Characterising menotactic behaviours in movement data using hidden Markov models

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Abstract

1. Movement is the primary means by which animals obtain resources and avoid hazards. Most movement exhibits directional bias that is related to environmental features (defined as taxis when biased orientation is voluntary), such as the location of food patches, predators, ocean currents or wind. Numerous behaviours with directional bias can be characterised by maintaining orientation at an angle relative to the environmental stimuli (menotaxis), including navigation relative to sunlight or magnetic fields and energy-conserving flight across wind. However, new methods are needed to flexibly classify and characterise such directional bias.

2. We propose a biased correlated random walk model that can identify menotactic behaviours by predicting turning angle as a trade-off between directional persistence and directional bias relative to environmental stimuli without making a priori assumptions about the angle of bias. We apply the model within the framework of a multi-state hidden Markov model (HMM) and describe methods to remedy information loss associated with coarse environmental data to improve the classification and parameterisation of directional bias.

3. Using simulation studies, we illustrate how our method more accurately classifies behavioural states compared to conventional correlated random walk HMMs that do not incorporate directional bias. We illustrate the application of these methods by identifying cross wind olfactory foraging and drifting behaviour mediated by wind-driven sea ice drift in polar bears (Ursus maritimus) from movement data collected by satellite telemetry.

4. The extensions we propose can be readily applied to movement data to identify and characterise behaviours with directional bias towards any angle, and open up new avenues to investigate more mechanistic relationships between animal movement and the environment.

Keywords
behaviour, hidden Markov models, movement ecology, orientation, remote tracking, taxis, telemetry
1 | INTRODUCTION

Behaviour is the primary way by which animals interact with their external environment to meet their needs. Nearly all biological activity manifests in the form of movement, from fine scale behaviours (e.g. grooming or prey handling) to large-scale changes in location to access resources (e.g. food and mates) or avoid factors that increase energy expenditure or pose risk of injury (e.g. predation or hazardous environments; Wilmers et al., 2015). The improvement of tracking technology increases our ability to accurately identify and characterise behaviour, which is central to understanding animal ecology (Kays et al., 2015; Wilmers et al., 2015). To answer key ecological questions, movement models should incorporate both internal conditions and environmental contexts to effectively leverage this wealth of data (Kays et al., 2015; Schick et al., 2008).

Animals tend to maintain heading (i.e. the orientation is auto-correlated), which can be modelled using a correlated random walk (CRW; Benhamou, 2006; Schick et al., 2008). When searching for resources in sparse environments, animals may alternate between different movement strategies. For example, in the absence of a desired resource, animals may enter an exploration phase (e.g. ranging or olfactory search), when they sense that they are near a target they may enter a localised exploitation phase (e.g. area restricted search), and when they reach the target, they may enter an exploitation phase (e.g. grazing or prey handling; Auger-Méthé, Derocher, et al., 2016; Bartumeus et al., 2016; Schick et al., 2008). These types of movements are typically influenced or informed by the external environment. At the basic level, the environment may alter movement speed or trigger switching between different movement modes/beaviours without influencing directionality. For example, polar bears (Ursus maritimus) may increase their time resting in low quality habitat to balance energy expenditure given prey availability (Ware et al., 2017). Movement orientation, measured as turning angle between successive locations, can also be affected by or modulated in response to environmental stimuli or cues (e.g. foraging patches, nest sites, predators and directions of ocean current, wind and sunlight; Benhamou, 2006; Codling et al., 2008). In the animal movement literature, preference for moving in a particular direction is defined as bias. Directional response to the external stimuli is a special case of bias defined as taxis (Codling et al., 2008). The degree of bias among different behaviours occurs along a spectrum from being primarily biased towards a preferred direction or an external factor (biased random walk; BRW), to a trade-off between directional persistence and directional bias (biased correlated random walk; BCRW), to being primarily governed by directional persistence (CRW; Benhamou, 2006; Codling & Bode, 2016; Codling et al., 2008). Research has explored movement where bias is directly towards (i.e. positive taxis) or away (i.e. negative taxis) from a target/focal point—for example, bias relative to light (phototaxis; e.g. Park & Lee, 2017), sound (phototaxis, e.g. Diego-Rasilla & Luengo, 2004) and water currents (rheotaxis; e.g. Mauritzen et al., 2003; Savoca et al., 2017).

In contrast to simple taxis, which usually assume movement is directly towards (or away from) the target, some behaviours exhibit bias towards a constant angle relative to stimuli or target (menotaxis). For example, the microalga Chlamydomonas reinhardtii exhibits movement at an angle to light to maintain preferred luminosity (Figure 1a; Arrieta et al., 2017). Loggerhead sea turtle (Caretta caretta) hatchlings exhibit positive phototaxis to get to shore following nest emergence, followed by movement perpendicular to waves to move away from shore, then using magnetic fields for large-scale navigation (photomotaxis; Figure 1b; Lohmann et al., 2008; Mouritsen, 2018). Some seabirds exhibit bias relative to wind direction (anemotaxis); fly approximately 50° relative to wind to maximise ground speed during transitory flights, and fly crosswind to maximise the chance of crossing an odour plume during olfactory search (Figure 1c; Nevitt et al., 2008; Ventura et al., 2020). Similar crosswind olfactory search has been observed in several other taxa (Figure 1c,d; Baker et al., 2018; Kennedy & Marsh, 1974; Togunov et al., 2017, 2018). In mobile environments (i.e. aerial or aquatic systems), the observed motion determined from remote tracking reflects both voluntary movement and advection by the system, and also influences the apparent orientation of movement (Auger-Méthé, Lewis, et al., 2016; Gaspar et al., 2006; Schick et al., 2008). For example, the motion of a stationary polar bear on sea ice reflects sea ice drift (Auger-Méthé, Lewis, et al., 2016), which tends to move 20° relative to wind, the primary driver of drift (Figure 1d; Bai et al., 2015).

Identifying behaviours in movement data is a field of active development, and there is a need to develop more sophisticated movement models that consider the perceptual and cognitive capacities of animals (Auger-Méthé, Derocher, et al., 2016; Bracis & Mueller, 2017; Gaynor et al., 2019; Kays et al., 2015). Hidden Markov models (HMMs) are well-developed statistical models used to describe behavioural changes using movement data. HMMs and other movement models that integrate relationships between environmental data and movement characteristics (e.g. speed and orientation) have proven to be effective at elucidating interactions between movement and the environment (Kays et al., 2015; McClintock et al., 2020). Thus far, HMMs have only been used to model positive and negative taxis in animal movement paths. The detection of biased behaviours may also be confounded by mismatched spatial and temporal resolutions among data streams. Mismatched, multi-stream, multi-scale data are widespread in the field of spatial ecology and there is a need for statistical tools to integrate disparate data sources (Adam et al., 2019; Bestley et al., 2013; Fagan et al., 2013; Wilmers et al., 2015). In this paper, we first present an extension to BCRW HMMs that relaxes the direction of bias and allows modelling movement towards any angle relative to stimuli (i.e. menotaxis). Second, we propose incorporating a one-step transitional state in HMMs when faced with low resolution environmental data to improve characterising the direction of bias in BRWs. We investigate the accuracy of our model in two simulation studies and illustrate its application using polar bear telemetry data as a case study. Finally, we provide a detailed tutorial for these methods with reproducible R code in Appendix D.
2 | MATERIALS AND METHODS

2.1 | Model formulation

2.1.1 | Introduction to modelling CRW, BRW and basic BCRW

Animal movement observed using location data (i.e. latitude and longitude) is typically described using two data streams: step length \( l_t \in (0, \infty) \) (distance between consecutive locations) and turning angle \( \phi_t \in (-\pi, \pi] \) (change in bearing between consecutive steps), where \( t = 1, \ldots, T \) represents the time of a step (Figure 2; the notation used in this paper is described in Table 1). The probability of the step length \( l_t \), from location at time \( t \) to \( t+1 \), is often modelled with a Weibull or gamma distribution (Langrock et al., 2012; McClintock & Michelot, 2018). We assume that \( l_t \) is distributed as follows:

\[
l_t \sim \text{gamma}(\mu_t^{(1)}, \sigma_t^{(1)}),
\]

where \( \mu_t^{(1)} \in (0, \infty) \) and \( \sigma_t^{(1)} \in (0, \infty) \) are the mean and standard deviation of the step length (these parameters can also be derived from shape and scale parametrisation of the gamma distribution). Animal movement is often influenced by external factors that result in complex movement patterns (Auger-Méthé, Lewis, et al., 2016). For example, some animals reduce speed when travelling through deep snow, increase speed when flying downwind, modulate orientation towards a foraging patch or moving away from predators (Duchesne et al., 2015; McClintock & Michelot, 2018; McClintock et al., 2012). The influence of these factors on movement can be represented by modelling the movement parameters as functions of external factors (e.g. McClintock & Michelot, 2018). We can model behaviours where the mean speed of observed movement is associated with external factors using:

\[
\ln(\mu_t^{(1)}) = \beta_1 + \beta_2 r_t,
\]

where \( \beta_1 \in (-\infty, \infty) \) is an intercept coefficient for step length mean and \( \beta_2 \in (-\infty, \infty) \) is a slope coefficient representing how the mean step length is affected by magnitude of external stimulus \( r_t \) (e.g. wind speed, or speed of neighbouring individuals in a school of fish).

The probability of turning angle \( \phi_t \) is often modelled with a wrapped Cauchy or von Mises distribution (McClinott et al., 2020). We assume that \( \phi_t \) follows a von Mises distribution as follows:

\[
\phi_t \sim \text{vMises}(\mu_t^{(2)}, \kappa_t^{(2)})
\]

where \( \mu_t^{(2)} \in (-\pi, \pi] \) is the mean turning angle parameter at time \( t \) and \( \kappa_t^{(2)} \in (0, \infty) \) is the concentration parameter around \( \mu_t^{(2)} \) (Figure 2a). In a basic CRW, \( \mu_t^{(2)} \) is assumed to equal zero and only the concentration parameter \( \kappa_t^{(2)} \) is modelled. In BRW and BCRW with simple positive or negative taxis (i.e. bias towards or away from a target), the mean turning angle \( \mu_t^{(2)} \) can be modelled as a function of the orientation relative to a stimulus \( \psi_t \) (e.g. direction of den site; Figure 2; McClintock & Michelot, 2018); we assume \( \phi_t \) follows a circular-circular von Mises regression model based on Rivest et al. (2016):

\[
\mu_t^{(2)} = \text{atan2}(\alpha_2 \sin \psi_t, 1 + \alpha_2 \cos \psi_t)
\]
FIGURE 2 Illustration of the proposed menotactic BCRW for one step (a) and a sample three-state track (b). Panel (a) presents the notation used in this paper along with their values. Bold vectors represent values obtained from the data (animal track, blue vectors, and external stimulus, purple vector) and thin vectors represent values estimated by the model. \( l_t \) and \( l_{t-1} \) represent the step length, the light grey unit vector represents directional persistence from which turning angle \( \phi_t \) is calculated. \( \psi_t \) (purple arc) represents the angle of stimulus with magnitude \( r_t \) relative to the bearing at \( t-1 \) (vector of persistence; light grey vector). The green vector represents the vector of attraction with a magnitude of attraction \( M \) and angle \( \theta \) relative to stimulus, which are obtained from the estimated bias parallel, \( \alpha_1 \), and perpendicular, \( \alpha_2 \), to the stimulus (teal). \( \mu^{(b)}_t \) (dark grey arc) represents the expected mean turning angle and reflects a trade-off between persistence (light grey vector) and bias towards \( \theta \) (green vector). \( M^* \) represents the scaled magnitude of attraction. Panel (b) presents a sample track with a BCRW state with bias \( \delta_{2v+1} = 45^\circ \) left of stimulus \( S^{(45^\circ)} \) (orange). A second BRW behaviour \( (B) \) with bias towards \( \delta_B = -22^\circ \) relative to stimulus is divide into a BRW state for the first step \( (B^0; \text{blue}) \) and a CRW state for consecutive steps \( (B^0; \text{light blue}) \). Green vector represents the scaled magnitude of attraction \( M^* \) with direction \( \theta \) relative to the stimulus. To represent environmental error, the true direction of the stimulus (not shown) rotates \(-10^\circ\) each step, while the estimated stimulus (purple) rotates \(-5^\circ\) each step.

where \( \psi_t \in (-\pi, \pi] \) is the observed angle of stimulus at \( t \) relative to the movement bearing at \( t-1 \) and \( \alpha_1 \in (-\infty, \infty) \) is the bias coefficient in the direction \( \psi_t \) (Figure 2a).

2.1.2 Extending the BCRW to allow for menotaxis

The BCRW described above can capture many behaviours exhibiting positive or negative taxis. However, many species exhibit menotactic movement where bias may be towards any angle relative to a stimulus (Figure 1). To capture behaviours with a bias towards an unknown angle of attraction \( \theta \) relative to \( \psi_t \), we propose modelling the mean turning angle as a trade-off between directional persistence, bias parallel to the direction of the stimulus and bias perpendicular to the stimulus (Figures 2a and 3) following:

\[
\mu^{(b)}_t = \alpha_1 \sin \psi_t + \alpha_2 \cos \psi_t, \quad 1 + \alpha_1 \cos \psi_t - \alpha_2 \sin \psi_t,
\]

where \( \alpha_1 \) represents the bias coefficient parallel to \( \psi_t \) as in Equation (4), and \( \alpha_2 \in (-\infty, \infty) \) represents the bias coefficient towards \( 90^\circ \) anti-clockwise of \( \psi_t \). In this framework, the centre angle of attraction relative to a stimulus is represented by \( \theta = \tan \mu^{(b)}_t \). Figures 2 and 3 depict how the mean turning angle is controlled by the two bias coefficients \( \alpha_1 \) and \( \alpha_2 \) and the angle of stimuli \( \psi_t \).

Given the nonlinear circular–circular link function, the slope of Equation (5) varies with \( \psi_t \) and results in artefacts that may not be ecologically meaningful (e.g. a negative slope or slopes approaching \( \infty \); see Appendix A). We present an alternate formulation of \( \mu^{(b)}_t \) with a constant slope in Appendix A, however, this cannot currently be implemented in user-friendly R packages such as momentuHMM.

We can represent where along the spectrum of CRW and BRW a behaviour lies with the magnitude of attraction \( M = \sqrt{\alpha_1^2 + \alpha_2^2} \in [0, \infty) \). A value of \( M = 0 \) represents a CRW, values around 1 represent BCRWs with equal weight for directional persistence and bias towards \( \theta \), and values approaching infinity represent BRWs towards \( \theta \). For a more intuitive metric, we can scale \( M \) to the unit interval using:

\[
M^* = \frac{M}{1 + M}
\]

where \( M^* \in [0, 1) \) represents the scaled magnitude of attraction. The CRW and BRW are limiting cases of Equation (6), where \( M^* \to 0 \) and \( M^* \to 1 \), respectively, while a BCRW would have an intermediate value of \( M^* \).

2.1.3 Integrating multiple states using hidden Markov models

Animal movement is behaviour specific, and HMMs can be used to model telemetry data spanning multiple behaviours (Langrock et al., 2012; Patterson et al., 2008). Using HMMs, we can combine multiple behaviours with distinct types of biased and correlated movement patterns. HMMs are defined by two components: an
unobserved state process (or hidden/latent process) and an observed state-dependent process. The state process assumes that animal behaviours are discrete latent states, $S_i \in \{1, \ldots, N\}$, whose probabilities at any given time $t$ depend only on the state at the previous time step. That is, the state sequence $\mathbf{S}(1, \ldots, T)$ follows a Markov chain governed by state transition probabilities $\gamma_{ij} = \Pr(S_{t+1} = j | S_t = i)$ for $i, j \in \{1, \ldots, N\}$, which are summarised by the $N \times N$ transition probability matrix, $\Gamma = (\gamma_{ij})$. Second, the state-dependent process $\mathbf{X} = (X_1, \ldots, X_T)$ (where $X_i = \{l_i, \phi_i\}$) assumes that the probability of any given observation $X_i$ also known as the emission probability, depends only on the underlying latent state $S_t$ (Langrock et al., 2012; Patterson et al., 2008; Zucchini et al., 2016). That is, the step length and turning angle parameters and their respective coefficients (i.e. $\mu^{(li)}(t), \sigma^{(li)}(t), h_{x_{l_t}}^{(li)}, k_{x_{l_t}}^{(li)}, \beta_1, \beta_2, \alpha_1, \alpha_2$) are assumed to be state specific (i.e. $\mu^{(li)}(t), \sigma^{(li)}(t), h_{x_{l_t}}^{(li)}, k_{x_{l_t}}^{(li)}, \beta_1, \beta_2, \alpha_1, \alpha_2$).

For some behaviours, we may expect animals to have two different, but related, angles to stimuli. For example, during crosswind movement, we may expect the animal to move $90^\circ$ to the left or right of the wind (i.e. $\mu^{(li)} = \psi_l \pm 90^\circ$). Such behaviours will have a bimodal distribution for their turning angle $\mu^{(li)}$ relative to stimulus $\psi_l$, which would be difficult to model with a single distribution. However, we can model such behaviour with two states: biased left of stimulus ($\mathcal{S}^{(li)}$) with bias towards $\psi_l + \theta_{28}$ and biased right of stimulus ($\mathcal{S}^{(ri)}$ with bias towards $\psi_l - \theta_{28}$). To reduce the number of estimated coefficients, these two states can share their parameters: $\mu^{(li)}(t), \sigma^{(li)}(t), h_{x_{l_t}}^{(li)}, k_{x_{l_t}}^{(li)}, \beta_1, \beta_2, \alpha_1, \alpha_2$ and transition probabilities into and out of those states $\gamma_{ij}$. If $\theta_{28}$ and $\theta_{28}$ are assumed to be symmetrical about $\psi_l$, $a_{1,28}$ and $a_{2,28}$ could be shared between symmetrical states by ensuring that $a_{1,28} = a_{2,28}$ and $a_{2,28} = -a_{2,28}$ in Equation (5).

### 2.1.4 Accounting for mismatch in resolutions of data streams

By definition, the direction of bias in a BRW is primarily determined by external factors rather than the direction of the preceding step. However, because the direction of external factors is also correlated in many cases (e.g. bias towards a distant target or towards temporally correlated stimulus; Figure 2b), there is often ambiguity between movement correlated in orientation and movement biased towards a correlated factor, making it difficult to distinguish between BRWs and CRWs (Benhamou, 2006). This ambiguity in the driver of

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**TABLE 1** Description of acronyms and notation used in this paper and their interval, if applicable

| Acronym/variable | Interval | Description |
|------------------|----------|-------------|
| CRW              | –        | Correlated random walk |
| BRW              | –        | Biased random walk |
| BCRW             | –        | Biased correlated random walk |
| TBCRW            | –        | Biased correlated random walk incorporating transitional states |
| $T$              | $\{1, 2, \ldots\}$ | Total number of time steps |
| $t$              | $[1, T]$ | A time step |
| $X_t$            | –        | Set of observations at time $t$ |
| $X$              | –        | The set of all observations ($X_1, \ldots, X_T$) |
| $l$              | $(0, \infty)$ | Step length between consecutive locations |
| $\phi$           | $(-\pi, \pi]$ | Turning angle (i.e. change in bearing) between consecutive steps |
| $r$              | $(0, \infty)$ | Magnitude of the stimulus |
| $\psi$           | $(-\pi, \pi]$ | Direction of a stimulus relative to the bearing of the previous time step |
| $\mu^{(li)}$     | $(0, \infty)$ | Mean parameter of step length |
| $\sigma^{(li)}$  | $(0, \infty)$ | Standard deviation parameter of step length |
| $\beta_1$        | $(-\infty, \infty)$ | Intercept coefficient for mean step length |
| $\beta_2$        | $(-\infty, \infty)$ | Slope coefficient for mean step length and $r$ |
| $\mu^{(li)}(t)$  | $(-\pi, \pi]$ | Mean parameter of turning angle |
| $h_{x_{l_t}}^{(li)}$ | $(0, \infty)$ | Concentration parameter of turning angle |
| $a_1$            | $(-\infty, \infty)$ | Bias coefficient in the same direction as the stimulus |
| $a_2$            | $(-\infty, \infty)$ | Bias coefficient $90^\circ$ left of the stimulus |
| $\theta$         | $(-\pi, \pi]$ | The direction of bias relative to stimulus |
| $M$              | $(0, \infty)$ | Magnitude of attraction |
| $M^*$            | $(0, 1)$ | Scaled magnitude of attraction |
| HMM              | –        | Hidden Markov model |
| $N$              | $\{1, 2, \ldots\}$ | Total number of behavioural states |
| $S$              | $[1, N]$ | Behavioural state |
| $\gamma_{ij}$   | $(0, 1)$ | Transition probability from state $i$ to state $j$ |
| $\Gamma$         | –        | $N \times N$ Transition probability matrix |
| $B^{(li)}, B^{(ri)}$ | –        | A BRW state, a state for the first step in the BRW, and a state for consecutive BRW steps, respectively |
| $D, D^{(li)}, D^{(ri)}$ | –        | The drift state, a state for the first step in drift, and a state for consecutive drift steps, respectively |

(Continues)
turning angle orientation is particularly true when there is error in the environmental data. If there is a significant mismatch in the resolutions among data streams, BCRW models may favour the higher resolution data streams, potentially at the expense of biological accuracy. If persistence explains more of the observed orientation than environmental data, BCRW models may incorrectly classify BRWs as CRWs (Benhamou, 2006; Codling et al., 2008). This misclassification can occur if location resolution is very high or significantly higher than the environmental data, if environmental error is higher than the location data, or if the direction of stimulus remains relatively homogenous such that only the initial change in orientation exhibits taxis (Figure 2b). We know a priori that for the first step in a BRW, the direction is independent of the prior step. Therefore, the first step in a BRW should be better explained by the environment than persistence even in the presence of error in environmental data (Figure 2b). In other words, the first step in a BRW contains information that can help disambiguate the driver of orientation.

To remedy the information loss associated with inadequate environmental data, we propose leveraging the information in the initial change in orientation by modelling the first step of a BRW state $B^{(f)}$ as a separate transition state from consecutive steps $B^{(c)}$. To ensure $B^{(f)}$ is modelled as a BRW, we must fix $a_{1,B^{(f)}}$ or $a_{2,B^{(f)}}$ to a large (positive or negative) value depending on the expected value of $\theta_{B^{(f)}}$. Second, to ensure that $B^{(f)}$ is fixed to just the first step in a BRW, we must ensure all states go through $B^{(f)}$ to get to $B^{(c)}$, that $B^{(f)}$ instantly transitions to $B^{(c)}$, and that $B^{(c)}$ cannot transition to $B^{(f)}$. These relationships can be enforced by ensuring the transition probability matrix $\Gamma$ follows:

$$\begin{align*}
B^{(f)} & \begin{bmatrix}
0 & 0 & \ldots & 0
\end{bmatrix} \\
B^{(c)} & \begin{bmatrix}
0 & \gamma_{B^{(c)},B^{(f)}} & \gamma_{B^{(c)},2} & \ldots & \gamma_{B^{(c)},N}
\end{bmatrix} \\
\Gamma & = \begin{bmatrix}
\gamma_{3,B^{(f)}} & 0 & \gamma_{3,2} & \ldots & \gamma_{3,N} \\
& \vdots & \vdots & \ddots & \vdots \\
N & \gamma_{N,B^{(f)}} & 0 & \gamma_{N,2} & \ldots & \gamma_{N,N}
\end{bmatrix}
\end{align*}$$

To reduce the number of coefficients, the step length coefficients in Equation (1) can be shared between $B^{(f)}$ and $B^{(c)}$. This method can be applied to any BRW state where the orientation of first step in the state is largely independent of the preceding step; including passive states driven by advection or strongly biased active states.

2.2 | Simulation study

We conducted simulation studies to test two aspects of our proposed menotactic HMM. First, we conducted a basic ‘sanity check’ to confirm that our menotactic BCRW HMM functions as intended in a controlled setting (i.e. using data simulated from the model), and that it can accurately recover its own simulated states when menotaxis is present and well represented by our model. For comparison, we explored the state accuracy of a misspecified null model (a CRW HMM with no bias).

![Figure 3](image-url)
that was applied to data simulated with our model. Second, we investigated the effect of coarse environmental data on state detection and the ability of incorporating a one-step transitional state to mediate the effects of environmental error. We used our polar bear case study as a base to develop the framework of our simulation studies.

### 2.2.1 Polar bear ecology background

We investigated three key behaviours: a passive BRW drift state, a BCRW olfactory search state and a CRW area restricted search state. The prime polar bear foraging habitat is the offshore pack ice during the winter months (approximately January to May, depending on regional phenology; Pilfold et al., 2012; Stirling & McEwan, 1975). The persistent motion of pack ice creates perpetual motion in the observed tracks, even when bears are stationary (e.g. still hunting, prey handling, resting). One of the key drivers of sea ice motion is surface winds, whereby drift speed is approximately 2\% that of wind speed and approximately –20° relative to the wind direction (Tschudi et al., 2010). Passive drift can be modelled as a BRW, with a predicted θ ≈ ±20° (Figure 1d).

In the spring, polar bears’ primary prey, ringed seals (Pusa hispida) occupy subnivean lairs for protection from predators and the environment (Chambellant et al., 2012; Florko et al., 2020; Smith & Stirling, 1975). Due to the large scale of the sea ice habitat and the cryptic nature of seals, polar bears rely heavily on olfaction to locate prey (Stirling & Latour, 1978; Togunov et al., 2017, 2018). The theoretical optimal movement of seals, polar bears rely heavily on olfaction to locate prey (Stirling & Latour, 1978; Togunov et al., 2017, 2018). Due to the large scale of the sea ice habitat and the cryptic nature of seals, polar bears rely heavily on olfaction to locate prey (Stirling & Latour, 1978; Togunov et al., 2017, 2018). Olfactory search can be modelled as a BCRW, with a predicted drift speed is approximately 2\% that of wind speed and approximately –20° relative to the wind direction (Tschudi et al., 2010). Passive drift can be modelled as a BRW, with a predicted θ ≈ ±20° (Figure 1d).

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### 2.2.2 Track simulation

We simulated movement tracks using a four-state HMM with drift $D$, olfactory search left of wind $O^{(L)}$, olfactory search right of wind $O^{(R)}$ and area restricted search ARS. The $D$ and $O^{(L/R)}$ states were biased in relation to uniquely simulated wind fields. Wind fields were generated in four steps: simulating pressure fields, deriving longitudinal and latitudinal pressure gradients, re-scaling the pressure gradients to represent wind velocities and finally applying a Coriolis rotation to obtain final wind vectors (see Appendix B for detail).

The $D$ state was defined as a passive BRW with mean step length determined by wind speed following Equation (2), and turning angle following Equation (6) with bias towards $θ_D = -15°$, as estimated from the polar bear case study below. $O^{(L)}$ and $O^{(R)}$ were defined as BCRWs following Equation (6) with biases towards $θ_{OL} = 90°$ and $θ_{OR} = -90°$ relative to wind and a large mean step length. Last, ARS was defined as a CRW with no bias relative to wind and low mean step length. All coefficients used in the simulation are presented in Table 2. All tracks were simulated using the momentuHMM package (see Appendix D for details; McClintock & Michelot, 2018).

In the first simulation study, movement relative to wind, $ψ_w$, was estimated from interpolated longitudinal and latitudinal pressure fields. In the second simulation study, the longitudinal and latitudinal wind fields were first spatially averaged to six resolutions (1, 2, 4, 8, 16 and 32 km) using the raster package (Hijmans & van Etten, 2016) then interpolated. For both simulation studies, we evaluated model accuracy by first predicting states from fit HMMs using the Viterbi algorithm (Zucchini et al., 2016), merging analogous states (i.e. first drift $D^{(L)}$ and consecutive drift $D^{(C)}$, and $O^{(L)}$ and $O^{(R)}$), then calculating the proportion of correctly identified states (number of correctly identified steps / total number of steps). We also calculated recall (proportion of a simulated state correctly identified) for $D$ following $\sum($correctly predicted $D)/ \sum($simulated $D)$.

### 2.2.3 Fitting HMMs to simulations

The first simulation validated the ability of our extended BCRW HMM to accurately recover states by comparing our model to a simpler CRW HMM. We fit 100 simulated tracks with two models: a three-state CRW HMM where mean drift speed was determined by wind but no states exhibit bias (e.g. Ventura et al., 2020) and a four-state BCRW HMM with wind-driven drift speed and bias in two states.

### TABLE 2 Coefficients used to simulate the four-state BCRW HMM movement track (left side) and the corresponding bias parameters (right side)

| State  | $β_{1S}$ | $β_{2S}$ | $σ^{(L)}_S$ | $σ^{(R)}_S$ | $α_{1S}$ | $α_{2S}$ | $κ^{(L)}_S$ | $κ^{(R)}_S$ | $θ_0(°)$ | $M^*$ |
|--------|----------|----------|-------------|-------------|----------|----------|-------------|-------------|----------|------|
| D      | -2.2     | 0.1      | -2.4        | 100         | -26.8    | 5        | 2           | 90          | -15      | 0.99 |
| $O^{(L)}$ | 0.1     | -        | -0.5        | 0           | 5        | 2        | -90         | 0.83        |
| $O^{(R)}$ | 0.1     | -        | -0.5        | 0           | 5        | 2        | -90         | 0.83        |
| ARS    | -2.5     | -        | -2.8        | 0           | -        | 0.5      | -           | 0           |

Note: Non-applicable values are indicated by ‘-‘.
As the CRW HMM assumes no bias is present, the mean turning angle was fixed to zero and not estimated for any state \( \mu_2^{(b)} = 0 \). The BCRW HMM was formulated following the methods described in 2.2.2, with the \( D \) and \( O^{(L)} \) and \( O^{(R)} \) states defined as biased relative to wind with both \( a_1 \) and \( a_2 \) being estimated. As we are primarily interested in differentiating the effect of incorporating menotaxis, the \( D \) state step length was modelled as a function of wind speed as in Equation (2) in both CRW and BCRW HMMs.

The second simulation study evaluated the effect of incorporating a transition state to alleviate information loss with lower environmental resolution. We down-scaled 100 simulations to six resolutions and fit two HMMs: the same four-state BCRW HMM used to simulate the tracks and a five-state HMM with drift divided into state for the first drift step \( D^{(l)} \) and consecutive drift steps \( D^{(i)} \) (hereafter, TBCRW HMM). Each simulated track was fit to the BCRW and TBCRW HMMs, which were compared by calculating the difference between their respective accuracies.

Drift was assumed to be a passive BRW relative to wind, which was ensured by fixing \( a_{D^{(p)}} \) to a large constant (in our case, \( a_{D^{(p)}} = 100 \)) as described in 2.1.4. \( D^{(l)} \) was modelled as a biased state with respect to wind, however, given the low resolution of wind data, no assumption was made on the direction of the bias relative to wind. Olfactory search was modelled as two states \( O^{(L)} \) and \( O^{(R)} \) that were biased with respect to wind, and we assumed these to be symmetrical about \( 0^\circ \). Finally, we assumed ARS to be a CRW independent of wind. These were modelled by modifying Equation (5) to:

\[
\phi_{s_{k}}^{(b)} = \begin{cases} 
0 & \text{if } S = \text{ARS} \\
\text{atan}(100 \sin \psi_1 + a_{2.5} \cos \psi_1, 1 + 100 \cos \psi_1 - a_{2.5} \sin \psi_1) & \text{if } S = D^{(l)} \\
\text{atan}(a_{1.5} \sin \psi_1 - a_{2.5} \cos \psi_1, 1 + a_{1.5} \cos \psi_1 + a_{2.5} \sin \psi_1) & \text{if } S = O^{(L)} \\
\text{atan}(a_{1.5} \sin \psi_1 + a_{2.5} \cos \psi_1, 1 + a_{1.5} \cos \psi_1 + a_{2.5} \sin \psi_1) & \text{otherwise.}
\end{cases}
\]

\[
\Gamma = \begin{bmatrix}
D^{(f)} & D^{(c)} & O^{(L)} & O^{(R)} & ARS \\
0 & 1 & 0 & 0 & 0 \\
0 & \gamma_2,2 & \gamma_2,3 & \gamma_2,3 & \gamma_2,5 \\
\gamma_3,1 & 0 & \gamma_3,3 & \gamma_3,4 & \gamma_3,5 \\
\gamma_3,1 & 0 & \gamma_3,4 & \gamma_3,3 & \gamma_3,5 \\
\gamma_5,1 & 0 & \gamma_5,3 & \gamma_5,3 & \gamma_5,5
\end{bmatrix}
\]

To reduce the number of estimated coefficients, the coefficients for step length \( \rho_{j}^{(l)} \) were shared between \( D^{(l)} \) and \( D^{(i)} \) and between \( O^{(L)} \) and \( O^{(R)} \). For \( O^{(L)} \) and \( O^{(R)} \), \( \lambda^{(w)} \), \( a_{1.5} \) and \( a_{2.5} \) were also shared along with the state transition probabilities \( \gamma_{j}^{(l)} \). To ensure \( D^{(l)} \) lasts one step, we fixed the transition probabilities following Equation (7). The transition probability matrix contained nine coefficients to be estimated following:

### 2.3 Case study—Polar bear olfactory search and drift

We illustrate the application of our HMM using global positioning system (GPS) tracking data from one adult female polar bear collared as part of long-term research on polar bear ecology (Lunn et al., 2016). The performed animal handling and tagging procedures were approved by the University of Alberta Animal Care and Use Committee for Biosciences and by the Environment Canada Prairie and Northern Region Animal Care Committee (Stirling et al., 1989). We limited the analysis to 1 month during the peak foraging period between 5 April 2011 and 5 May 2011. The collar was programmed to obtain GPS locations at a 30 min frequency. To obtain the continuous environmental data necessary for HMMs, missing locations \( n = 8 \) (56\%) were imputed by fitting a continuous-time correlated random walk model using the `crawal` package in R (Johnson & London, 2018; Johnson et al., 2008; R Core Team, 2020). GPS locations were annotated with wind data using the ERA5 meteorological reanalysis project, which provides hourly global analysis fields at a 31 km resolution (Hersbach et al., 2020). Wind estimates along the track were interpolated in space and time as described in Togunov et al. (2017, 2018). We modelled the polar bear track as a five-state TBCRW HMM as in the second simulation. All statistical analyses were done in R version 4.0.2 (R Core Team, 2020). Reproducible code is presented in Appendix D.

### 3 RESULTS

#### 3.1 Simulation

The first simulation served as a basic confirmation that the proposed BCRW HMM can accurately recover its own states when compared to a misspecified null model without bias. The accuracy (mean and [2.5%, 97.5%] quantiles) of the BCRW HMM (0.96 [0.96, 0.96]) was higher than that of the unbiased CRW HMM (0.77 [0.77, 0.78]). In both models, olfactory search was the most accurately identified state (Table C1). The BCRW HMM had higher precision in estimating all states compared to the CRW HMM. The CRW HMM had the lowest precision rate when predicting \( D \), where it more frequently confused it for ARS (Table C1).

When there was no environmental error, the basic BCRW HMM outperformed the TBCRW HMM (Fig. 4). As the environmental resolution declined, the accuracy of both models also declined, however, the TBCRW HMM outperformed the BCRW HMM at resolutions coarser than 4 km (Figure 4). At finer resolutions, recall (mean and [25%, 75%] quantiles) of \( D \) in the BCRW HMM was higher than in TBCRW HMM (e.g. recall\(_{\text{BCRW},1km} = 0.88[0.84,0.91] \)
At resolutions coarser than 8 km, recall of $D$ in the BCRW HMM was lower than in the TBCRW HMM (e.g. recall $BCRW,32\text{ km} = 0.40[0.31, 0.46]$ vs. recall $TBCRW,32\text{ km} = 0.61[0.54, 0.67]$).

In both the BCRW HMM and TBCRW HMM, the mean estimates of $\theta_D$ and $M^*$ across the 100 simulated tracks were close to the simulated $-15^\circ$, however, there was a marked difference in the spread of estimates across the simulations (Figure 5a). At resolutions 4 km or finer, the BCRW HMM provided reasonable estimates of $\theta_D$ and $M^*$ ($\geq 79\%$ of $\theta_D \in \theta_D \pm 5^\circ$; Figure 5). At resolutions coarser than 4 km, the spread of estimated values increased with $\leq 30\%$ of $\theta_D \in \theta_D \pm 5^\circ$ (Figure 5a). According to the BCRW HMM, at a 16 km resolution, $D$ would be characterised as a BCRW ($M^*_D \approx 0.5$) and a BRW at 32 km ($M^*_D \approx 0$; Figure 5b). These patterns were exaggerated for the $D^{(f)}$ state in the TBCRW HMM, with the estimates of $\theta_D$ widening at 4 km resolutions and coarser and the rate of change $M^*_D$ suggested $D^{(f)}$ was a CRW (Figure 5). In contrast, the transitionary $D^{(c)}$ state in the TBCRW HMM was estimated more accurately than either $D^{(f)}$ or $D$, with more estimates of $\theta_D$ closer to the simulated $-15^\circ$ at all resolutions (Figure 5a).

### 3.2 Case Study: Polar bear olfactory search and drift

The fitted HMM showed distinct movement characteristics among the five modelled states. Based on the stationary state
The bear spent about 35% of its time between $D^{(c)}$ and $D^{(f)}$, 47% between $O^{(L)}$ and $O^{(R)}$, and 17% in ARS. The only notably differences in transition probabilities were that $D^{(c)}$ was more likely to be followed by $O^{(L,R)}$ than ARS and that the transition between $O^{(L)}$ and $O^{(R)}$ was significantly less likely than the probability of remaining within the same olfactory search state (Table 3).

First drift, $D^{(f)}$, was characterised as a passive BRW with mean direction and speed determined by wind. As described in 2.2.3, the downwind bias coefficient was fixed to $a_{1,D^{(f)}} = 100$ to ensure it was a BRW and crosswind bias coefficient was estimated at $a_{2,D^{(f)}} = -27.65$, corresponding to an overall bias towards $\theta_{D^{(f)}} = -15^\circ$ relative to wind (Figures 7b and 8a; Table 4). Turning angle concentration was moderate ($\kappa_{D^{(f)}} = 1.61$) and scaled magnitude of attraction was very high ($M^*_D = 0.99$), best characterising $D^{(f)}$ as a BRW (Figure 8a; Table 4).

The mean observed direction of drift relative to wind was $13^\circ$ (estimated from a von Mises distribution fit to the direction of wind for steps classified as $D^{(f)}$ or $D^{(c)}$). However, turning angle during $D^{(c)}$ showed almost no bias relative to wind ($a_{1,D^{(c)}} = -0.02$ and $a_{2,D^{(c)}} = 0.03; M^*_D = 0.03$) and turning angle concentration was very high ($\kappa_{D^{(c)}} = 75.60$), thus best characterising $D^{(c)}$ as a CRW with high persistence (Figures 7b and 8a; Table 4). These results mirror those observed in the second simulation, which characterised $D^{(f)}$ as a BRW and $D^{(c)}$ as a CRW (Figure 5). The step length of $D^{(f)}$ and $D^{(c)}$ was characterised by a small step length that was explained by an exponential
relationship to wind speed (Figure 9). At the median wind speed of 21.0 km h⁻¹, the mean step length of $D^{(0)}$ was $0.22 \pm 0.09$ km m⁻¹ ($\mu^{(0)} \pm \sigma^{(0)}$), or about 2% of wind speed (Figure 7a; Table 4).

Olfactory search was characterised as a fast BCRW relative to wind. The estimated mean step length was $1.09 \pm 0.63$ km ($\mu^{(0)} \pm \sigma^{(0)}$, Figure 7a; Table 4). Bias downwind during olfactory search was $a_{O}^{(0)} = -0.332$ and bias crosswind was $a_{C}^{(0)} = 1.385$, corresponding to an overall bias towards $\theta^{(0)} = 103^\circ$ relative to wind (Figures 7b and 8b; Table 4). The turning angle concentration was moderate ($k^{(0)} = 2.324$) as was the scaled magnitude of attraction ($M^{(0)} = 0.588$), best characterising olfactory search as a BCRW (Figure 8b; Table 4).

ARS was characterised as a slow CRW with no bias relative to wind. The estimated mean step length was $0.08 \pm 0.06$ km ($\mu^{(0)} \pm \sigma^{(0)}$, Figure 7a; Table 4). Mean turning angle was fixed to zero and the turning angle variance was the lowest among the states ($k^{(s)}_{ARS} = 1.61$), best characterising ARS as a CRW with low persistence (Figures 7b and 8c; Table 4).

### 4 | DISCUSSION

Behaviours with biased movement are common among animals for obtaining resources and avoiding costs (Bailey et al., 2018; Michelot et al., 2017; Ylitalo et al., 2020). Here, we described two extensions to HMMs to identify and characterise menotactic behaviours and

| TABLE 4 Estimated parameters and coefficients for five-state polar bear HMM |
|---|
| Data stream | Parameter | Coefficient | States | Estimate (SE) |
| Step length | $\mu^{(0)}$ | $\beta_1$ | $D^{(f)}, D^{(c)}$ | $-2.118 (0.042)$ |
| | | $\beta_2$ | $D^{(f)}, D^{(c)}$ | $0.107 (0.004)$ |
| | | $\beta_3$ | $O^{(f)}, O^{(r)}$ | $0.087 (0.027)$ |
| | $\beta_4$ | ARS | $D^{(f)}, D^{(c)}$ | $-2.445 (0.037)$ |
| | | $O^{(f)}, O^{(r)}$ | $-0.462 (0.044)$ |
| | | ARS | $-2.804 (0.153)$ |
| Turning angle | $\kappa^{(a)}$ | $\alpha_1$ | $D^{(f)}$ | $100 (0)$ |
| | | $\alpha_2$ | $D^{(f)}$ | $-27.645 (8.409)$ |
| | | $\alpha_3$ | $D^{(f)}$ | $-0.020 (0.015)$ |
| | | $\alpha_4$ | $O^{(f)}, O^{(r)}$ | $0.027 (0.008)$ |
| | | $\alpha_5$ | $O^{(f)}, O^{(r)}$ | $-0.332 (0.062)$ |
| | | $\alpha_6$ | $O^{(f)}, O^{(r)}$ | $1.385 (0.125)$ |
| | | $\alpha_7$ | ARS | $0 (0)$ |
| | | $\alpha_8$ | ARS | $1.131 (0.158)$ |
| | | $\alpha_9$ | ARS | $4.325 (0.112)$ |
| | | $\alpha_{10}$ | ARS | $0.843 (0.068)$ |
| | | $\alpha_{11}$ | ARS | $0.476 (0.138)$ |

![FIGURE 9](image)

**FIGURE 9** Curve representing the estimated mean step length parameter $\mu^{(0)}$ (in km 30 m⁻¹) as a function of wind speed $r_w$ (in km h⁻¹). Shaded area represents 95% confidence interval. Points represent observed step lengths for first drift ($D^{(f)}$) and consecutive drift ($D^{(c)}$) states.

BRWs. By modelling turning angle bias with a component parallel to and a component perpendicular to stimuli, menotactic behaviours with bias towards any angle can be modelled. Second, we outline the use of a one-step ‘transitionary’ state for tactic BRWs, which can improve the accuracy of state detection and estimation of the direction of bias when the resolution of the environmental data is coarse relative to the animal track. We illustrated the application of these methods for detecting olfactory search and passive drift from both simulated data and polar bear tracking data using the readily accessible and well documented momentHMM package in R (McClintock & Michelot, 2018). To further aid in the implementation of these methods, we have provided a tutorial with reproducible R code in Appendix D.

Given the ubiquity of taxes exhibited among animals, other studies have integrated bias into their movement models. However, these have usually been simple attractive or repulsive bias (i.e. positive and negative taxis; e.g. Benhamou, 2014; McClintock & Michelot, 2018; Michelot et al., 2017). Furthermore, although there has been much investigation into mechanisms and consequences of behaviours with nonparallel bias relative to the direction of stimuli, such metaxises has yet to be mechanistically integrated in a movement model. Typically, menotaxis has been studied independently of the movement process or using post hoc analysis and is identified either using visual assessment or basic descriptive statistics (e.g. Mestre et al., 2014; Paiva et al., 2010; Togunov et al., 2017, 2018; Ventura et al., 2020). Such methods are appropriate for some analyses, however, they may prohibit investigating more nuanced relationships between animals, their behaviour and the environment. The direction of taxis may be unknown, incorrectly assumed a priori, or may be affected by other factors (e.g. environmental covariates, internal state). Not
accounting for these interactions may lead to incorrectly classifying movement or incorrectly estimating the direction or strength of bias. For instance, conventional methods for analysis of tracking data in mobile environments account for involuntary motion by simply subtracting the component of drift from the movement track (e.g. Blanchet et al., 2020; Gaspar et al., 2006; Klappstein et al., 2020; Safi et al., 2013). However, this type of correction does not account for the error often in the environmental data (Dohan & Maximenko, 2010; Togunov et al., 2020; Yonehara et al., 2016). Our methods overcome some of these limitations by building on the robust framework of HMMs, which are relatively flexible to uncertainty in both the track and environmental data by distinguishing between latent state and state-dependent processes (McClintock et al., 2012; Zucchini et al., 2016).

Our first simulation study indicated that our proposed BCRW HMM (i.e. integrating anemotaxis into predicting the turning angle) can accurately identify states in cases where menotactic movement is well represented by our model. Our model reliably identified its own three behavioural states and outperformed the simpler unbiased HMM (i.e. the misspecified null model). In cases where the speed of movement (i.e. step lengths) among different behaviours become more similar, a conventional HMM using only step length and turning angle may be completely unable to differentiate states, while our model may still be able to differentiate taxes. This was evident in our results where we observed a marked increase in accuracy for the drift state (60 percentage points), which had a comparable mean step length to area restricted search. Given that the data were generated from the model that was fit, we expected the high performance of our model. If an animal does not exhibit biased orientation, or if the mechanism behind their menotaxis is very different from the one we simulated, a simpler CRW model might perform better.

When modelling measured data, the estimated parameters reflect both the underlying process of interest (e.g. a connection between movement, wind and drift) as well as any underlying error in the data (Bestley et al., 2013). For instance, a low coefficient for a covariate may correctly reflect a weak ecological relationship or be an incorrect artefact of data with high error (Bestley et al., 2013). Our second simulation study demonstrated that at coarser resolutions of environmental data, a simpler BCRW HMM was prone to incorrectly characterising BRWs as CRWs. We showed that the use of a one-step transitional state can help recover some of the information lost for tactic BRWs in the presence of environmental error. The use of a transitional state yielded two advantages: reduced misclassification of BRWs and improved estimation of the direction of bias. Although the use of a transitional drift state caused consecutive drift steps to be misclassified as a CRW, the transitional state was able to recover information on bias that would otherwise be lost entirely using conventional models. Employing a transitional state for BRWs has one important caveat: because the transitional state lasts for precisely one step, the model requires there to be a sufficient number of state transitions to the BRW for sufficient power to accurately estimate bias coefficients. To obtain a sufficient number of BRW transitions may require longer tracking or sharing coefficients among different animals. The utility of employing a transitional state method depends on the system, but generally, it may be advantageous if the temporal resolution of the environmental data is coarser than the tracking data, if the angular error in the environmental data tends to be greater than the turning angle or if high homogeneity in the environmental data carries error across multiple steps. In our case, the use of a transitional state was beneficial as soon as the track data resolution was equal to or higher than the temporal resolution of the wind data (data not shown).

Different behaviours have unique fitness consequences and unique relationships with the environment, thus identifying the underlying behavioural context is critical to effectively interpret observed data (Roever et al., 2014; Wilson et al., 2012). This study was the first to identify stationary behaviour in polar bear tracking data, which made up a notable 35% of the track duration. The drifting state encapsulates several distinct behaviours including rest, sheltering during adverse conditions, still hunting by a seal breathing hole, or prey handling (Stirling, 1974; Stirling et al., 2016). To distinguish between this mixture of behaviours we may investigate the effect of time or environmental conditions on the transition probabilities between states (i.e. relaxing the model assumption of homogenous state transition probability matrix). In some cases, the strength or direction of bias may depend on other factors. For example, bias to the centre of an animal’s home range may depend on its distance from that centre (McClintock et al., 2012), or the strength of bias relative to wind during passive advection being proportional to wind speed (e.g. Yu et al., 2020). Such interactions with the bias can be accomplished by modelling bias coefficients, $a_1$ and $a_2$, as functions of covariates (e.g. distance to target, or magnitude of stimuli). Another important extension is to model multiple biases simultaneously, as animal movement is often driven by several competing goals (e.g. navigation in flocking birds; Nagy et al., 2010). These extensions can all be readily accommodated using moment-HMM (McClimont & Michelot, 2018). If in cases where simultaneous biases interact in complex ways, more advanced extensions may be required (Mouritsen, 2018). In mobile environments, such as birds in flight, the movement of the animal itself contains information on the flow since it is influenced by the currents and advection may affect the appearance of movement in all behaviours (Goto et al., 2017; Wilmers et al., 2015; Yonehara et al., 2016). If the magnitude of advection is comparable to the speed of voluntary movement, explicitly accounting for advection in all behaviours becomes increasingly important (Auger-Méthé, Lewis, et al., 2016; Gaspar et al., 2006; Yonehara et al., 2016). Our model can serve as a starting point for modelling menotactic BCRWs without making assumptions on the strength or direction of bias or assuming error-free movement and environmental data. The methods we present in this paper are simple extensions to conventional movement models. They can be readily applied to animal tracking data to characterise menotactic behaviours and open new
venues to investigate more nuanced and mechanistic relationships between animals and their environment.

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AUTHOR CONTRIBUTIONS
R.R.T. and MAM conceived the ideas and designed methodology; NJL and AED conducted fieldwork; RRT conducted the analyses and prepared the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST
The authors have no conflict of interest to report.

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DATA AVAILABILITY STATEMENT
The location data of the polar bear case study are available on UAL Dataverse Derocher (2021). Code to reproduce the simulations and the case study is available on Zenodo Togunov et al. (2021). Wind data were obtained from the ERA5 meteorological reanalysis project (Hersbach et al., 2020).

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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