

RESEARCH ARTICLE

Modelling individual variability in habitat selection and movement using integrated step-selection analysis

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Abstract

1. *Integrated step-selection analysis* (ISSA) is frequently used to study habitat selection using animal movement data. Methods for incorporating random effects in ISSA have been developed, making it possible to quantify variability among animals in their space-use patterns. Although it is possible to model variability in both habitat selection and movement parameters, applications to date have focused on the former despite the widely acknowledged and important role that movement plays in determining ecological processes from the individual to ecosystem level. One potential explanation for this omission is the absence of readily available software or examples demonstrating methods for estimating movement parameters in ISSA with random effects.
2. We demonstrated methods for characterizing among-individual variability in both movement and habitat-selection parameters using a simulated data set and by fitting two models to an acoustic telemetry data set containing locations of 35 red snapper (*Lutjanus campechanus*). Movement kernels were assumed to depend on either the type of benthic reef habitat in which the fish was located (model 1) or the distance between the fish's current location and the nearest edge habitat (model 2). In both models, we also quantified habitat selection for different benthic habitat classes and distance to edge habitat, and we allowed for individual variability in movement and habitat-selection parameters using random effects.
3. The simulation example highlights the benefits of a mixed-effects specification, namely, we can increase precision when estimating individual-specific movement parameters by borrowing information across like individuals. In our applied example, we found substantial among-individual variability in both habitat selection and movement parameters. Nonetheless, most red snapper selected for hardbottom habitat and for locations nearer to edge habitat. They also moved less when in hardbottom habitat. Turn angles were frequently near $\pm \pi$ but were more dispersed when fish were far away from edge habitat.

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4. We provide code templates and functions for quantifying variability in movement and habitat-selection parameters when implementing ISSA with random effects. In doing so, we hope to encourage ecologists conducting ISSA to take full advantage of their ability to model among-individual variability in both habitat-selection and movement patterns.

KEYWORDS

animal movement, individual variability, integrated step-selection analysis, *Lutjanus campechanus*, mixed-effect, random effect, red snapper, step-selection function

1 | INTRODUCTION

Our understanding of how individuals move and select for different habitat features has been enhanced by technological advances, including smaller and better tracking devices (Kays et al., 2015), widespread availability of remote sensing data products (Dodge et al., 2013; Neumann et al., 2015), and new statistical methods and software for modelling animal movement (Hooten et al., 2017; Joo et al., 2020). By tracking individuals in the context of dynamic environmental conditions, we can identify the drivers of movement and predict how movements and species distributions will change as the environment changes (Cagnacci et al., 2010).

Importantly, individuals frequently exhibit variation in the extent of their movements, which can have implications for survival and fitness. For example, Fraser et al. (2001) found that Trinidad killifish (*Rivulus hartii*) identified in the laboratory as being more bold also moved more when released into their native streams; killifish movements were also positively correlated with individual growth in areas of the stream where predators were present. Individual variation can often be accommodated using hierarchical models with random effects, but since most animal movement models are non-linear in the parameters (e.g. Tracey et al., 2005), this leads to statistical likelihoods with intractable integrals over the random effects distribution, and thus, no closed form solution exists (note, general purpose software has been developed in the case of generalized linear mixed-effects models which suffer from this same issue; see e.g. discussions in Bolker et al., 2009; Fieberg et al., 2009). Thus, users must typically rely on numerical approximation techniques and custom-written code to estimate parameters (Auger-Méthé et al., 2017; Jonsen et al., 2019). Alternatively, many studies have explored individual variation in animal movement data using linear mixed-effects models with simple movement metrics (e.g. mean daily distance moved) as the response variable (Hertel et al., 2020, 2021; Tucker et al., 2018). Although useful for quantifying variation across individuals and species, these applications focus on variation in emergent movement patterns rather than the mechanistic drivers of movement variation at finer spatial and temporal scales.

Integrated step-selection analysis (ISSA) offers an appealing framework for modelling complex movements in response to local environmental features (Avgar et al., 2016; Fieberg et al., 2021; Muff et al., 2020; Northrup et al., 2022). Similar to species distribution

models and resource-selection functions, ISSA infers the importance of environmental covariates by comparing their distribution at used versus available locations. However, ISSA offers several advantages over the former approaches by: (1) allowing for temporally dynamic covariates that drive species distribution patterns to be included in the model; (2) using an individual's movements to determine available habitat; and (3) relaxing the assumption of independence among locations to an assumption of independent 'steps' or movements between sequential locations. Another advantage of ISSA is the ability to model both habitat selection, using covariates at the end of the movement step, and habitat-dependent movement, by allowing an animal's step lengths (distances between sequential locations) and turn angles (changes in direction) to depend on habitat at the start of the movement step (Avgar et al., 2016; Fieberg et al., 2021). This strength has been widely recognized, and ISSA has been used to explore how individuals alter their step lengths and turn angles in response to linear features such as roads and seismic lines (Dickie et al., 2020; Prokopenko et al., 2017; Scrafford et al., 2018).

Integrated step-selection analysis can be implemented using statistical software capable of fitting conditional logistic regression models, but the likelihood becomes difficult to maximize when random effects are included (Craiu et al., 2011; Duchesne et al., 2010). This led Craiu et al. (2011) to develop a two-step approach for fitting mixed conditional logistic regression models in this context. More recently, Muff et al. (2020) developed an approach for incorporating random effects in ISSA by exploiting the equivalence between Poisson regression with stratum-specific intercepts and conditional logistic regression. This approach has quickly become commonplace when modelling habitat selection using data sets that include many individuals, and allows for both individual- and population-level inference. For example, one can estimate coefficients for a typical individual by setting all random effects to 0 (Fieberg et al., 2009, 2010), estimate variance parameters that capture among-individual variability in the habitat-selection coefficients (Muff et al., 2020), and explore functional responses in habitat selection by considering how individual-specific coefficients vary with habitat availability or other landscape metrics (Aarts et al., 2013; Matthiopoulos et al., 2011). A nice exemplification is Jones et al. (2020), who used random effects to explore whether variation among individual spotted owls (*Strix occidentalis*) in their habitat-selection parameters was related to patch size and configuration in a post-fire landscape.



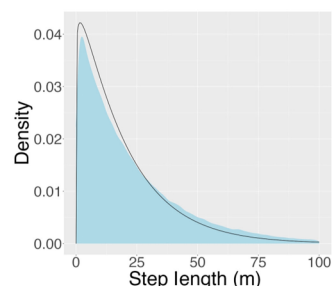
Although many studies have explored individual variation in habitat-selection parameters, little to no attention has been given to studying variation in movement parameters when using ISSA with random effects (hereafter 'mixed ISSA'). One likely reason for this lack of attention is that the estimation of movement parameters in ISSA is typically done using a complicated two-step process (Avgar et al., 2016; Fieberg et al., 2021). Tentative movement parameters are first estimated using observed step lengths and turn angles, ignoring the effect of habitat selection on observed movements, and then movement parameters are updated using additional coefficients from the fitted conditional logistic regression model (Figure 1). This approach is analogous to using importance sampling

to approximate the likelihood of the data (Michelot et al., 2023). The *amt* package (Signer et al., 2019) provides functions for implementing this two-step approach, but they only work when fitting models to individual animals. Furthermore, it is not immediately clear how this process should be implemented when the goal is to estimate individual-specific movement parameters.

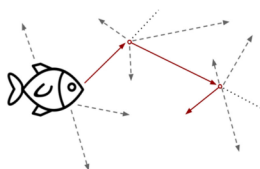
Here, we demonstrate how mixed ISSA can be used to study among-individual variation in both movement and habitat-selection parameters using a simulation example and by analysing an acoustic telemetry data set of 35 red snapper (*Lutjanus campechanus*). We show how one can visualize individual variation in movement and habitat-selection patterns, and provide functions within an

Step one: Prepare data & fit model

1. Fit single sampling kernel for observed step lengths and turn angles using **amt::fit_distr**.



2. Generate time-dependent random points and form strata of observed and random steps using **amt::random_steps**.

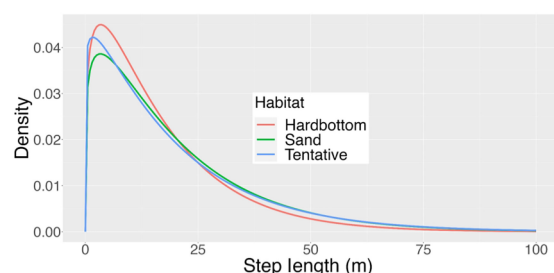


3. Fit mixed-effects conditional logistic regression model using **glmmTMB::fitTMB**, assuming step lengths come from a gamma distribution and turn angles from a von Mises distribution,

$$\begin{aligned} \text{case} &\sim \text{sl} + \log(\text{sl}) + \cos(\text{ta}) + \\ \text{x_start} &:(\text{sl} + \log(\text{sl}) + \cos(\text{ta})) + \\ &\quad \text{x_end} + \\ &\quad (1 \mid \text{step_id}) + \\ (0 + \text{sl} + \log(\text{sl}) + \cos(\text{ta}) \mid \text{id}) &+ \\ (0 + \text{x_end} \mid \text{id}) & \end{aligned}$$

Step two: Update movement parameters

- 4a. **Typical Individual** – Update movement parameters for a typical individual for fixed effects with all random effects set to zero using **mixedSSA::update_dist**.



- 4b. **Individuals** – Update movement parameters for tracked individuals using fixed- and random-effects using **mixedSSA::update_dist** with the **random_effects_var_name** argument set.

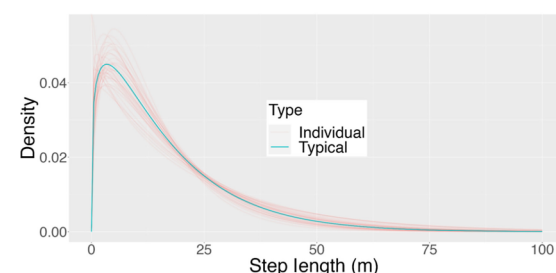


FIGURE 1 Schematic diagram of proposed workflow for estimating individual-specific movement parameters from a mixed-effects integrated step-selection analysis. Although we focus here on visualizing step-length distributions in different environments and across different individuals in the population, the same process can be used to visualize variation in turn-angle distributions. In Step One-third box (upper right panel), *sl*, $\log(\text{sl})$, and $\cos(\text{ta})$ and interactions are terms used to estimate the parameters of the movement kernel, *x_start*:(*sl* + $\log(\text{sl})$ + $\cos(\text{ta})$) allows the movement kernel to depend on habitat at the start of the step, *x_end* is used to model habitat selection, (1|*step_id*) codes for a fixed-effects intercept making the model equivalent to a conditional logistic regression (Muff et al., 2020), (0+*sl*+ $\log(\text{sl})$ + $\cos(\text{ta})$ | *id*) specifies random effects that allow each individual to have its own movement kernel and (0+*x_end*|*id*) specifies random effects that allow each individual to have its own habitat selection parameters.

associated R package (mixedSSA) to facilitate the application of these methods to other data sets.

2 | INTEGRATED STEP-SELECTION ANALYSIS

Integrated step-selection analysis assumes that animal space use is captured by the product of two functions, a movement-free habitat-selection function, $w(\cdot)$, that represents habitat preferences and a selection-free movement kernel, $\phi(\cdot)$, that quantifies how the animal would move in the absence of habitat selection (Augar et al., 2016; Fieberg et al., 2021):

$$u(s, t + \Delta t | s', t, \psi) = \frac{w(x(s, t + \Delta t); \beta) \phi(s, s', x(s', t), \psi; \gamma)}{\int_{\tilde{s} \in G} w(x(\tilde{s}, t + \Delta t); \beta) \phi(\tilde{s}, s', x(s', t), \psi; \gamma) d\tilde{s}}, \quad (2.1)$$

where $u(s, t + \Delta t | s', t, \psi)$ represents the conditional probability of an animal being present at location s at time $t + \Delta t$, given that it was at location s' at time t and arrived there via the bearing ψ ; $x(s', t)$ and $x(s, t + \Delta t)$ are habitat covariates measured at the start and end of the movement step, respectively; and β and γ are sets of parameters that quantify habitat selection and movement tendencies respectively. Finally, note that the denominator in Equation (2.1) integrates over the geographic area, G , that represents the area in which an animal could have potentially moved based on its prior observed movements and ensures that the right-hand side is a proper probability distribution; \tilde{s} is a dummy variable for integration.

3 | EXAMPLE APPLICATION TO SIMULATED DATA

To demonstrate the application of mixed ISSA that allows for individual variability in movement parameters (Figure 1), we simulate trajectories following Equation (2.1) for a population of individuals with individual-specific, known parameter values. We also compare the estimates from the mixed ISSA to those obtained by fitting a separate model to data from each individual. Doing so highlights the benefits of using random effects; namely, the ability to borrow information across like individuals, which leads to improved estimates of individual-specific parameters (Gelman & Hill, 2006; Harrison et al., 2018).

3.1 | Simulated movements

We generated a set of tracking data for 30 individuals. To do so, we created a landscape with a single categorical variable representing two habitat types (A and B). We then simulated movements in which each individual had its own set of movement and habitat selection parameters, and in which movements were more directed, on average, when individuals were in habitat of type B.

Let sl_{ik} and θ_{ik} represent step lengths and turn angles, respectively, for individual i in habitat class k ($k = 1, 2$ for habitats A and B). The sl_{i1} follow a gamma distribution with individual-specific shape and scale parameters, α_{i1} and v_{i1} , respectively, and θ_{i1} follow a von Mises distribution with mean 0 and with individual-specific concentration parameters, κ_{i1} :

$$\begin{aligned} sl_{i1} &\sim \text{gamma}(\alpha_{i1}, v_{i1}) \\ \theta_{i1} &\sim \text{von Mises}(0, \kappa_{i1}) \end{aligned} \quad (3.1)$$

We assumed the parameters $(\alpha_{i1}, v_{i1}, \kappa_{i1})$ for each individual followed a multivariate Normal distribution:

$$\begin{bmatrix} \alpha_{ik}, v_{ik}, \kappa_{ik} \end{bmatrix}^T \sim N(\mu_\gamma, \Sigma_\gamma), \text{ with } \mu_\gamma = \begin{bmatrix} \bar{\alpha} \\ \bar{v} \\ \bar{\kappa} \end{bmatrix} \text{ and } \Sigma_\gamma = \begin{bmatrix} \sigma_\alpha^2 & \sigma_{\alpha,v}^2 & \sigma_{\alpha,\kappa}^2 \\ \sigma_{\alpha,v}^2 & \sigma_v^2 & \sigma_{v,\kappa}^2 \\ \sigma_{\alpha,\kappa}^2 & \sigma_{v,\kappa}^2 & \sigma_\kappa^2 \end{bmatrix} \quad (3.2)$$

The diagonal elements of Σ_γ quantify among-individual variability in the movement parameters, and the off-diagonal elements quantify how these parameters covary; non-zero covariances allow individuals that tend to move more to also exhibit more directed movements (or, vice versa depending on the sign of the covariance parameters). We assumed that step lengths and turn angles for movements starting in habitat B also followed individual-specific gamma and von Mises distributions, respectively. The parameters of these distributions were shifted relative to parameters in habitat A using an additive model:

$$(\alpha_{i2}, v_{i2}, \kappa_{i2}) = (\alpha_{i1}, v_{i1}, \kappa_{i1}) + (a, n, k),$$

where $(a, n$ and $k)$ are constants. Thus, we allowed each type of movement parameter (α , v and κ) to vary by individual, while forcing differences in parameter values for the two habitat classes to be consistent across individuals. For example, $\alpha_{i2} - \alpha_{i1} = a$ for all individuals. Finally, we assumed $w(x_{t+1}) = \exp(0.5)$ when individuals were in habitat B and $w(x_{t+1}) = \exp(0)$ when in habitat A. Thus, all individuals preferred habitat B to habitat A.

We generated random parameters, $(\alpha_{i1}, v_{i1}, \kappa_{i1})$, for each individual using the `mvrnorm` function in the MASS R package (Venables & Ripley, 2002). Sample sizes (number of steps) for each individual were then generated by rounding random values sampled from a Normal distribution with mean 2000 and standard deviation equal to 250, resulting in sample sizes ranging between 1633 and 2627. We then generated random trajectories using the `redistribution_kernel` and `simulate_path` functions in the `amt` package of R (Signer et al., 2019, 2023). We set the parameter values used to simulate the trajectories as follows:

$$\mu_\gamma = \begin{bmatrix} 3 \\ 1 \\ 4 \end{bmatrix} \text{ and } \Sigma_\gamma = \begin{bmatrix} 0.25 & 0.15 & 0.15 \\ 0.15 & 0.20 & 0.15 \\ 0.15 & 0.15 & 0.25 \end{bmatrix}$$

Lastly, we set $(a, n$ and $k) = (0.05, 0.05, 0.05)$.



3.2 | Parameter estimation

3.2.1 | Mixed ISSA

We used the following workflow to estimate the parameters in the mixed ISSA (Figure 1):

1. We parameterized a sampling kernel, $\phi^*(s, s', \psi; \hat{\gamma})$, using the observed step lengths and turn angles pooled across all individuals. Here, $\hat{\gamma}$ consisted of a single shape (α_0), scale (ν_0) and concentration parameter (κ_0). We set the mean of the von Mises distribution to 0.
2. Using `amt`'s `random_steps` function, we generated time-dependent random locations by simulating 10 potential movements from each previously observed location using the sampling kernel, $\phi^*(s, s', \psi; \hat{\gamma})$ from [1] above.
3. We formed strata by matching each observed step with its set of random steps. We then used the `glmmTMB` function in the `glmmTMB` package (Magnusson et al., 2017) to fit the equivalent of a mixed-effects conditional logistic regression model using these strata and the 'Poisson trick' from Muff et al. (2020). We included the habitat class measured at the end of the movement step to quantify relative selection for the two habitat types. As described in Avgar et al. (2016) and Appendix C of Fieberg et al. (2021), we can obtain estimates of movement parameters that account for habitat selection if we include specific movement characteristics in our conditional logistic regression model; these characteristics depend on the assumed distributions used to model step lengths and turn angles. For our model specification using the gamma and von Mises distributions, we need to include step length, $\log(\text{step length})$ and $\cos(\text{turn angle})$. Further, to allow the movement parameters to depend on habitat class, we need to include interactions between these movement characteristics and the habitat class at the start of the movement step. Finally, we included random effects for step length, $\log(\text{step length})$ and $\cos(\text{turn angle})$ to allow each individual to have its own set of movement parameters.
4. We estimated the movement parameters in $\phi(s, s', \psi; \gamma)$ using the sampling kernel, the regression coefficients associated with movement characteristics (step length, $\log(\text{step length})$ and $\cos(\text{turn angle})$), and their interactions with habitat class as outlined in Avgar et al. (2016) and Appendix C of Fieberg et al. (2021). Let β_{sl} , $\beta_{\log(sl)}$ and $\beta_{\cos(\theta)}$ represent the fixed-effects coefficients associated with step length, $\log(\text{step length})$ and $\cos(\text{turn angle})$ respectively. Further, let b_{sl_i} , $b_{\log(sl)_i}$, $b_{\cos(\theta)_i}$ represent individual-specific random effects associated with these variables. We estimated updated movement parameters for the reference class (habitat A) for each individual, i , using:

$$\alpha_{1i} = \alpha_0 + \beta_{sl} + b_{sl_i} \quad (3.3)$$

$$\nu_{1i} = \frac{1}{\frac{1}{\nu_0} - (\beta_{\log(sl)} + b_{\log(sl)_i})} \quad (3.4)$$

$$\kappa_{1i} = \kappa_0 + \beta_{\cos(\theta)} + b_{\cos(\theta)_i} \quad (3.5)$$

Similarly, we could estimate updated parameters for habitat B by including the coefficients for the interaction terms in the above equations (see e.g. Appendix B of Fieberg et al., 2021 or Appendix S1 for a similar application to the snapper data).

3.2.2 | Individual models

We followed a similar workflow when fitting models to individuals, except that we estimated a separate sampling kernel using each individual's data in Step 1, and we used the `fit_issf` function in the `amt` package when fitting models to each individual's data rather than `glmmTMB` in Step 3; the `fit_issf` function serves as a wrapper function for the `clogit` function in the `survival` package (Therneau, 2023).

4 | APPLICATION OF MIXED ISSA TO RED SNAPPER

Red snapper are an economically and ecologically important species distributed in the Gulf of Mexico and along the eastern coasts of North America, Central America and northern South America. They are a reef-associated, demersal, gonochoristic fish species that can live 50+ years, maturing around 2 years, and they can exceed 1000 mm and 12 kg (White & Palmer, 2004; Wilson & Nieland, 2001). They are generalist predators, with adults feeding primarily on benthic invertebrates and other reef-associated fishes (Szedlmayer & Lee, 2004; Wells et al., 2008). In the United States, red snapper are targeted by both recreational and commercial sectors, and these fisheries are managed in the Gulf of Mexico by the Gulf of Mexico Fishery Management Council and in the Atlantic Ocean by the South Atlantic Fishery Management Council. Previous studies of red snapper have found an affinity for areas of high to moderate relief near edges of hardbottom habitat (Bacheler et al., 2021; Bohaboy et al., 2022; Williams-Grove & Szedlmayer, 2016, 2017).

4.1 | Study area

Our study site comprises reef habitat in approximately 37 m deep water off the coast of North Carolina, USA, between Cape Hatteras and Cape Lookout (Figure 2). The seafloor of the study site is composed of a patchy mix of rocky pavement and ledges in a matrix of sand (Figure 2). We used a high-resolution bathymetric map for the classification of benthic habitat into either sand or hardbottom.

4.2 | Data collection and processing

We caught red snapper from May through September, 2019 using hook-and-line methods or baited fish traps and tagged them with



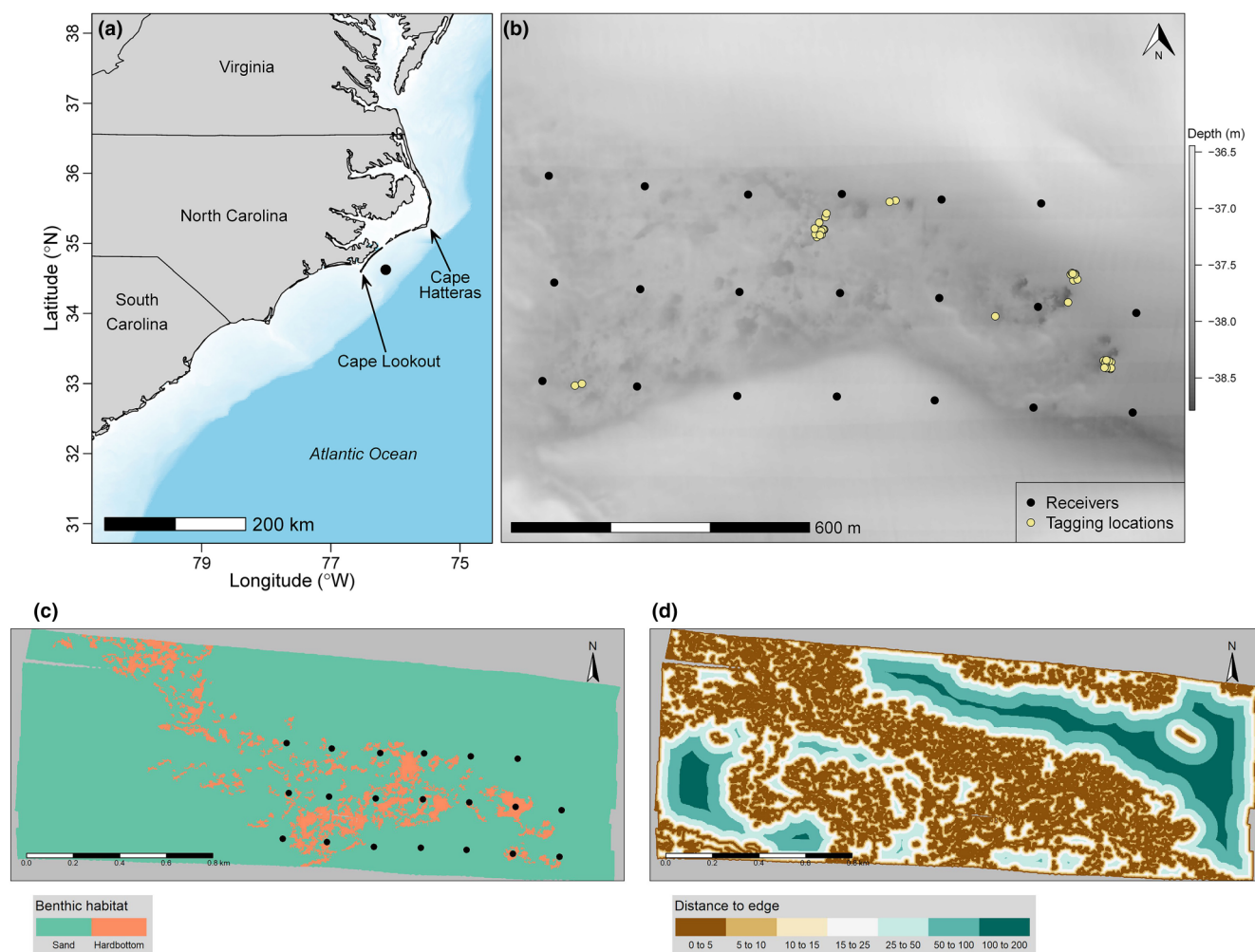


FIGURE 2 (a) Broad-scale location of study (filled black circle) on the continental shelf between Cape Lookout and Cape Hatteras, North Carolina, USA, in 2019. Water depth is shown in blue: the lightest blue indicates water less than 5m deep, while the darkest blue is greater than 100m deep. (b) Close-up view of the study area where a Vemco positioning system was used to estimate fine-scale positions of red snapper (*Lutjanus campechanus*). Background shows a multibeam sonar map that is scaled to depth (right y-axis), submersible receivers are represented by filled black circles, and tagging and release locations are represented by light yellow points. Environmental variables used in the habitat-selection modelling (c) benthic habitat class (sand or hardbottom) with the submersible receivers represented by filled black circles; and (d) distance-to-edge habitat.

13g externally attached Vemco V13P-1x transmitters that had an average battery life of 613 days and a pulse interval of 130–230s. Locations were collected from May 2019 to December 2019 using a 400×1200m regularly spaced grid array of 20 VR2AR acoustic receivers placed on the sea floor (Figure 1, Bacheler et al., 2021). We used an additional V13P-1x reference transmitter to quantify the accuracy of data collection between transmitters and acoustic receivers by deploying it at a known location and quantifying the horizontal error of all estimated positions over the duration of the study.

We converted the location data to a set of steps representing movements between sequential observations and dropped any steps that had a step length >100m and a turn angle >170 degrees, assuming these steps likely resulted from erroneous locations with large measurement error (Bjørneraas et al., 2010). We then thinned the telemetry data to equally spaced intervals of 6 ± 1 min using the

track_resample function in the amt R package (Signer et al., 2019). Finally, we created a distance-to-edge habitat covariate measuring the nearest distance to habitat separating sand and hardbottom habitat classes (Figure 2).

4.3 | Mixed ISSA

We expected that both movement and habitat-selection parameters would vary by individual, but that most individuals would (1) prefer hard bottom habitat near the edge of reef-sand habitat transition and (2) move in a more directed manner (longer step lengths with turn angles near 0) when in sandy habitats or far from the edge of reef-sand habitat. To accommodate individual variation and test these assumptions, we used two different mixed ISSAs. In the first,

we assumed step lengths and turn angles depended on the categorical benthic habitat class variable measured at the start of the movement step, similar to our simulation example. In the second mixed ISSA, we modelled the distribution of step lengths and turn angles as a function of a continuous variable quantifying the distance between the current location and the nearest edge habitat. To allow the movement kernels, $\phi(\cdot)$, to depend on the habitat at the start of the movement step, we included step length, $\log(\text{step length})$ and $\cos(\text{turn angle})$ as well as interactions between these terms and the benthic habitat class (model 1) or distance to edge (model 2). In both models, we also included random effects for step length, $\log(\text{step length})$ and $\cos(\text{turn angle})$, thus allowing each individual to have their own set of movement parameters. We did not, however, include random effects for interaction terms between step length, $\log(\text{step length})$, $\cos(\text{turn angle})$ and habitat class (model 1) or distance to habitat edge (model 2). Although in principle, these interactions could also be modelled using random effects, this would lead to a substantially larger number of variance/covariance parameters that would need to be estimated with relatively few individuals.

For both mixed ISSAs, we modelled the habitat-selection function, $w(\cdot)$, as a log-linear function of benthic habitat class and distance to edge measured at the end of the movement step:

$$w(x(s, t + \Delta t); \beta) = \exp((I(\text{Hardbottom}(t + \Delta t))_{ij}\beta_{1i} + d_{ij}(t + \Delta t)\beta_{2j}),$$

where i indexes the different individuals and j indexes the movement steps, $d_{ij}(t + \Delta t)$ is the distance to edge habitat at the end of the movement step and $I(\text{Hardbottom}(t + \Delta t))_{ij}$ is equal to 1 if the end of the movement step falls in the Hardbottom habitat class, and 0 otherwise. We used random effects to allow each individual to have its own set of habitat-selection parameters. We assumed the coefficients for Hardbottom habitat varied independently from the distance-to-edge coefficients and that both habitat-selection parameters varied independently of the movement parameters. Again, alternative specifications of the random effects structure are possible, and the specific choice should depend on the effective sample size (e.g. number of individuals) and the user's underlying research questions. We return to this point in the Section 7.

We estimated parameters using the same workflow as outlined in Figure 1 and implemented in the application to the simulated data. We noted, however, that the peak of the snapper turn-angle distribution was centred on $\pm \pi$. This can occur when individuals are largely stationary or moving back and forth along linear features. To allow for a more flexible specification of the von Mises distribution, we set the estimated mean of the turn-angle distributions to $\pm \pi$ and κ to $|\kappa|$ when estimates of κ were negative and 0 otherwise. Finally, we estimated the mean step length for a typical individual (i.e. one with all random effects set equal to 0) in sand and hardbottom habitat classes (model 1) and for quantiles of $d_{ij}(t)$ (model 2). We used the delta method to quantify uncertainty in these estimates.

We provide a full set of equations describing the two models along with the R code needed to implement them in Appendix S1.

5 | SOFTWARE AND DATA AVAILABILITY

We developed an R package, mixedSSA (available at <https://github.com/smithfrmn/mixedSSA>) to facilitate the estimation and visualization of updated movement parameters. All analyses were carried out in R 4.0 (R Core Team, 2020). Data and code for reproducing all of the analyses have been archived in the Data Repository of the University of Minnesota (<https://conservancy.umn.edu/handle/11299/261582>; Chatterjee et al., 2024).

6 | RESULTS

6.1 | Simulation example

As expected, the mixed ISSA resulted in more accurate estimates of the movement parameters than when fitting separate models to each individual. Deviations between the estimated and true parameters were smaller, on average, for the mixed ISSA (Figure 3), with root mean-squared errors (RMSEs) that were roughly half that of the individual model fits. The RMSEs for the shape, scale and kappa parameters were 0.09, 0.035 and 0.10 for the mixed-effects model versus 0.18, 0.077 and 0.21 for the individual models.

6.2 | Application to red snapper

A total of 35 individuals were acoustically tagged in this study. The number of relocations (range 265–52,189) and the number of tracking days (range 3–223) were substantially different across individuals (Appendix S2: Table 1). Median horizontal error from 18,026 detections of the reference transmitter was 0.8m with a range of approximately 0.6–2.0m (Bacheler et al., 2021). We dropped a total of 13,802 observations (4% of the total) that did not meet the expected movement criteria (step length <100 meters and turn angle <170 degrees).

There was substantial variability in the estimated individual-specific habitat-selection parameters, with both positive and negative coefficients for each explanatory variable (Figure 4, Appendix S2: Figure 2). Comparing mean coefficients and their SEs, we see that the 'typical individual' prefers hardbottom to sand habitat (Figure 4), though the coefficient for $I(\text{hardbottom})$ was negative for three individuals.

Evaluating movement kernels for an individual with random effects=0 (Figure 5, Appendix S2: Table 3), we see that the typical snapper also tends to move less when in hardbottom habitat and as they get closer to edge habitat. The distribution of turn angles also becomes more dispersed when fish are farther from habitat edges ($\hat{\beta}_{\cos(\theta);d} = 0.006$; $p < 0.001$; Figure 5). Similar to habitat selection, there was substantial among-individual variability in both the distributions of step lengths and turn angles (Figure 6, Appendix S2: Figure 3) in both models.



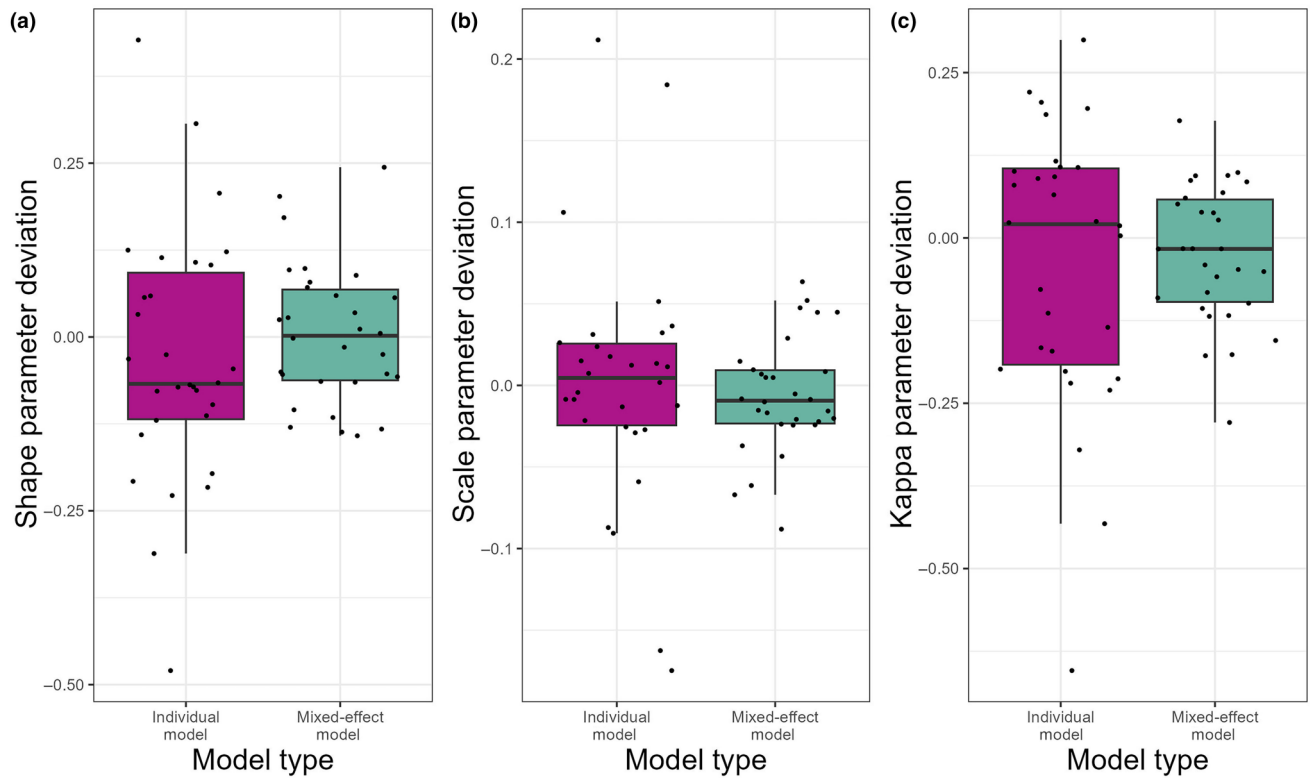


FIGURE 3 Deviations (estimated–true) in the shape (α), scale (ν) and concentration (κ) movement parameters estimated using the individual (purple) and mixed ISSA (green) models (a–c) for 30 simulated individual tracks.

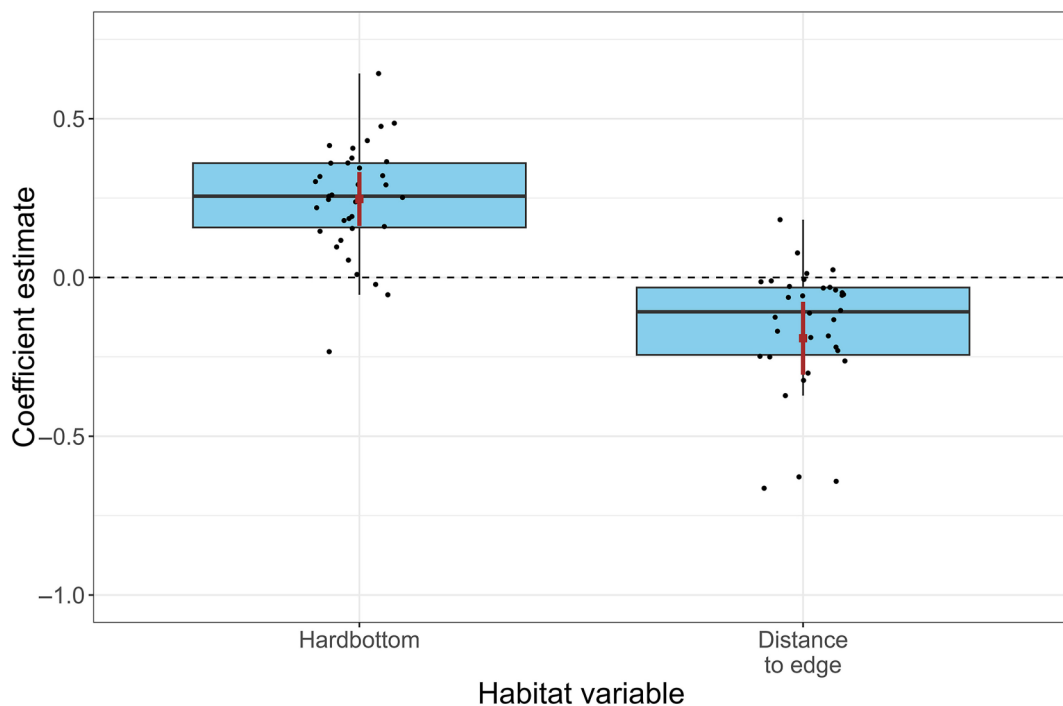


FIGURE 4 Boxplots summarizing the individual habitat-selection coefficients (black dots) associated with hardbottom habitat and the distance-to-edge covariate from Model 1. Boxes bound the 25th and 75th percentiles, solid line within the box indicates the median, and the whiskers extend to 1.5 times the interquartile range of the observations. The mean coefficient, along with a 95% confidence interval for the mean, is depicted in brown.



7 | DISCUSSION

An understanding of the causes and consequences of variability in animal movement and habitat selection is important for addressing many questions in applied and theoretical ecology (Shaw, 2020). For example, behavioural ecologists are increasingly interested in studying personalities and behavioural syndromes using mixed-effect models applied to metrics of animal movement and habitat selection (Hertel et al., 2020, 2021). Consistent and quantifiable intra- and inter-individual variability in movement also drives many important ecological processes, including individual foraging rates, social interactions, disease dynamics and spread of invasive species (Spiegel et al., 2017; Webber et al., 2020, 2023).

In the behavioural ecology literature, it is common to use the intraclass correlation coefficient from a fitted linear mixed-effects model, often referred to as repeatability, to quantify the proportion of variation in a response variable that can be attributed to the individual-level random effects (e.g. Hertel et al., 2020, 2021). The ability to use a single summary metric is an attractive feature of this approach as it can facilitate comparisons across studies and species (e.g. Stuber et al., 2022). Similar metrics have been suggested in the context of generalized linear mixed-effects models

(e.g. Nakagawa et al., 2017; Stoffel et al., 2021), and it is intriguing to consider whether they could be adapted to quantify repeatability in the context of mixed ISSA, particularly those that use the two-step approach to parameter estimation. Rather than focus on a single summary measure, however, we encourage users of mixed ISSA to explore in more detail the various sources of within- and between-individual variability captured by their models.

Our application to data from red snapper tracked on reef habitat demonstrates how mixed ISSA can be used to study both intra- and inter-specific variation in animal movements. By including interactions between movement attributes and environmental covariates (benthic habitat class or distance to edge of hardbottom habitat), we were able to quantify how individuals altered their movements depending on local habitat features. Interestingly, we found that individuals tended to have shorter average step lengths in the most strongly selected habitat (i.e. hardbottom habitat). Turn angles also tended to be more dispersed when fish were close to edges of reef habitat. This combination of shorter step lengths and more dispersed turn angles is consistent with area restricted search patterns, suggesting that these locations may serve as important foraging areas. Similarly, interactions with temporal covariates can be used to study how individuals alter their

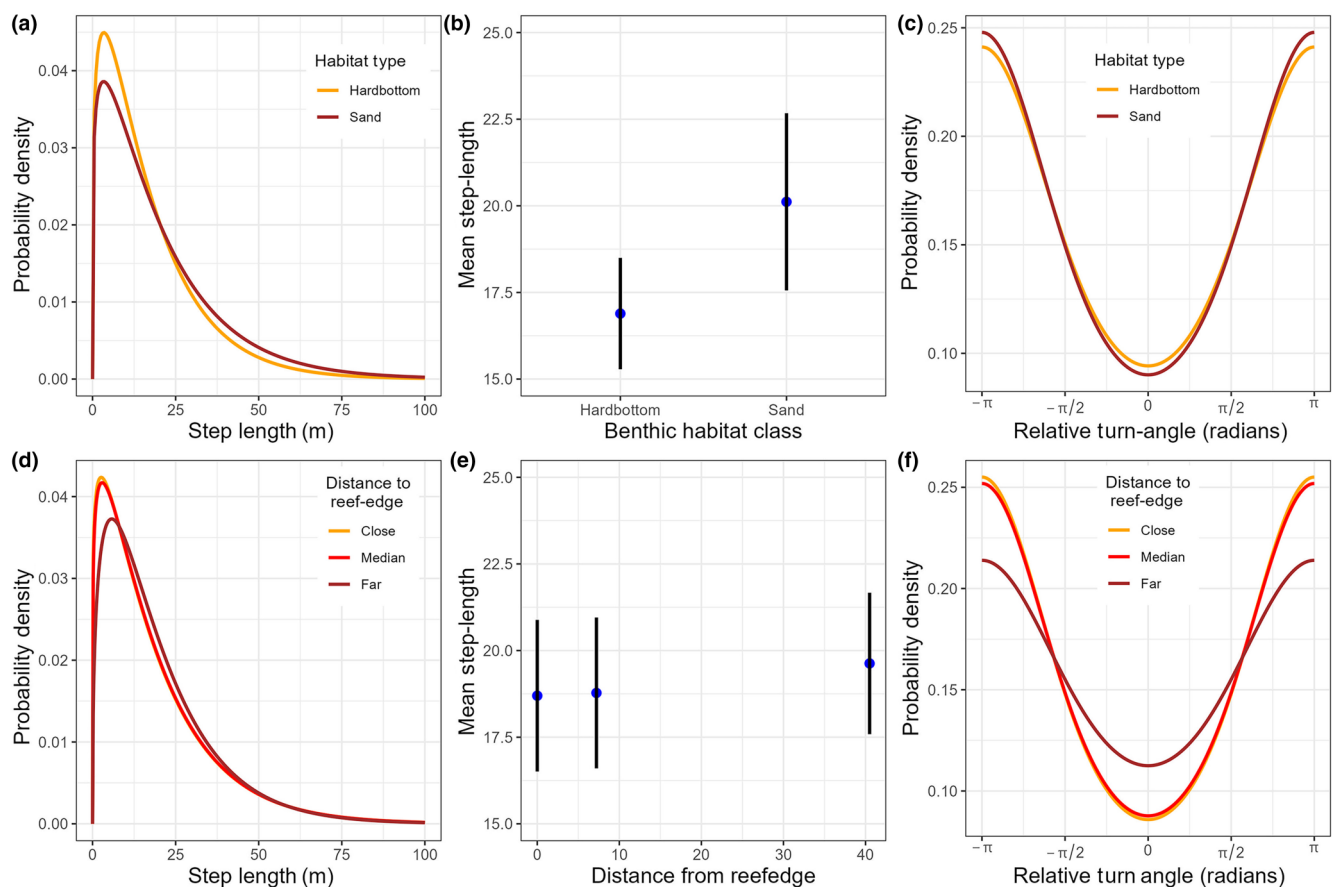


FIGURE 5 Estimated step-length and turn-angle distributions for a typical red snapper, that is, one with all random effects equal to 0, for sand and hardbottom habitat classes (a, c) and different distances to edge habitat (d, f) with estimates of mean step length (i.e. speed) for sand and hardbottom habitat class (b) or for different quantiles of distance to edge habitat (e). Close, median and far represent the 5th, 50th and 95th percentiles in panels (d and f).

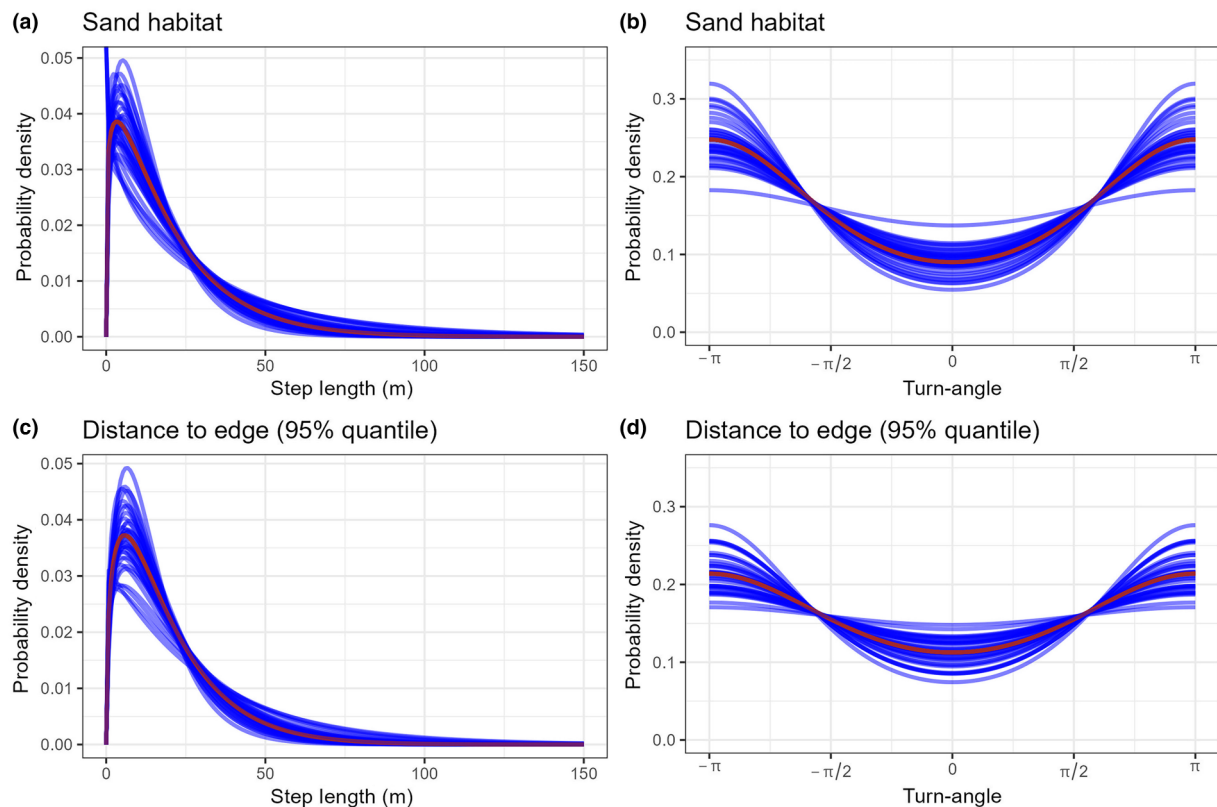


FIGURE 6 Estimated step-length and turn-angle distributions for different individuals (blue) and for a typical individual (i.e. an individual with all random effects set to 0) (red) in sandy habitat (a, b) and at 95% distance quantile from edge habitat (c, d).

movements through time. For example, Prokopenko et al. (2017) included an interaction between time of day and $\log(\text{step length})$ to model increased movements of elk (*Cervus elaphus*) during twilight hours. Giroux et al. (2023) conducted an ISSA with interactions between movement characteristics and temperature, time of day and habitat type, finding giant anteaters (*Myrmecophaga tri-dactyla*) had more directed movements (longer step lengths, turn angles more concentrated near 0) when temperatures decreased during daylight hours, but that temperature decreases were likely to result in resting behaviours (smaller step lengths and more dispersed turn angles) at night.

Random effects associated with each individual allowed us to quantify among-individual variability in both habitat-selection parameters and movement kernels. As is often the case, we found substantial among-individual variability in habitat-selection parameters; we also found substantial variability in individual movement kernels. Individual variability in red snapper movement and habitat use likely has important management implications. For instance, red snapper vulnerability to capture by fishers is likely related to their movement and habitat use, which could create the potential for evolutionary effects of fishing (Claireaux et al., 2018). Similarly, individual variability in behaviour likely affects detection probabilities of red snapper sampled by surveys, and this heterogeneity may bias abundance estimates. Indeed, abundance estimates from surveys are the most important data source on population dynamics for stock assessments, which are used by resource managers to inform regulatory

decisions. The large degree of individual variability we observed also suggests that random effects may be important to properly account for statistical dependencies arising from having repeated measures on the same individuals. Ignoring these dependencies will typically result in the estimators of uncertainty that are biased low (Fieberg et al., 2010).

The simplest method for accommodating individual variation in habitat-selection studies is to fit separate models to each individual (Fieberg et al., 2010). Yet, a complication with this approach is that it becomes more challenging to estimate population parameters that quantify among-individual variability. For example, the variance of the individual coefficients will be impacted by both true variability and sampling error (Davidian, 2017; Muff et al., 2020). Using the mixed ISSA, we can directly estimate these variance parameters and also use the same model for both individual and population-level inference. Furthermore, as our simulation example illustrates, we can obtain better estimates of individual-specific parameters by borrowing information from like individuals (Gelman & Hill, 2006; Harrison et al., 2018). Yet, the application of mixed ISSA can be challenging, especially when analysing data sets containing small numbers of individuals. Complex models with many random effects can lead to computational challenges and convergence issues, and users may need to carefully consider which parameters they allow to vary across individuals; these types of choices are commonplace when fitting generalized linear mixed-effects models (Bolker et al., 2009). Steps used to improve the likelihood of model convergence in linear



mixed-effects models (e.g. centring and scaling predictors, increasing the number of iterations) are also likely to prove useful for mixed ISSA (see e.g. Brauer & Curtin, 2018).

In our models, we included random effects for step length, $\log(\text{step length})$ and $\cos(\text{turn angle})$ but not their interactions with habitat class or distance to nearest edge habitat. This decision not only reduced the number of variance parameters that needed to be estimated but also constrained the degree of inter-individual variability that was included in our models. There are other ways that we could have simplified our model. For example, we could have assumed that only the scale parameter of the gamma distribution varied across individuals. This choice would have eliminated the need for a variance parameter (for the shape of the gamma distribution) and a covariance parameter (for the shape and concentration parameters). We could achieve a similar reduction in model complexity by switching to an exponential distribution for modelling step lengths. On the other hand, it might be of interest to explore how movement and habitat-selection parameters covary. Models could be constructed to explore this possibility, but doing so would require additional covariance parameters which we assumed to be 0.

Additional research to guide model-building strategies (e.g. methods for determining an appropriate level of model complexity) would be helpful. The two-step approach to parameter estimation (Avgar et al., 2016; Fieberg et al., 2021) and the Poisson trick for implementing mixed ISSA (Muff et al., 2020) also complicates parameter interpretation and model inference. Recently, Klappstein et al. (2024) demonstrated how a variety of ISSAs with random effects can be fit using the *mgcv* package (Wood, 2017) though computation times were longer than when fitting Poisson models using the *glmmTMB* package (Magnusson et al., 2017). Mixed ISSA could also potentially be implemented using Template Model Builder with the Laplace approximation to integrate over the random effects distribution (e.g. Auger-Méthé et al., 2017; Jonsen et al., 2019). General purpose software implementations that directly fit models for mixed ISSA in a single step would be a welcome advance.

Although several statistical frameworks have been suggested for modelling animal movement (Hooten et al., 2017; Patterson et al., 2017), including state-space models (Patterson et al., 2008) and diffusion processes in continuous time (Blackwell, 1997; Michelot et al., 2019), ISSA is arguably the most widely used method in applied ecology. Its popularity likely stems from the ability to link movements directly to environmental features and the availability of robust statistical software for model fitting. Hidden Markov models (HMMs) offer another popular alternative for modelling animal movement data (Langrock et al., 2012; McClintock & Michelot, 2018). In contrast to ISSA, which allow users to directly model the effects of local environmental features on movements via a habitat-selection function and a (potentially habitat-dependent) movement kernel, HMMs rely on latent (unobserved) states to model temporal variability in movement characteristics (e.g. step lengths and turn angles). Movement-based

HMMs are typically not spatially explicit, and while spatial covariates can be used to model the transition probabilities and/or state-dependent movement distributions, this typically leads to models with many parameters that are challenging to interpret (Glennie et al., 2023). Random effects can be used to model individual variability in either the state transition probabilities or the state-dependent distributions, but the former approach can be computationally challenging and unreliable for small sample sizes (<100 individuals; McClintock, 2021) and the latter approach has been shown to suffer from parameter identifiability issues (Glennie et al., 2023). Thus, although software for fitting HMMs with random effects is now available (Michelot, 2022), it is more common to fit a single model to data pooled across individuals. Alternatively, one can fit separate models to data from each individual, but then there is no guarantee that the latent states identified by the individual-level models will have similar interpretations (Glennie et al., 2023).

Individual variability has long been recognized as fundamental to understanding broad patterns in ecology, including those that emerge from the aggregation or interactions of smaller-scale individual units (Levin, 1992). Recent attention has been given to methods that scale individual movement models to broader levels of animal space use or ecological dynamics. These studies include the use of step-selection analyses to derive utilization distributions and infer broad-scale patterns in space use (Potts & Börger, 2023), and the integration of intra-specific variation from movement data in larger contexts such as community ecology (Costa-Pereira et al., 2022) and biodiversity studies (Jeltsch et al., 2013). Mixed ISSA can be used to parameterize movement models for a population of individuals, which can then be simulated to explore population-level space-use patterns (Signer et al., 2017, 2023). By providing annotated code with functions to easily fit and visualize models of animal movement using mixed ISSA, we hope ecologists will take full advantage of their ability to quantify within- and among-individual variability in both movement and habitat-selection parameters to better understand ecological phenomena and species responses to changing environments.

AUTHOR CONTRIBUTIONS

Nilanjan Chatterjee led the analysis with contributions from David Wolfson, Dennis Kim, Smith Freeman, Juliana Velez and John Fieberg; Kyle Shretzer, J. Christopher Taylor and Nathan M. Bacher collected the data; Smith Freeman created schematic diagram and functions for implementing the analyses in the R package (*mixedSSA*); John Fieberg, Nilanjan Chatterjee and Nathan Bacher led the writing of the manuscript. All authors discussed, edited, read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14321>.

DATA AVAILABILITY STATEMENT

The data associated with the study are available at the Data repository of the University of Minnesota (DRUM; Chatterjee et al., 2024, <https://doi.org/10.13020/27hq-zx30>).

DECLARATIONS

All tagging protocols were approved by the Institutional Animal Care and Use Committee (# NCA19-002) of the North Carolina Aquariums. Research activities were carried out under a Scientific Research Permit issued to Nathan Bacheler by the Southeast Regional Office of the US National Marine Fisheries Service, in accordance with the relevant guidelines and regulations on the ethical use of animals as experimental subjects. Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA. The scientific results and conclusions, as well as any views and opinions expressed herein, are those of the authors and do not necessarily reflect those of any government agency.

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SUPPORTING INFORMATION

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

Appendix S1. Details of the framework with equations and codes used for application of the mixed ISSA model to the empirical data.

Appendix S2. Supplementary tables and figures with detailed information of the study, fitted models and movement parameter distribution.

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