

Central place foragers and moving stimuli: A hidden-state model to discriminate the processes affecting movement

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Abstract

1. Human activities can influence the movement of organisms, either repelling or attracting individuals depending on whether they interfere with natural behavioural patterns or enhance access to food. To discern the processes affecting such interactions, an appropriate analytical approach must reflect the motivations driving behavioural decisions at multiple scales.
2. In this study, we developed a modelling framework for the analysis of foraging trips by central place foragers. By recognising the distinction between movement phases at a larger scale and movement steps at a finer scale, our model can identify periods when animals are actively following moving attractors in their landscape.
3. We applied the framework to GPS tracking data of northern fulmars *Fulmarus glacialis*, paired with contemporaneous fishing boat locations, to quantify the putative scavenging activity of these seabirds on discarded fish and offal. We estimated the rate and scale of interaction between individual birds and fishing boats and the interplay with other aspects of a foraging trip.
4. The model classified periods when birds were heading out to sea, returning towards the colony or following the closest boat. The probability of switching towards a boat declined with distance and varied depending on the phase of the trip. The maximum distance at which a bird switched towards the closest boat was estimated around 35 km, suggesting the use of olfactory information to locate food. Individuals spent a quarter of a foraging trip, on average, following fishing boats, with marked heterogeneity among trips and individuals.
5. Our approach can be used to characterise interactions between central place foragers and different anthropogenic or natural stimuli. The model identifies the processes influencing central place foraging at multiple scales, which can improve our understanding of the mechanisms underlying movement behaviour and characterise individual variation in interactions with a range of human activities that may attract or repel these species. Therefore, it can be adapted to explore the movement of other species that are subject to multiple dynamic drivers.

KEYWORDS

animal telemetry, Bayesian, central place foraging, *Fulmarus glacialis*, hidden-state modelling, movement attractors, multiscale

1 | INTRODUCTION

Animal movements may change in response to various human activities operating in their environment. These may have a repelling or an attracting effect on wildlife depending on whether they interfere with natural behavioural patterns or enhance access of food (Bartumeus et al., 2010; Hays et al., 2016). Aspects of these interactions that are particularly relevant to inform management include the scale at which they occur, the prevalence among individuals and their interplay with other biological and ecological functions (Crowder & Norse, 2008).

Assessing the movement of free-ranging animals towards or away from particular centres of attraction in their landscape is challenging. An animal's decision to head towards attractors depends on a series of contextual factors, including the individual's body condition, reproductive needs, previous experience, current activity and underlying motivation at a given time and over a longer time-scale (McClintock et al., 2012; Michelot et al., 2017; Nathan et al., 2008). The assessment is further complicated when these attractors move, because their continuously varying distance from an animal will impact the individual's ability to sense their presence and, when within detectable distance, will be traded-off against the potential benefit they represent (Bodey et al., 2014). Understanding this complex decision-making thus requires discriminating among the different processes that influence how and why the animals move at different scales (Nathan et al., 2008) and disentangling their interaction with new attracting components entering the landscape.

Many species act as central place foragers (Orians & Pearson, 1979), including seabirds and pinnipeds (Boyd, Punt, Weimerskirch, & Bertrand, 2014; Patrick et al., 2014). These animals exploit food resources around a particular location to which they are bound to return, often due to reproductive requirements (Stephens, Brown, & Ydenberg, 2007). Particularly in the early phases of their life, young depend on parents for food and protection, and adults are constrained to perform regular return trips to the colony, den or nest. When they encounter profitable patches along these trips, their fine-scale movement changes, often becoming slower and more convoluted (Michelot et al., 2017). This behavioural mode is known as area-restricted search (ARS) and is believed to reflect foraging activity in a patchy landscape (Kareiva & Odell, 1987). Therefore, characterising the interaction of central place foragers with human activities and other moving attractors in the environment needs to account for the interplay of the various attracting processes and multiscale drivers of movement.

Hidden-state models are routinely applied to animal telemetry data with the aim of identifying periods during which an individual is travelling through unprofitable areas (transit mode) and periods spent searching for food in profitable patches (resident or ARS mode) (Beyer, Morales, Murray, & Fortin, 2013; Jonsen et al., 2013; McClintock et al., 2012; Patterson, Thomas, Wilcox, Ovaskainen, & Matthiopoulos, 2008). The two modes can be distinguished based on the movement features estimated from the track, whereby transit mode is faster and more directed and resident mode is slower and

more convoluted (Jonsen et al., 2013). However, in addition to fine-scale step lengths and turning decisions (i.e., the movement steps) that define the current behavioural mode, an individual's movement will also be influenced by a broader attraction process that determines its movement phase (Nathan et al., 2008). Particularly, central place foragers will first depart from the home base (hereafter central place), heading out towards available foraging patches, and, after having spent some time travelling and foraging, will return towards the central place (Michelot et al., 2017). The overall bearing during different phases of a trip (e.g., heading away from or towards the central place) can be decoupled from the process determining transit versus resident behaviour, in that an animal might engage in either of the two modes irrespective of where it is broadly heading. As a result, two state processes can be thought as occurring concomitantly: first, a larger-scale process determining the overall bearing of the animal as the trip progresses, reflecting the different phases of the trip; second, a finer-scale process affecting the animal's residency in a given area, reflecting the movement mode at any moment in time (Nathan et al., 2008). Failing to distinguish the two may confound the estimation of the state-specific parameters and, ultimately, the identification of the corresponding states.

In this study, we developed a modelling framework for the analysis of the movements of central place foragers, where the process affecting an animal's bearing was treated separately from the process affecting its residency in an area. We illustrate this approach using a case study that explores how seabird movements are influenced by the presence of fishing boats. Discarding by commercial fisheries has been recognised as one of the key challenges to achieving the sustainable use of marine resources (Kelleher, 2005). Species, populations and individuals differ in their reliance on discards (e.g., Bodey et al., 2014; Granadeiro, Brickle, & Catry, 2014; Patrick et al., 2015; Phillips et al., 1999; Tew Kai et al., 2013; Votier et al., 2004, 2010). The fine-scale analysis of seabird movement behaviour in relation to fishing boats can reveal whether birds are actively following the boats and permit quantification of key features of these interactions, for example the scale, frequency and individual heterogeneity (Bodey et al., 2014; Collet, Patrick, & Weimerskirch, 2017a,b; Patrick et al., 2015; Votier et al., 2010). Developing a modelling framework to evaluate the dependency of individual seabirds on discards is therefore critical for evaluating demographic effects and the potential consequences that changes in international regulation may have on marine food webs (Bicknell, Oro, Camphuysen, & Votier, 2013; Cohen et al., 2014; Tew Kai et al., 2013; Votier et al., 2004).

By recognising the distinction between movement steps at a finer scale and movement phases at a larger scale, our model can identify periods when an animal is actively following a fishing boat, irrespective of its movement mode. We apply the framework to GPS data collected on a central place forager, the northern fulmar *Fulmarus glacialis* (hereafter "fulmar"), paired with anonymised locations of fishing boats operating contemporaneously to the tracking data. Fulmars are known to feed on a variety of prey, including offal and non-target fish discharged by commercial fisheries (Phillips et al., 1999) and are therefore one of the species expected to interact with

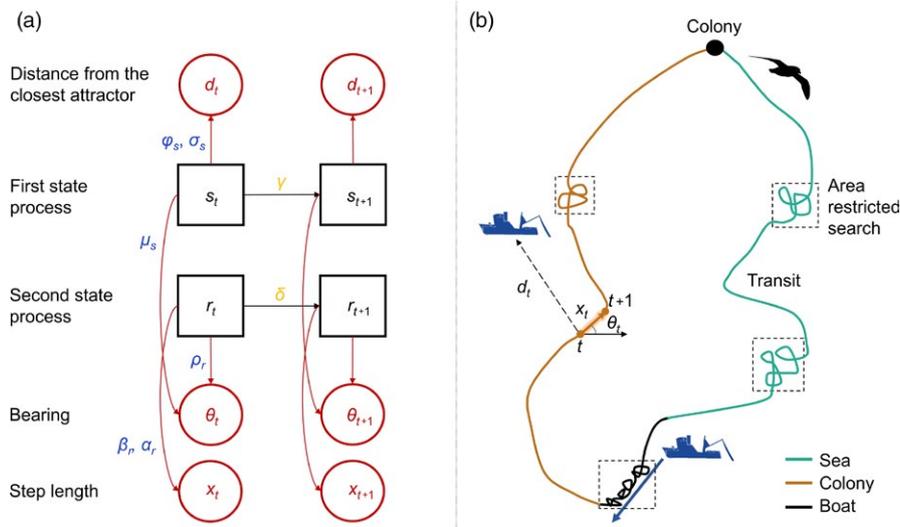


FIGURE 1 (a) Schematic representation of the hidden Markov model. The black squares indicate the two hidden-state processes, s and r . The transition between states over time is indicated with black arrows, and the corresponding probabilities (γ and δ) are in yellow. State-dependent distributions (red arrows), characterised by state-dependent parameters (in blue; described in the text), determine the observations (step lengths x , bearing θ and distance from the closest attractor d ; red circles) at each time step t . (b) Schematic representation of a fulmar's foraging trip. The first state process regulates the movement phase: moving out to sea (green), towards a boat (black) or towards the colony (red). In this example, the bird followed one boat. The blue arrow indicates the direction of movement of the closest boat during this interaction. The second state process regulates the characteristics of the movement steps, distinguishing between resident (area-restricted search; dashed boxes) and transit behaviour. State-dependent observations (step lengths x , bearing θ and distance from the closest boat d) are exemplified for one time step t [Colour figure can be viewed at wileyonlinelibrary.com]

fishing boats to at least some extent. We illustrate how this modelling framework can be used to estimate the rate of interaction between individual animals and moving attractors in their environment, the scale at which these interactions occur and their interplay with other aspects of a foraging trip, such as foraging activity or the need to return to the central place.

2 | MATERIALS AND METHODS

2.1 | Model structure

We developed a modelling framework for the foraging trips of central place foragers where movement phase and movement steps were treated as separate, hidden-states (Nathan et al., 2008) (Figure 1). We assumed that a first hidden-state variable, $s_{i,t}$, defined the mean bearing of the animal at each time step t of trip i , while a second hidden-state variable, $r_{i,t}$, affected the step length and the variability around the mean bearing (Table S1). Under the first state process, an individual could be heading either away from the central place ($s_{i,t} = 1$), towards the central place ($s_{i,t} = 2$) or towards the closest moving attractor ($s_{i,t} = 3$). When the animal was moving away from the central place, we assumed that the state-specific mean bearing $\mu_{s,i,t}$ was drawn from a wrapped Cauchy distribution centred on the angle ν_i between the central place and the furthest location reached during trip i , with unknown trip-specific concentration parameter ε_i , that is $\mu_{1,i,t} \sim \text{WC}(\nu_i, \varepsilon_i)$. If the animal was moving towards the central place, it moved with mean bearing $\mu_{2,i,t}$, which was the angle between the current location and the central place. Finally, if the

animal was moving towards the closest attractor, the mean bearing $\mu_{3,i,t}$ represented the angle between the current location and that attractor. The mean bearing under state $s_{i,t} = 1$ was not fixed because preliminary exploration of the available data showed that the degree of directedness when moving away from the central place could vary among different trips (Figure 2). Taken together, this made it possible to distinguish the two processes affecting angle concentration, that is an individual's current behavioural mode and the variation in directedness among different trips. However, when running a model with fixed bearing for state 1, all other estimates were largely unchanged (Table S9). We assumed that, in the first time step of a trip, an individual was moving away from the central place ($s_{i,1} = 1$).

Under the second state process, an individual could be in transit ($r_{i,t} = 1$) or resident mode ($r_{i,t} = 2$). Following Morales, Haydon, Frair, Holsinger, and Fryxell (2004), McClintock et al. (2012) and McClintock, Russell, Matthiopoulos, and King (2013), the step length at time t of trip i , $x_{i,t}$, was assumed to emerge from a Weibull distribution with state-specific scale (α_i) and shape (β_i) parameters, that is $x_{i,t} \sim W(\beta_i, \alpha_i)$, and steps in transit mode were assumed to be larger than steps in resident mode, that is $\alpha_1 > \alpha_2$. The movement mode also affected the concentration parameter of the bearing distribution ρ_r , and transit mode was assumed to be more directed than resident mode, that is $\rho_1 > \rho_2$. We assumed that, in the first time step, an individual leaving the central place was in transit mode ($r_{i,1} = 1$). The two state processes in combination affected the observed bearing $\theta_{i,t}$, which emerged from a wrapped Cauchy distribution (McClintock et al., 2012, 2013; Morales et al., 2004) with mean $\mu_{s,i,t}$ and concentration parameter ρ_r , that is $\theta_{i,t} \sim \text{WC}(\mu_{s,i,t}, \rho_r)$. Other distributions

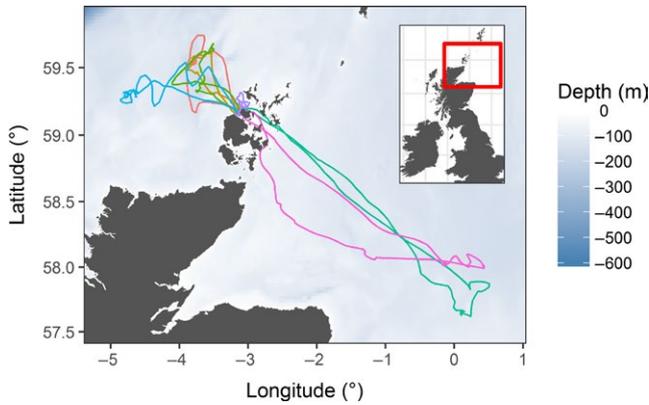


FIGURE 2 Map of the study area and fulmar GPS tracks, coloured by trip [Colour figure can be viewed at wileyonlinelibrary.com]

could alternatively be used to model step lengths and bearings (Beyer et al., 2013; Michelot, Langrock, & Patterson, 2016; Michelot et al., 2017). To assess whether the choice of such distributions affected the results, we ran an alternative version of the model that used a von Mises distribution for the animal's bearing at each time step and a Gamma distribution for its step length (detailed in Appendix S4).

The first state process was also informed by the observed distance, $d_{i,t}$, between an individual and the closest attractor, which had state-dependent log-normal distribution $d_{i,t} \sim \log N(\varphi_s, \sigma_s)$. This distribution was chosen to account for the fact that distance values can only be positive and their distribution will thus tend to be rightly skewed (Figure S1). Specifically, under state $s_{i,t} = 1$ and $s_{i,t} = 2$ (i.e., when not moving towards an attractor), distance from the closest attractor was expected to have the same statistical distribution, but be larger and more variable than under state 3 on average, that is $\varphi_1 = \varphi_2 > \varphi_3$ and $\sigma_1 = \sigma_2 > \sigma_3$.

The temporal sequences of both hidden-states were treated as Markov processes (i.e., the state at a moment in time only depended on the previous state), regulated by two separate sets of transition probabilities among states (Figure 1). The transition probabilities for the first process constituted a 3×3 matrix Γ , where each element, $\gamma_{h,j}$, indicated the probability that $s_{i,t} = j$ given that $s_{i,t-1} = h$. Because the chance of an individual moving towards the central place increases as time progresses, the transition probabilities towards state 2 (i.e., heading towards the central place) were assumed to depend on the elapsed proportion $p_{i,t}$ of the total trip. Similarly, the transition probabilities towards state 3 (i.e., heading towards the closest attractor) were assumed to depend on the distance to the closest attractor, $d_{i,t}$. To model these effects, a multinomial logit formulation was used. Specifically, the transition probabilities to state 2 at time t of trip i were modelled as $\text{logit}(\gamma_{h,2,i,t}) = a_{h,2} + b_{h,2} \cdot p_{i,t}$, where $s_{i,t-1} = h$, $a_{h,2}$ is the basal probability of transitioning from state h to state 2 on the logit scale and $b_{h,2}$ represents the effect of the elapsed proportion of the trip. The transition probabilities to state 3 at time step t of trip i were formulated as $\text{logit}(\gamma_{h,3,i,t}) = a_{h,3} + b_{h,3} \cdot d_{i,t}$, where $s_{i,t-1} = h$, $a_{h,3}$ is the basal probability of transitioning from state h to state 3 on the logit scale, and $b_{h,3}$ is the effect of the distance of

the closest attractor. Transition probabilities to state 1 were then derived as $\gamma_{h,1,i,t} = 1 - \gamma_{h,2,i,t} - \gamma_{h,3,i,t}$. The transition probabilities for the second process formed a 2×2 matrix Δ , where each element, $\delta_{k,l}$, was the probability that $r_{i,t} = l$ given that $r_{i,t-1} = k$.

We use a formulation similar to McClintock et al. (2013) to express the joint conditional likelihood (f) of all observations (step lengths \mathbf{x} , turning angles $\boldsymbol{\theta}$, distances from the closest attractor \mathbf{d}) and unknown state sequences (\mathbf{s} and \mathbf{r}) as the product of their independent likelihoods:

$$f(\mathbf{x}, \boldsymbol{\theta}, \mathbf{d}, \mathbf{s}, \mathbf{r} | \boldsymbol{\omega}) = \prod_{i=1}^I \prod_{t=2}^{T_i} [f(\mathbf{x}_{i,t} | \boldsymbol{\omega}, r_{i,t}) \cdot f(\boldsymbol{\theta}_{i,t} | \boldsymbol{\omega}, s_{i,t}, r_{i,t}) \cdot f(d_{i,t} | \boldsymbol{\omega}, s_{i,t}) \cdot f(s_{i,t} | \boldsymbol{\omega}, s_{i,t-1}) \cdot f(r_{i,t} | \boldsymbol{\omega}, r_{i,t-1})],$$

where $\boldsymbol{\omega}$ denotes the set of all model parameters, I is the total number of trips, and T_i is the duration of each trip.

2.2 | Case study: data collection and processing

We used fulmar tracking data collected on Eynhallow, Scotland (59.12°N, 3.1°W; Figure 2), as part of a long-term demographic study (Thompson & Ollason, 2001) to demonstrate the application of the analytical approach. All bird handling, marking and telemetry tagging was carried out under Home Office and British Trust for Ornithology licences. Adult fulmars were caught on the nest during early chick rearing between the 12th and the 17th of July 2009 using a net or noose. A GPS logger (iGot-U GT-120, MobileAction®, Taipei, Taiwan; 18 g) was attached to mantle feathers using tape (Tesa® 4651, Hamburg, Germany). GPS devices were set to record one position every 10 min. Tagged birds were recaptured after one or multiple foraging trips, and location data were downloaded using the manufacturer's software.

Under EC Regulation No. 2244/2003 and Scottish Statutory Instrument (SI) 392/2004 the geographical position, identity, course and speed of all fishing boats above a given size (15 m in 2009) must be reported at least every 2 hr. Satellite tracking via vessel monitoring system (VMS) is used to record such information (Witt & Godley, 2007). Anonymised VMS locations of fishing boats operating concurrently to fulmar GPS deployments in July 2009 were provided by Marine Scotland Science. Only VMS locations associated with fulmar data were analysed, making it impossible to identify specific boats from our data and results.

Hidden-state models require data collected at regular time intervals. Therefore, fulmar tracks were linearly interpolated at a 10-min resolution using package ADEHABITATLT (Calenge, 2006) in R (R Development Core Team, 2016). Ninety-four per cent of the observed intervals between consecutive bird GPS positions were shorter than the chosen time step, ensuring limited interpolation over long unobserved periods. The step length, that is the distance between consecutive locations in degrees, and the bearing, that is the absolute angle of each step measured from 0 radians, were calculated for each location. VMS data were also linearly interpolated at the same temporal resolution to match fulmar data. Regardless

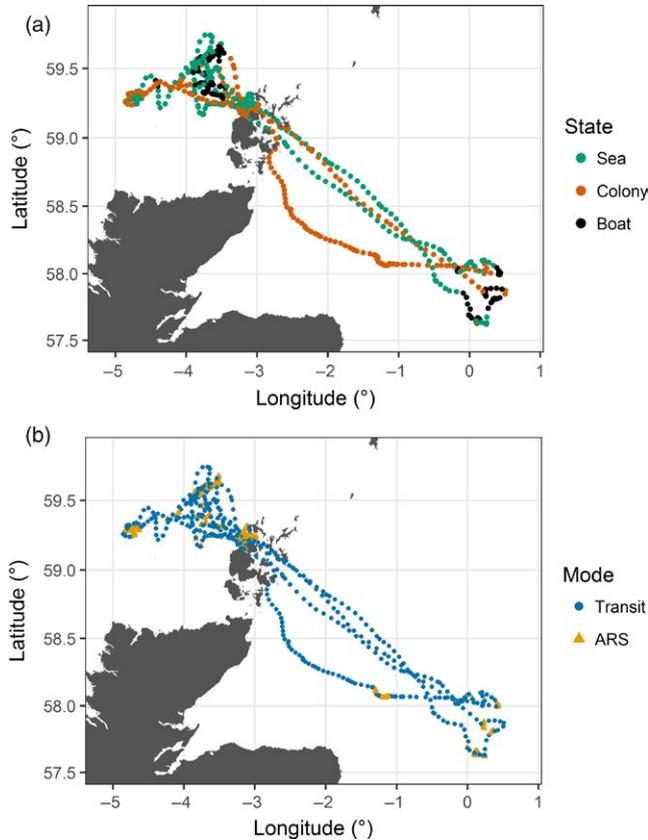


FIGURE 3 Fulmar tracks coloured by the latent behavioural states estimated by the model. In (a), locations are classified based on the first state process, defining mean movement bearing. An individual can be in one of three states: heading out to sea (state 1), heading towards the colony (state 2) and heading towards the closest boat (state 3). In (b), locations are classified based on the second state process, defining fine-scale movement mode. An individual can either be in transit (state 1) or in area-restricted search (ARS) mode (state 2) [Colour figure can be viewed at wileyonlinelibrary.com]

of their distance from a bird, all boats occurring within a 5-min time window around a fulmar's 10-min fix were identified. The coordinates and distance in kilometres of the closest boat were associated with the corresponding fulmar location.

Our analysis aimed to classify fulmar behaviour within a foraging trip. Therefore, a bird's movements in inshore waters around the colony were excluded. Moreover, only one individual was tracked over two different foraging trips, so these were treated separately in the analysis. The overall bearing of each trip was calculated as the angle between the starting location and the location furthest from the colony reached during that trip.

Because the resolution of fishing boat data was relatively coarse (mean interval between VMS locations: 110 min; standard deviation: 91 min), their interpolation at the same temporal scale of fulmar GPS tracks introduced an unknown degree of error over periods between consecutive VMS locations. We tested whether such uncertainty affected the conclusions drawn from our model, using the approach developed by Torres et al. (2011) to generate circular spatial buffers encompassing the area where a boat could have been

at each unobserved time step. We developed a modified version of the model that accounted for the resulting uncertainty in angle and distance to the closest boat, as described in detail in Appendix S3.

2.3 | Model fitting

Models were fitted in a Bayesian framework using OpenBUGS run from R (package R2OPENBUGS; Sturtz, Ligges, & Gelman, 2005). A Bayesian approach was chosen because of its flexibility, which allows concomitantly fitting multiple state processes affecting different components of behaviour. This implementation also facilitates potential extensions to include a hierarchical structure (see Discussion). Prior distributions for model parameters are listed in Table S2. Markov chain Monte Carlo (MCMC) algorithms were iterated until convergence of the states and parameters. Three chains were run in parallel, each starting at different initial values. The proportions $\lambda_{1,1-3}$ and $\lambda_{2,1-2}$ of time steps classified under each state were used to monitor the convergence of both state variables. Convergence was assessed by visually inspecting trace and density plots (Lunn, Jackson, Best, Thomas, & Spiegelhalter, 2013) and confirmed using the Brooks–Gelman–Rubin (BGR) diagnostic and Monte Carlo (MC) error (Lunn et al., 2013). The package coda was used to assess convergence, calculate effective sample size and extract posterior estimates (Plummer, Best, Cowles, & Vines, 2006). Appendix S1 reports the code for the model in OpenBUGS format.

3 | RESULTS

Six individual fulmars were tagged during the study period, with a total of seven foraging trips available for analysis (Figure 2). Trips lasted 25 hr on average (range 18–34 hr). The final, regularised and filtered dataset included 1,061 locations. The median distance from the closest boat at any moment in time was 18 km, although this ranged widely (between 70 m and 57 km) and appeared to have a multimodal distribution (Figure S1).

The initial 10,000 iterations were discarded as burn-in, while 200,000 unthinned iterations were used for inference (Link & Eaton, 2012). The analysis required 18 hr (including model compiling and initialisation times) on 8 Intel(R) Core(TM) i7-4910MQ CPU @ 2.90 GHz processors, 16 GB RAM. For comparison, fitting the model to a subset of the data including four trips and approximately half of the data points (582 locations) required 8.5 hr. Convergence was confirmed by the relative diagnostics and the effective sample size was greater than 400 for all parameters (Lunn et al., 2013). Despite the large number of parameters in the model, these all converged adequately and were estimated with precision, possibly because a Bayesian approach allowed setting some broad constraints on the priors that facilitated mixing and state identification (Table S2). For example, we set state $r_{it} = 2$ to be more convoluted than $r_{it} = 1$ by specifying a constraint on angle concentration $\rho_1 > \rho_2$. We also set $\rho_1 \geq 0.5$ so that $r_{it} = 1$ represented directed movement. Similar constraints reflected a broad understanding of the biological processes underlying the data. However, some

FIGURE 4 Estimated effects of covariates on state transition probabilities. In (a), relationship between the elapsed proportion of a trip and the probability of switching from each state to state 2 (heading to the colony). In (b), relationship between the distance to the closest boat and the probability of switching from each state to state 3 (heading towards the closest boat) [Colour figure can be viewed at wileyonlinelibrary.com]

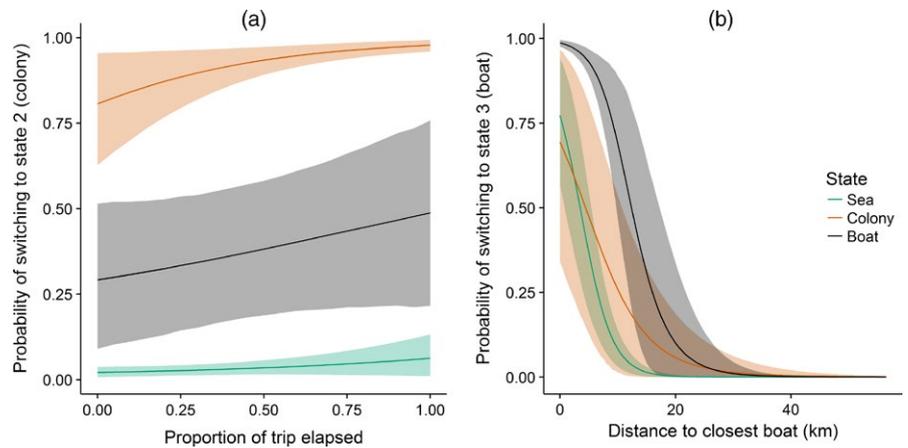
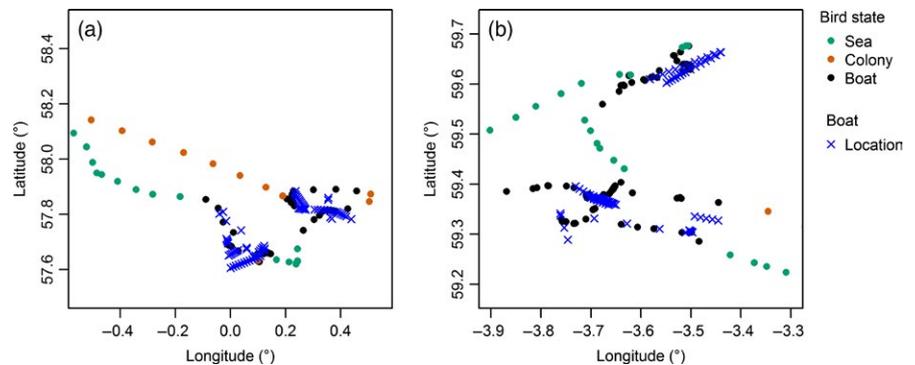


FIGURE 5 Examples of fulmar interactions with closest fishing boats estimated by the hidden-state model. In (a), a portion of the track from trip 4. In (b), a portion of the track from trip 3 [Colour figure can be viewed at wileyonlinelibrary.com]



of the trip-specific concentration parameters for the bearing of state 2 (heading out to sea), ε_p , showed relatively poorer chain mixing because movements tended to be highly directed during some portions of these trips (i.e., ε_i close to 1; Figure S2). Due to computing memory limitations, we retained only one in 20 iterations for both state variables. Posterior estimates of model parameters and associated uncertainty are summarised in Table S3.

The model correctly classified the periods when a bird was heading out to sea and moving towards the colony (Figure 3a), which were characterised by a log-normal distribution of distances from the closest boat centred on 3.1 km on the log scale (i.e., 22 km). In contrast, when a bird was following the closest boat, the mean distance was smaller (0.9 km on the log scale, i.e., 2.5 km). The probability of heading towards the colony increased as the trip progressed (Figure 4a), while the probability of switching towards a boat declined as the distance from the closest boat increased (Figure 4b). Specifically, the probability of a bird switching towards a boat if it was travelling towards the colony (state 2) approached 0 after 30 km, while in state 1 (when the bird was heading out to sea), the transition probability approached 0 before 20 km. The relationship with distance was also more variable in state 2 than under state 1. When heading towards a boat, an individual tended to remain in that state with high probability, up to a distance of more than 30 km. Animations of the tracks coloured by the median posterior estimate of state $s_{i,t}$ at each time step (particularly for trips 3, 4 and 7) illustrate the ability of the model to identify periods when a bird was actively following the closest fishing boat (Appendix S2; examples in Figure 5).

The distinction between transit and resident mode (state $r_{i,t}$) was also clear, with resident mode being characterised by small, convoluted steps ($\rho_2 = 0.37$, while $\rho_1 = 0.81$) (Figure 3b). When an individual was heading out to sea, 43% of locations were in transit mode, against 57% in resident mode (Table S4). Transit mode became more frequent while travelling towards the colony, representing 59% of locations in transit mode against 41% in resident mode. When following a boat, birds were mostly (76%) in resident mode, although in 24% of the time they showed directed movement with larger step lengths, corresponding to the initial approach phase (Table S4). On average, birds spent 24% of their time following fishing boats, but with marked differences among trips and individuals (Table S5). Boat interactions lasted between 10 min and 7.3 hr (mean = 2.7 hr; $SD = 2.1$); 33% of ARS behaviour occurred while following a boat, while the remaining 67% occurred while heading out to sea or towards the colony.

Results remained largely unchanged if a different set of distributions for the step length and bearing was used (Appendix S4). Similarly, the inclusion of uncertainty in boat interpolated locations following Torres et al. (2011) did not alter the conclusions of the model (Appendix S3).

4 | DISCUSSION

The modelling approach presented in this study allows the identification of the processes that regulate the movement of central place

foragers over the course of a foraging trip. These processes operate at different scales and result in heterogeneous movement steps (defining an individual's behavioural mode) nested within the broader phases that constitute a foraging trip. Therefore, the model explicitly acknowledges the multiscale nature of animal movement ecology, reflecting aspects of the short- and long-term motivation driving an individual's behavioural decisions as it moves in the environment (Nathan et al., 2008). Here, the approach was applied to classify periods when a marine central place forager, the northern fulmar, was actively following fishing boats, presumably to access offal and non-target fish discarded in the sea. More generally, this approach offers the potential to explore how various ecological agents and anthropogenic activities could influence movement patterns by either attracting or repelling individuals as they forage from their central place.

Discriminating the three attraction processes defining the movement phase of a foraging trip (away from the central place, towards the central place and towards moving attractors) was possible because these were explicitly decoupled from the process determining movement features at a small scale (i.e., the speed and directedness of movement steps). Therefore, movement mode and phase can be combined flexibly via the two hidden-state processes. Our model differs from the approach proposed by Michelot et al. (2017), who defined movement phases in conjunction with specific features of the associated steps. Their approach is effective when a foraging trip can be split into predefined segments. However, it could not accommodate scenarios where foraging areas are less localised, the interaction with attractors in the landscape occurs at irregular times and locations, and the attractors may move. The novel formulation presented here offers a general approach that does not require one to assume a stereotypical sequence of states during a trip, and further extends the framework proposed by McClintock et al. (2012) for biased movements. For example, in trip number 6 of this study, the tracked bird moved towards the colony, but then flew out again before returning to the colony and concluding the trip, a sequence of behaviours that was correctly classified by the model. Similarly, foraging bouts indicated by the ARS mode were not constrained to occur in predefined foraging areas. To our knowledge, this is the first example of telemetry data being used to model multiple state processes separately at different scales. Overlaying the two state processes highlighted that ARS behaviour occurred disproportionately in different phases of the trip. This mode corresponds to putative foraging activity (Kareiva & Odell, 1987), but possibly also includes resting and drifting on the sea surface. Understanding how movement modes are distributed over the course of a foraging trip is important to characterise the dynamic allocation of time and energy to different activities (Grémillet, Wright, Lauder, David, & Wanless, 2003). This could shed light on an individual's decision-making process, as well as provide information on the variable vulnerability to anthropogenic threats and disturbances at different moments in time (Dean et al., 2013). For species that only forage in well-defined regions (Michelot et al.,

2017), the approach could be modified to explicitly quantify the increased probability of switching to ARS mode as time or distance from the central place increases. Moreover, a fourth state could be added to the first state process to further distinguish movement that is not directed towards attractors or the central place into movement away from the central place and movement with unknown bearing (e.g., targeting foraging patches off the main course of the trip). We ran a model with this additional state and present results in the Supporting Information (Appendix S5, Table S8 and Figure S5). Overall, movement states under the two processes could be successfully described because of the high degree of separation between the corresponding distributions of the movement variables and the use of the ancillary variable distance from the closest attractor (Beyer et al., 2013).

We focused on seabirds' attraction to fisheries as an example of the relevance of the proposed approach to inform management of human activities at sea. Seabirds are known to occur in areas that are intensely used by fisheries, but it is often unclear whether the animals are directly exploiting fishery discards or relying on the same prey aggregations (Karpouzi, Watson, & Pauly, 2007; Tew Kai et al., 2013). Our analytical approach can be used to assess whether tracked animals changed their movement patterns and actively followed fishing boats. Because the movement mode is decoupled from the attraction towards a boat, the model both identifies the threshold distance at which an individual starts its approach and estimates the time spent putatively foraging around a boat. We applied the model to fulmar tracking data and found that, on average, tracked birds spent around a quarter of their trips in close proximity to fishing boats, with one bird actively following a boat for >7 hr. Moreover, a third of recorded ARS behaviour occurred while following a boat, suggesting that a substantial component of these birds' foraging activity could be dependent on discards. However, the time spent tracking boats varied widely among individuals and trips. Such variability could be ascribed to the differential occurrence of fishing boats within the detection range of an individual during a specific trip, but could also reflect individual differences in the propensity to approach boats and in the reliance on discards as a source of food (Granadeiro et al., 2014; Patrick et al., 2015; Votier et al., 2010). In turn, these individual differences in interaction rate could result in different exposure to by-catch risk (Lewison et al., 2014). In future, multiple trips by single individuals could be used to characterise such heterogeneity, paired with stable isotope analysis to verify resulting dietary differences (Granadeiro et al., 2014; Votier et al., 2010). To this purpose, the Bayesian formulation of the model will grant the flexibility required to include a hierarchical structure and accommodate individual random effects. With a larger tracking dataset, our model could also be extended to include age, sex, season and time of day as covariates potentially affecting transition probabilities among states, which could help clarify some of the observed differences among individuals (Collet et al., 2017b). The effects of a variable reliance on discards and by-catch risk on individual condition, survival and reproductive success could then be evaluated using life-history data collected via long-term population monitoring (Cohen et al., 2014; Collet et al., 2017b).

The ability of the model to capture the interplay of motivations driving individual decisions was demonstrated in this study with the inclusion of the effects of distance from the closest boat and proportion of the trip elapsed. The state-specific probability of switching towards the closest boat and its variable relationship with distance highlights the trade-offs an individual makes between the potential benefits of accessing discards, the distance to reach this source of food and the phase of the trip (Cohen et al., 2014). While travelling out to sea in the initial part of a foraging trip, fulmar propensity to switch towards a boat tapered off rapidly with distance, reaching 0 at around 20 km. In this phase, variability among individuals and trips was small. In contrast, the propensity to switch towards a boat when travelling back to the colony may be balanced against several other factors, such as the cumulative feeding success over the trip and the growing pressure to return to attend the chick. This could explain the estimated larger variability in the corresponding transition probability. An individual may also be more willing to travel long distances to reach a boat if a trip was particularly unsuccessful (Cohen et al., 2014), which would justify the probability of following a boat dropping to 0 at larger distances. Similarly, when a bird switched its movement towards a boat, it was unlikely to switch states, reflecting a relatively stable decision-making process. In general, the maximum ecological footprint of fishing boats' influence on birds' decisions was over three times greater for fulmars than previously estimated for northern gannets *Morus bassanus* (Bodey et al., 2014). Here, we estimated that a boat could attract a fulmar up to approximately 35 km, which could represent the maximum detection range for the species. This distance is comparable to the 30 km threshold identified by Collet et al. (2017b) for wandering albatrosses *Diomedea exulans* and black-browed albatrosses *Thalassarche melanophrys*. The inconsistency among species could reflect differences in the sensory system used to locate food, with *Procellariiformes* such as fulmars and albatrosses relying largely on olfaction as opposed to sight (Hutchison & Wenzel, 1980; Nevitt, 2008). Further work applying this modelling approach to other scavengers could quantify species- or population-specific parameters, which would support the investigation of the implications of discarding for different seabird communities.

Fishing boat locations were only available from VMS at a coarser temporal resolution than fulmar GPS tracks. Therefore, an unknown degree of uncertainty surrounds our interpolated boat locations. However, it is important to note that our approach detected direct interactions between birds and fishing boats despite such uncertainty and that the estimated scale and frequency of interactions between tracked birds and fishing boats did not vary when the method proposed by Torres et al. (2011) was used to capture the potential magnitude of interpolation errors. In addition, boat locations were not filtered on the basis of their activity state, which previous studies have inferred from the boats' movement patterns (e.g., Bodey et al., 2014). We did not take this approach because we did not want to assume a priori that birds only follow boats when the vessels are actively fishing. Collet et al. (2017a) did not find a relationship between attendance to fishing boats

and mass gain, suggesting that attraction might occur even in the absence of active fishing or discarding. Future work could explore the potential difference in attractiveness among different activities and types of fishing boats (e.g., trawling versus non-trawling), which also contribute to the trade-offs regulating behavioural decisions, thus shedding light on some of the heterogeneity among trips we detected.

The model developed here has broad applicability beyond the presented case study of seabird interactions with fisheries. Firstly, it could naturally be applied to quantify the attraction of other central place foraging species towards any static or mobile anthropogenic activity providing enhanced access to food, for example pinnipeds targeting underwater structures acting as reefs (Russell et al., 2014) or fish farms (Sepúlveda et al., 2015). The approach could also be modified to model individuals' avoidance of disturbing activities, such as intense noise sources (e.g., Russell et al., 2016). In addition, the role of dynamic environmental variables on movement decisions could be explored. For example, the characterisation of the first phase of seabirds' foraging trips could be improved by including an effect of wind direction in determining the overall bearing when leaving the colony. This will be especially important for species such as fulmars that rely on dynamic soaring for long-ranging flight (Furness & Bryant, 1996). In general, decoupling movement steps from movement phases allows disentangling the processes influencing movement at multiple scales (Nathan et al., 2008). As a result, the model may potentially be adapted to any setting in which a species uses separate habitats for different activities or life-history stages. For example, it could be reformulated for the movements of migratory species, where the patterns of attraction switch seasonally, to assess the effects of anthropogenic activities at different stages of migration (e.g., Schofield et al., 2010). Finally, external agents need not be anthropogenic, and the approach could thus be used to model the influence of predators' distance on prey movements (e.g., Breed et al., 2017), the location of conspecifics in groups of social species (Boinski & Garber, 2000) or the availability of carcasses on the ranging pattern of scavengers (Kane, Healy, Guillerme, Ruxton, & Jackson, 2017). In essence, the model requires the estimation of bearings representing competing attraction or repulsion processes affecting an individual over time, and extensive telemetry datasets are already available to develop many of these possible extensions. These applications will improve our understanding of the functional mechanisms driving animal behaviour and how both natural and anthropogenic drivers influence movement patterns.

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AUTHORS' CONTRIBUTIONS

All authors contributed to discussions that led to the development of the study. P.T. and E.E. designed and managed the data collection; E.P., E.E. and P.T. conceived the research question; E.P. and L.N. developed the modelling approach; E.P. led the analysis and the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/doi:10.5061/dryad.0d377r6> (Pirotta, Edwards, New, & Thompson, 2018).

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SUPPORTING INFORMATION

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