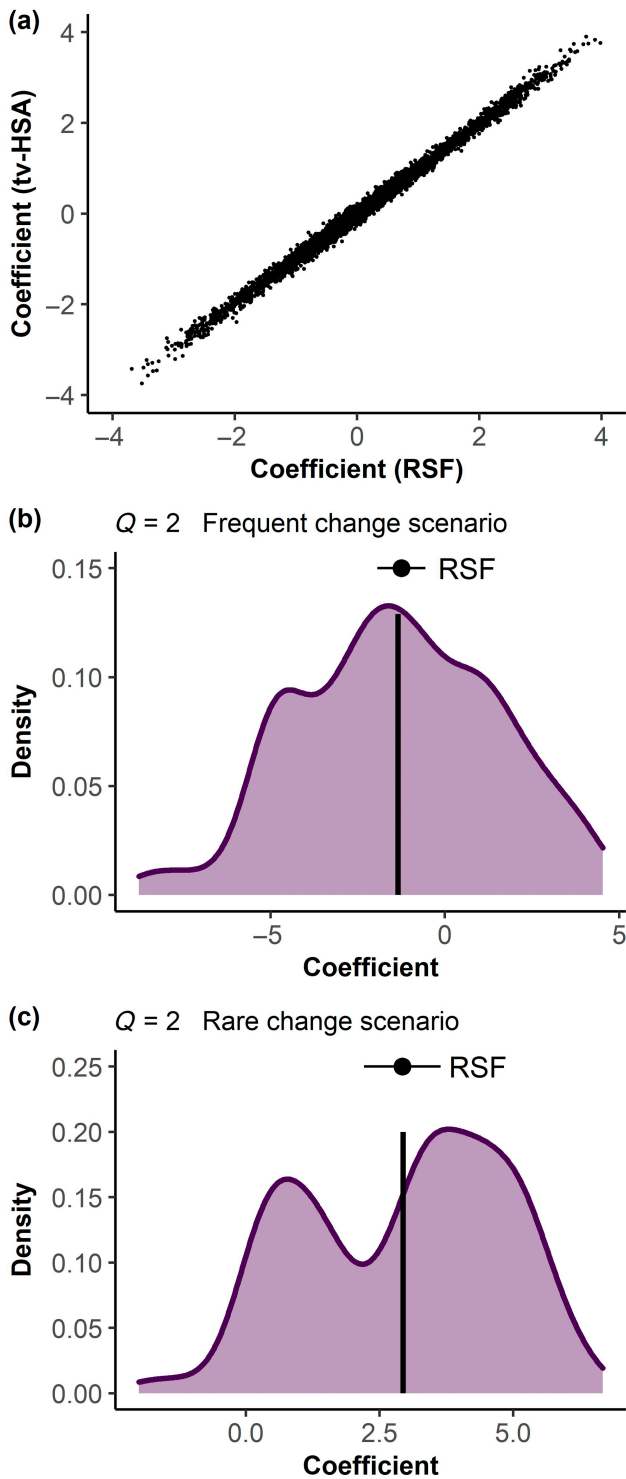


FIGURE 2 Comparison between time-varying habitat selection analysis (HSA) and conventional resource selection function (RSF). (a) Relationship between the coefficients of habitat selection estimated from time-varying HSA and averaged over the time series, to the RSF coefficient. Each dot shows the coefficients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

this wildebeest maintained the same overall strength of selection for open habitats from November to August, whereas this period covers months from both the dry and wet seasons (Figure 4a). Also, we note that during the dry season (April to June) this wildebeest did not preferentially use areas close to rivers, but selected areas close to rivers consistently from July to mid-August (green segment) and probably made back-and-forth trips to and away from the rivers from mid-August to October (yellow segment; Figure 4b).

Event-based variations: Post-release changes in habitat selection

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

DISCUSSION

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

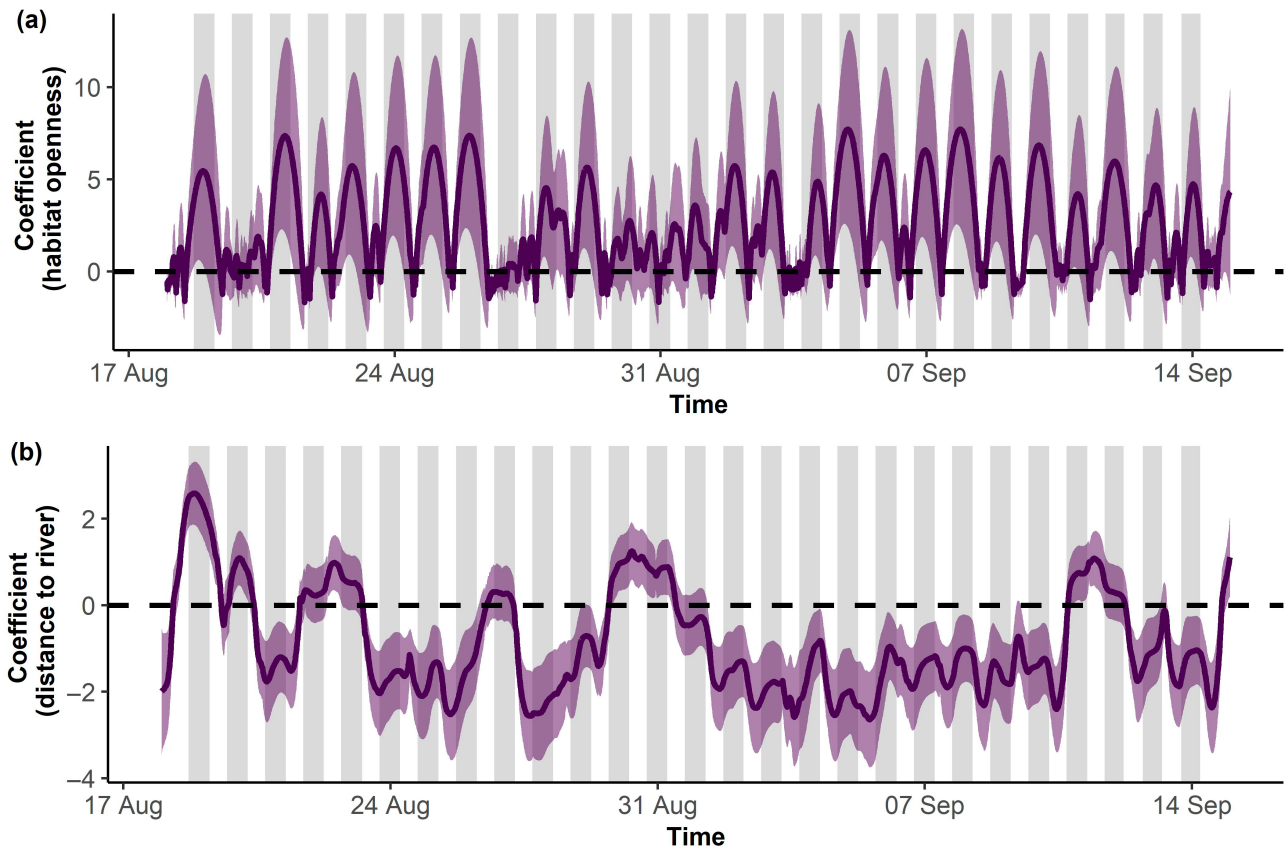


FIGURE 3 Estimations of short-term temporal variations of wildebeest's selection for open habitats (a) and areas close to rivers (b). Positive coefficients indicate selection for open habitats or areas far from rivers. Ribbons show 95% confidence interval. Note, however, that location data used in this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

With this time-varying HSA approach, one can simultaneously estimate both the timing and the amplitude of habitat selection changes. Estimation of the timing of change from the data is what makes this approach novel and attractive. Many times, *a priori* segmentation of time into distinct periods requires expert knowledge or is based on ancillary data (e.g., climate data) whose relevance for a particular dataset is not warranted. “Letting the data speak” allows for revealing the actual pattern of change. This may be of particular importance, for instance, in the study of interindividual variability, as the timing of change can be one of the differencing variables, as evidenced in our post-release study case. As recognized by Picardi et al. (2021), time-varying HSA opens a new avenue to broaden the scope of the studies of interindividual differences in space use, which has so far focused on movement characteristics or habitat selection strength. More generally, even when the relevance of an *a priori* segmentation of time into distinct periods is easier to ascertain, such as when comparing daytime to night-time habitat selection, time-varying HSA allows one to immediately identify unusual periods (e.g., night

of 27 August, when the wildebeest did not increase its selection for open habitat). These unusual periods may either be of interest (in such case, one would have to conduct one standard HSA per night to have discovered this), or be “noise” that should not affect the estimation of habitat selection strength during more “usual” periods (conversely to what occurs in a standard HSA).

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

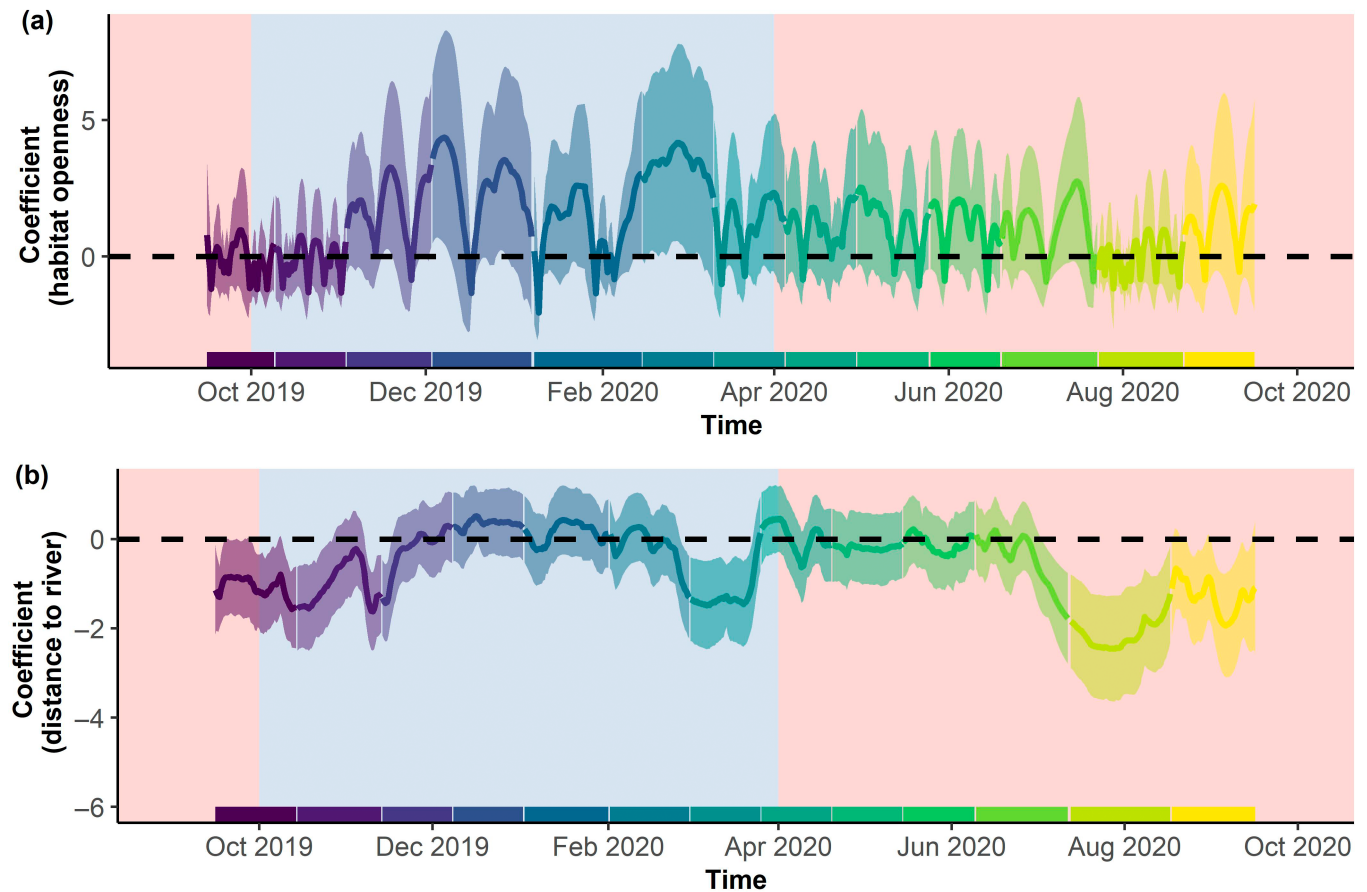


FIGURE 4 Estimations of long-term temporal variations of wildebeest's selection for open habitats (a) and areas close to rivers (b). Positive coefficients indicate selection for open habitats or areas far from rivers. Ribbons show 95% confidence interval. Data used in this analysis were subsampled to one location per night and one location per day to avoid issues with autocorrelation. Common definitions of wet (blue) and dry (red) seasons are shown in the background in panels (a, b). Lines and ribbons are colored on a purple-to-yellow gradient, with colors corresponding to segments of homogeneous habitat selection, as obtained with the *segclust2d* approach.

behavioral-mode detection approaches based on SSF (Klappstein et al., 2022; Nicosia et al., 2017; Prima et al., 2022), although by definition the temporal scale of selection considered is much different.

Despite that, rigorously, conventional RSF models are not time series models, our approach is closer to the RSF than to the SSF framework. Indeed, by generating random points within the whole animal's home range, the estimated time-varying coefficients measure when an animal is spending time in a "rare" habitat relative to its large-scale availability. The selection process measured here is the fact that animals move and stay in rare habitats over time, and not the "step" selection resulting from the animal's choice within the steps allowed by the sampling rate. Hence, we make the biological and statistical assumption that the animal's habitat selection at time t depends on the history of the animal's habitat selection up to t (Fahrmeir, 1994). An example of why such an assumption makes sense is animal migration: once established in a new range, coefficients from an SSF

(i.e., fine scale) would not show a selection for this new range, while coefficients from an RSF (i.e., large scale) would show a selection for such areas when considering the whole study area as available.

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

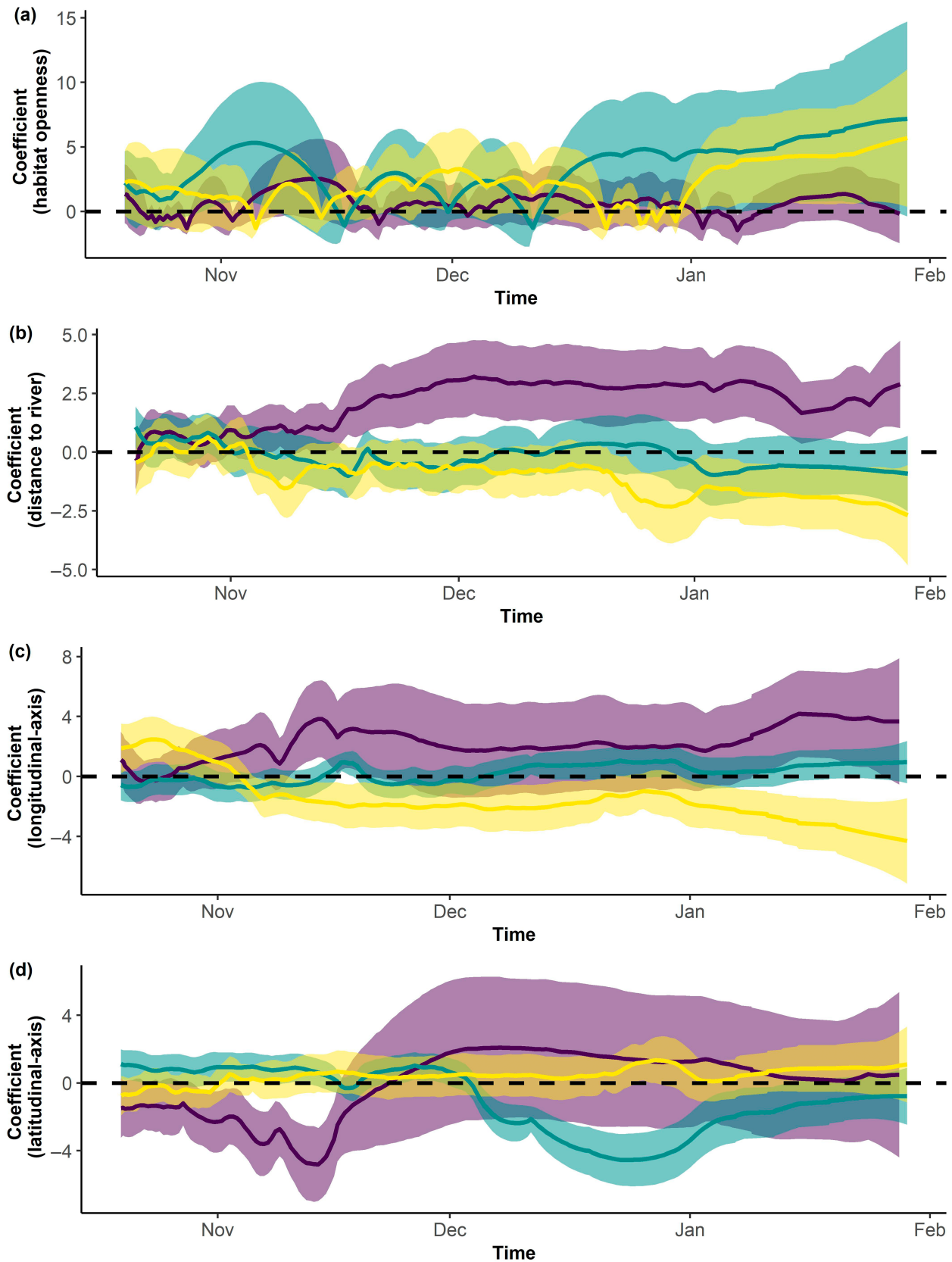


FIGURE 5 (a–d) Estimations of post-release variation of wildebeest’s selection for open habitats, areas close to rivers, longitude, and latitude. Positive coefficients indicate selection for open habitats, areas far from rivers, or areas at greater longitude and latitude. Estimated coefficients (line) and 95% confidence intervals (ribbons) are colored per individuals. Data used in this analysis were subsampled to one location per night and one location per day to reduce the autocorrelation between the used locations.

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

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

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Dejeante et al., 2023b) are archived in a Figshare collection at <https://doi.org/10.6084/m9.figshare.c.6365415.v5>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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