

A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement

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Summary

1. The recently developed Brownian bridge movement model (BBMM) has advantages over traditional methods because it quantifies the utilization distribution of an animal based on its movement path rather than individual points and accounts for temporal autocorrelation and high data volumes. However, the BBMM assumes unrealistic homogeneous movement behaviour across all data.
2. Accurate quantification of the utilization distribution is important for identifying the way animals use the landscape.
3. We improve the BBMM by allowing for changes in behaviour, using likelihood statistics to determine change points along the animal's movement path.
4. This novel extension, outperforms the current BBMM as indicated by simulations and examples of a territorial mammal and a migratory bird. The unique ability of our model to work with tracks that are not sampled regularly is especially important for GPS tags that have frequent failed fixes or dynamic sampling schedules. Moreover, our model extension provides a useful one-dimensional measure of behavioural change along animal tracks.
5. This new method provides a more accurate utilization distribution that better describes the space use of realistic, behaviourally heterogeneous tracks.

Key-words: behavioural change, encounter probability, GPS, home range, utilization distribution

Introduction

Animal movement is increasingly being studied by tracking individuals with electronic tags that produce a time series of sequential locations (Wikelski *et al.* 2007). The typical approach to analyse and visualize the area used by a tracked animal is to convert its movement into a 2-dimensional spatial representation originally referred to as a 'home range' (Burt 1943). Modern methods for home range estimation quantify not only the size of the area, but also how intensely animals use different areas within their home range, referred to as a utilization distribution (UD; Worton 1989). UDs are commonly estimated with kernel methods using a collection of spatial points that ignore the temporal structure (Worton 1989), requiring individual points to be either sampled from a

track at regular intervals or temporally independent (Fieberg 2007; Fieberg *et al.* 2010). However, kernel methods have not been useful for modern GPS data sets because the least square cross-validation method used for the parameter estimation is sensitive to large samples (Hemson *et al.* 2005). Thus, there is a need to develop new UD methods that can accommodate the more detailed animal tracks provided by modern GPS tracking (Kie *et al.* 2010).

The recent introduction of the Brownian bridge movement model (BBMM) improves on the traditional UD statistics by incorporating the temporal structure of tracking data and explicitly modelling the movement path (Bullard 1999; Horne *et al.* 2007). The BBMM does this by incorporating both the order of locations and the amount of time between them. The model approximates the movement path between two subsequent locations by applying a conditional random walk. The BBMM has been rapidly adopted because it provides straightforward results, is based on clear assumptions, can incorporate location errors and is simple to apply to a wide range of movements (Lonergan, Fedak & McConnell

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2009; Ovaskainen & Crone 2009; Willems & Hill 2009). Consequently, the BBMM has been recognized for its broad potential in ecological studies, for example, to calculate encounter rates of animals (e.g. Farmer *et al.* 2010) or model disease outbreaks (Takekawa *et al.* 2010).

However, the BBMM can be improved as it currently does not take full advantage of the information contained in animal tracks. In particular, the current BBMM assumes animal movement patterns within a track to follow one constant property defining the variance of the Brownian motion (σ_m^2), which quantifies how diffusive or irregular the path of an animal is. Using a leave-one-out approach, σ_m^2 is estimated from the distances between the actual location and the expected location of the point left out, under the assumption of a constant movement between the previous and next location (Horne *et al.* 2007). The σ_m^2 thus contains both information on how straight a movement path is, as well as how much a path varies in speed and the scale of movements. This parameter is estimated from the trajectory itself based on an average of all available data (Horne *et al.* 2007). However, animal movement is actually composed of a succession of behaviourally distinct movement patterns (Morales *et al.* 2004; Jonsen, Flemming & Myers 2005; Bailey *et al.* 2008; Gurarie, Andrews & Laidre 2009). For example, within a day, animals may move in different ways when foraging versus travelling between sites, and almost all species break their day into periods of movement and rest (i.e. nocturnal, diurnal; Jonsen, Myers & James 2007; Boyce *et al.* 2010). On broader scales many species change their movement over the year or lifetime, for example migratory animals move over a small range when breeding but then make long distance movements for migration. Thus, estimating σ_m^2 for an entire trajectory will cause this parameter to be overestimated in some parts along the trajectory and underestimated in others. Overestimating σ_m^2 leads to an imprecision in the UD and thus wider UD areas; whereas underestimating σ_m^2 results in a false precision and too narrow UD areas. The work of Benhamou (2011) expands on the variation estimation of the Brownian bridge method in two ways, the variance estimation separates advection and diffusion and the variance is separated for different habitats. Although differing variances are calculated, the variation is restricted to known habitats that are predefined and the varying variance is not used for UD calculations.

Recently, Gurarie, Andrews & Laidre (2009) introduced the behavioural change point analysis (BCPA) to statistically determine where along an animal's trajectory changes in the behavioural state occur based on changes in the underlying movement patterns. The BCPA uses likelihood comparisons in a moving window to identify change points and quantifies the variation in the underlying movement parameters along a trajectory. Here, we propose a method that combines the BBMM with an approach similar to the BCPA to provide a dynamic and more accurate estimate of σ_m^2 along a path. This new movement analysis improves the estimation of UD, particularly for long complex animal journeys. In addition,

adjusting σ_m^2 based on changes in movement patterns will provide insight into changes in behaviour along trajectories, very much like the original intention of the BCPA (Gurarie, Andrews & Laidre 2009).

Materials and methods

A Brownian bridge UD requires, in addition to the geographic position (x and y) and the timestamps (t) of the locations, the variance of the Brownian motion (σ_m^2) and the telemetry error (δ^2). The error δ^2 can be derived empirically from field tests and is a property of the locations. The geographic positions together form the matrix \mathbf{Z} where Z_i represents the x and y coordinates of location i ; i can range from 0 to n . The variance of the Brownian motion σ_m^2 is a property of the intervals between locations, hereafter referred to as segments, and is estimated from the trajectory for a series of locations \mathbf{Z} by maximizing the likelihood function (eqn 1; Horne *et al.* 2007) using only odd values for i , where $\mu_i(t_i) = Z_{i-1} + \alpha_i(Z_{i+1} - Z_{i-1})$; $\sigma_i^2(t) = T_i\alpha_i(1 - \alpha_i)\sigma_m^2 + (1 - \alpha_i)^2\delta_{i-1}^2 + \alpha_i\delta_{i+1}^2$; $\alpha_i = (t_i - t_{i-1})/T_i$; and $T_i = t_{i+1} - t_{i-1}$ (parameter definitions Table 1).

$$L(\sigma_m^2|\mathbf{Z}) = \prod_{i=1}^{n-1} \frac{1}{2\pi\sigma_i^2(t_i)} \exp\left\{-\frac{[Z_i - \mu_i(t_i)][Z_i - \mu_i(t_i)]^\top}{2\sigma_i^2(t_i)}\right\} \quad \text{eqn 1}$$

Until now, the model assumed σ_m^2 to be the same along the entire path. We suggest to use eqn 1 on subsections of trajectories to quantify a localized movement pattern of an animal and thus obtain a more refined UD.

To estimate the σ_m^2 parameter for a subsection of a trajectory, a sliding window that calculates the variance iteratively is not satisfactory, as it does not allow to follow any sudden changes (i.e. switches in behaviour) in the variance (see also: Gurarie, Andrews & Laidre 2009). To allow for sudden as well as gradual changes, we implemented an adjusted version of the BCPA (Gurarie, Andrews & Laidre 2009; Fig. 1).

Within a sliding window with w locations we compare model fit using either one or two estimates of σ_m^2 (Fig. 1). The log-likelihood of using just one value of σ_m^2 for the whole window (using eqn 1) is compared to the log-likelihood of a window split in two parts by comparing the Bayesian Information Criterion (BIC) values. The log-likelihood for a window described by two parameters changing at location b , the breakpoint, is calculated using eqn 2, where $Z_{i,j}$ is a subset of \mathbf{Z} .

$$\begin{aligned} \log(L(\sigma_m^2|Z_{1,w}, b)) = & \\ \log\left(\operatorname{argmax}_{\sigma_{m,1}^2 \in [0, \infty]} \left(L(\sigma_{m,1}^2|Z_{1,b})\right)\right) + & \\ \log\left(\operatorname{argmax}_{\sigma_{m,2}^2 \in [0, \infty]} \left(L(\sigma_{m,2}^2|Z_{b,w})\right)\right) & \quad \text{eqn 2} \end{aligned}$$

Table 1. Parameters used for calculating dynamic Brownian bridges

Parameter	Definition
\mathbf{Z}	Matrix containing x and y location (in equal area projection)
δ^2	Vector of location errors
t	Vector of timestamps
T_{total}	Total time of tracking period
σ_m^2	Brownian motion variance
w	Size of sliding window
b	Location of the breakpoint within the sliding window
m	Margin size

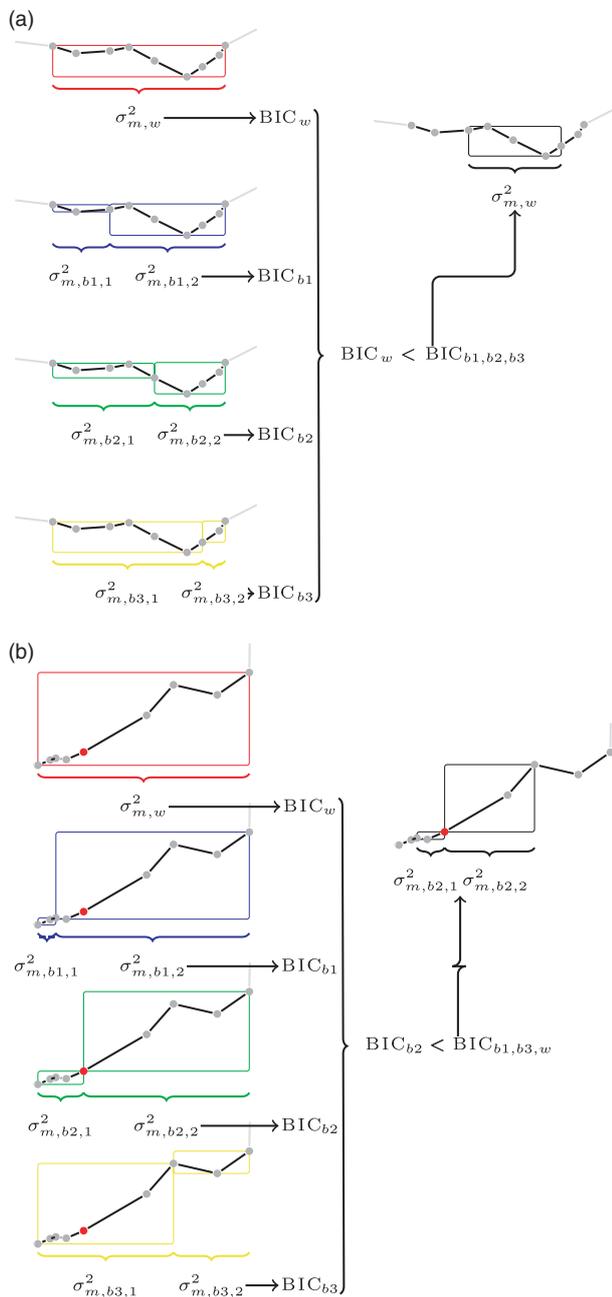


Fig. 1. Schematic description of σ_m^2 estimation in one window for dynamic Brownian bridges in a trajectory without a breakpoint (a), and one with a change in movement pattern (b). In both cases, σ_m^2 is calculated for the entire window and for all possible subsections, $\sigma_{m,w}^2$ refers to the σ_m^2 estimate for the whole window while $\sigma_{m,b3,2}^2$ refers to the σ_m^2 estimate after the third breakpoint in the window. In cases where a breakpoint occurs (red dot in (b)) the Bayesian Information Criterion (BIC) of the model consisting of two σ_m^2 estimates separating the window at the breakpoint is lowest. In such a case, the model with two parameter estimates (with d.f. = 2) is preferred over a model with only one parameter estimate (d.f. = 1) according to the BIC value. The appropriate σ_m^2 estimates are then associated with the track between the margins.

This equation can be calculated for any subset of the whole set of locations. When comparing the models, lower BIC values are preferred whereby the model without a breakpoint has one degree of

freedom (Fig. 1) and the model with two estimated parameters has two degrees of freedom.

Because, σ_m^2 is estimated by a leave-one-out method, a minimum of three locations is required by the likelihood calculation to estimate σ_m^2 . Thus, at the start and end of each window, a margin of size m with a minimum of three locations is required in which no breakpoints could be estimated. In addition, only odd values for b and w are allowed because the likelihood estimation of σ_m^2 works on the basis of using every second location as an independent observation, therefore, only an odd number of locations produces a valid likelihood. Using eqns 1 and 2, where b varies between m and $w-m$, we can search for an optimal description of the window considering σ_m^2 , and using BIC to identify potential breakpoints. Because we prohibit breakpoints from occurring in the margins of the sliding window, we obtain valid estimates for σ_m^2 only in the interval between m and the $w-m$ locations within the window. We apply the estimation for σ_m^2 to a window that is moved through the track. The sliding window produces several estimates for each segment, which we average into one mean value per segment. Because we do not obtain the same amount of σ_m^2 estimates at the beginning and end of the track, we omit those segments where we do not have the maximal amount of estimates for σ_m^2 .

Increasing the size of the sliding window (enlarging w) increases reliability in σ_m^2 estimation at the cost of missing short term changes in the variation parameter. Increasing the margin size (m), in contrast, enhances the power to identify ‘weak’ breakpoints at the cost of not detecting breakpoints within the margin. The choice of m and w should be biologically informed and is determined by the time interval that changes in behaviour are expected to occur. However, for regularly sampled tracks, equation $T_{\text{change}} > wT_{\text{int}}$ should be satisfied, where T_{change} is the smallest interval between expected behavioural changes and T_{int} the time between locations. This will ensure that every possible break can be described. Window sizes larger than T_{change} could result in detecting either the onset or offset of a behaviour but not both. Finally, after obtaining σ_m^2 for the segments, we can calculate the UD, according to Horne *et al.* (2007). The difference being that σ_m^2 varies, we therefore refer to it as dynamic Brownian bridge movement models (dBBMM).

VALIDATION

We evaluated the dBBMM for estimating σ_m^2 in trajectories with varying behavioural stages using both simulated and real animal trajectories. All analyses were written for and conducted within R 2.11.1 (R Development Core Team 2010) and based on the BBMM package (Nielson *et al.* 2011; see supplementary material for dBBMM code). First, we checked whether the dBBMM better described the UD by applying the model to a simulated track with two behavioural stages. Second, we investigated the potential for identifying breakpoints in a track with known properties, and the influence of window sizes (w) and margins (m).

We created 650 random tracks, using a correlated random walk (Kareiva & Shigesada 1983), that consisted of two stages to assess how well the dBBMM can describe a track with a behavioural change compared to the BBMM. Each track consisted of two ‘behavioural’ stages of 500 locations each. The first stage of each trajectory had a constant concentration for the wrapped normal distribution of turning angles ($r = 0.58$, on a scale from 0 to 1, where the standard deviation (SD) of the distribution is $\sqrt{-2 * \log r}$). The scaling parameter (step length) was kept constant using χ distribution multiplied by the scaling parameter ($h = 1$). In the second half of the track, the scaling parameter was changed to one of 13 differ-

ent values from a regular sequence ranging from 0.2 to 5. In one parameter combination, the scaling parameter was the same as in the first half (1). We simulated 50 replications for every parameter combination. To represent realistic sampling schemes, we sampled 250 locations from the entire trajectory, using both regular and random sampling. We added a normally distributed location error ($SD = 1$) to the sampled locations to represent observation errors. We then estimated the UD with the method described earlier (dBBMM) and with a constant σ_m^2 (BBMM), within a raster grid (maximal dimension = 2500 cells).

We assessed the performance of the dBBMM and the BBMM by comparing the ability of the two approaches to predict the locations of points, which were not used for the estimation of the models in a cross-validation. First, the initial data set was divided into two: one to calculate the UDs based on a dBBMM and a BBMM and the other part was used for the cross-validation. For each location that was not used for building the models, we calculated a cross-validation index by dividing the predicted UD probability value of the dBBMM (UD_{dBBMM}) approach by the probability value of BBMM (UD_{BBMM}) and took the n^{th} root of the product (geometric mean, eqn 3). Thus, values above one represent higher predicted UD probability for the observed locations using dBBMM and values below one higher probabilities using BBMM allowing us to compare the performance of the two approaches directly. The use of arithmetic mean is unsatisfactory, because it is biased towards changes in the numerator and the ratio of the arithmetic mean is biased towards locations with higher UD intersection.

$$\sqrt[n]{\prod_{i=1}^n \frac{UD_{dBBMM,i}}{UD_{BBMM,i}}} \quad \text{eqn 3}$$

To test how well breakpoints are identified with different window sizes and margins (w and m), we used another set of simulated tracks with two behavioural changes. The tracks consisted of a correlated random walk with 80 locations with a scaling of 1, then changed to a scaling of 5 for 30 locations and back again to a scaling of 1 for 80 locations. The concentration of the correlated random walk was kept constant at 0.6. We evaluated 250 replicates of the track for all possible window sizes ranging from 7 to 71 and margins from 3 to 31. We used the F-statistic of an analysis of variance (ANOVA) to test how constant σ_m^2 remained within one part of the track and differed between the different parts. This could be seen as a proxy to evaluate how well σ_m^2 identifies changes in behaviour.

APPLICATION TO FIELD DATA

To evaluate the effect of window and margin size on the UD, we used the trajectory of a fisher (*Martes pennanti*) tracked in Albany, New York. We sampled the track and based on that calculated Brownian bridges with different window and margin sizes. The relative performance was calculated using the cross-validation index as described earlier. The experimental GPS tag (E-obs GmbH) was motion sensitive and recorded a GPS location every 2 min when the animal was active, every 10 min at medium activity and every hour at low activity (4881 locations total). We sampled every fourth location for calculating the UD and used the others for the cross-validation. The grid cell size for mapping the UD was 25 m.

We used two tracks for comparing the UD estimated by the dBBMM and the BBMM. A lesser black-backed gull (*Larus fuscus*) trajectory was obtained using an Argos GPS tag (Microwave telemetry) that was programmed to take 4 fixes per day and produced

940 locations over a duration of 243 days. The gull migrated from Finland to lake Victoria in fall 2009 where it overwintered. A fisher track was obtained using a GPS logger with remote download (E-obs GmbH) and was programmed to take a fix every 15 min and produced 919 locations over a period of 21 days during February 2009 in Albany, New York. The location error for the GPS logger was determined in a field test as 23.5 m. Because no field measurement on the location error was available for the gull tag, we assumed the same error, which is reasonable for GPS quality data (Frair *et al.* 2010). Although we used one single location error along the track, there is no technical limitation to using differing location errors with the dynamic Brownian Bridge movement model as used by Lewis *et al.* (2011) in combination with the Brownian Bridge movement model. For both tracks, we used a window size of 33 locations with margins of 11 locations, which translated into a window length of 8 days for the gull and 8 hours for the fisher. For comparison, we assessed the resulting UDs visually and calculated the volume of intersection. The volume of intersection is the shared volume of the UD between the dBBMM and BBMM (Millsbaugh *et al.* 2000, 2004a,b). To assess what a varying σ_m^2 could reveal about the behaviour of an individual, we plotted σ_m^2 over time. We also investigated whether the environment affected the movement modes by comparing the difference in σ_m^2 between landscape characteristics for the fisher. Land use data were obtained from the 30 m resolution NLCD 2006 data set (http://www.mrlc.gov/nlcd_2006.php). We used the average σ_m^2 from the segment before and after each location where the fisher was observed and associated the land use at that location. We only used locations during the night to minimize the influence of resting during the day. Differences in average σ_m^2 at that location as a product of the environment were tested using a nonparametric Kruskal–Wallis test. We only used land use categories that occurred at least 10 times to adhere to the assumptions of the Kruskal–Wallis test. In total 7 land use categories met these criteria: developed open space, developed medium intensity, deciduous forest, evergreen forest, mixed forest, cultivated crops and woody wetlands.

Results

VALIDATION

The dBBMM performed better than, or at least as well as, the traditional BBMM with a constant σ_m^2 . The performance of a dynamic estimation of σ_m^2 increased as the characteristics of the path before and after the breakpoint became increasingly dissimilar. The maximal mean cross-validation index was 1.153 ($SD = 0.271$) with irregularly sampled tracks and the largest change in the scaling parameter. In 21 of 26 cases, the mean cross-validation index was significantly ($P < 0.05$) higher than 1 according to a Student's *t*-test, indicating the superior performance of the dBBMM. The index was significantly below 1 in only one case, with the regular sampled track and unchanged scaling parameter, but the effect size was very small (cross-validation index of: 0.9974). This shows that the dBBMM and BBMM perform similar on tracks with low variation in movement pattern. It is important to highlight that the dBBMM produced better estimation of the home range particularly in cases where locations were randomly sampled, proving its power for nonregularly sampled tracks (e.g. missed GPS fix attempts).

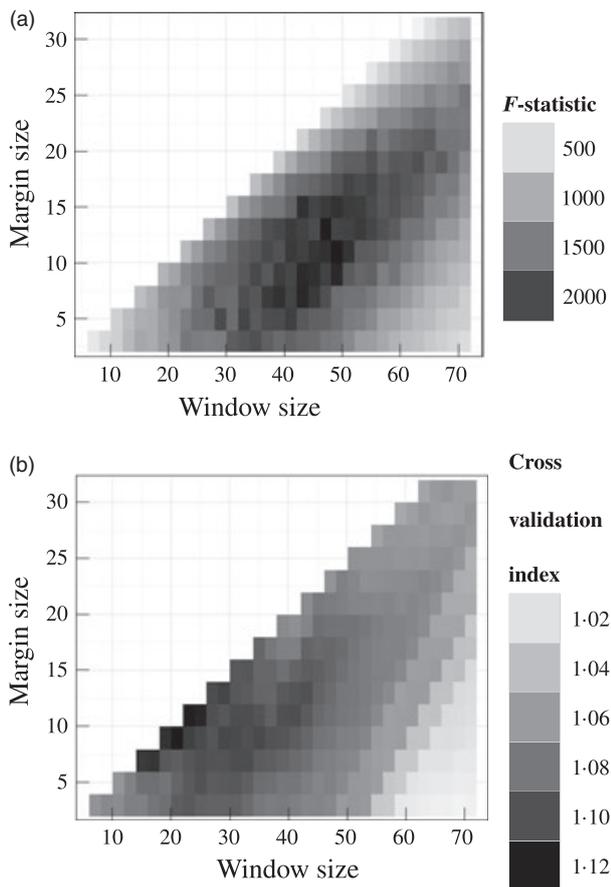


Fig. 2. Plots for evaluating optimal parameter settings for distinguishing behavioural changes (a) and comparing the performance of the new dBBMM vs the traditional BBMM (b). (a) Higher values for the F -statistic indicate better performance of the dBBMMs σ_m^2 to separate a movement track into different behaviours. These settings vary depending on species and sampling intensity, and should be evaluated before each use of the dBBMM. (b) The higher cross-validation index values show the increasing improvement offered by the dBBMM versus the BBMM with small to intermediate window sizes. This value is always larger than one, showing that the dBBMM is never a worse model, but offers less improvement when the window size is so large that it masks the underlying heterogeneity of the fishers movement.

Predicting the breakpoints in the simulated track suggested that the method best separated the two behavioural stages with intermediate window sizes (41–47) and relatively small margins (7–9) (Fig. 2). Slightly better separation performance was generally achieved with slightly larger window sizes than predicted by the suggested optimum ($T_{\text{change}} > wT_{\text{int}}$; $w = 30$ in this case). This discrepancy is probably due to the fact that the locations within the margins were not used for the calculations of the final σ_m^2 . In addition, slightly larger values stabilized the estimates for σ_m^2 . This means that w can be up to 1.5 times larger than suggested and still clearly identify changes in behaviour.

APPLICATION TO FIELD DATA

The cross-validation index for all combinations of margins and window sizes using the sampled fisher track is higher

than 1, showing that the dBBMM was always better in predicting the location of the individual. The sampled fisher track suggested that relatively small margins (9–13) and small to intermediate window sizes (19–31) were producing the highest cross-validation index (Fig. 2). It must be noted that the highest CV values are generally not obtained using the smallest possible margins. The cross-validation index was maximally 1.121 indicating that the dBBMM produced a considerably better fitting UD. It is important to note that optimal values for w and m are track specific and should not be generalized across projects and/or species. The main consideration should be the time scale of targeted behavioural changes. Therefore, if there are no *a-priori* expectations, we suggest exploring different parameter combinations. The cross-validation approach could give indications as to which combinations of w and m provide the best fit to the data. However, this approach is computationally costly and requires temporally well resolved trajectories.

UTILIZATION DISTRIBUTION

By calculating σ_m^2 for the segments, the dynamic model was better able to describe space use. We qualitatively compared how changes in σ_m^2 used in dBBMM changed the UD compared with a fixed σ_m^2 in the current BBMM by visual inspection of the UD contours of tracks from both a fisher and a migratory lesser black-backed gull (Figs 3 and 4). The UD probabilities around the fisher rest sites became more concentrated using a dynamic σ_m^2 compared with a fixed σ_m^2 (Fig. 3a,b). This is not surprising, but shows that using a fixed UD tends to overestimate the size of these resting areas because it assumes movement when in fact there was none. This translated in a volume of intersection of 0.86 between the BBMM and the dBBMM.

The dynamic model by calculating σ_m^2 for the different periods separately was better able to describe space use. Comparing the resulting UD between a fixed and a dynamic σ_m^2 estimation for the gull, showed that the fixed σ_m^2 causes an unrealistically high confidence level in the long migration segments (Fig. 4, upper detailed map). This high confidence level was caused by a σ_m^2 value strongly influenced by movements during the breeding (i.e. nonmigratory) period of the animal. The dBBMM resulted in more uncertainty in the exact path between the two distant locations during migration, which is more likely to represent a realistic scenario. Further, the UD derived with the dynamic σ_m^2 estimation described the movement patterns within the wintering area (Fig. 4, lower detailed map) much better. The volume of intersection between the BBMM and dBBMM UD was 0.55.

BEHAVIOUR

We also assessed the utility of σ_m^2 as a metric for identifying potential behaviours of a moving animal. The σ_m^2 values from the gull showed two very clear spikes, coinciding with migra-

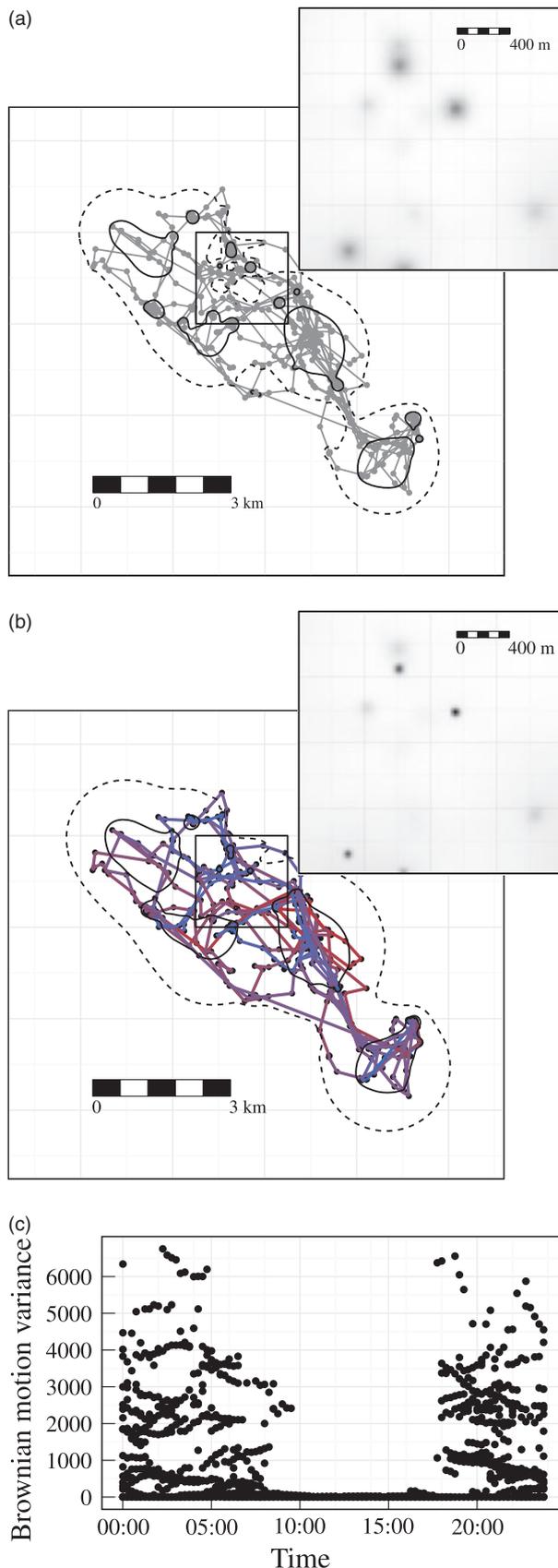


Fig. 3. The utilization density for a fisher (*Martes pennanti*) estimated with the BBMM (a) and the dBBMM (b). Black lines indicate the 50 and 95% contours, the grey line is the track of the fisher. The colour of the track (b) corresponds to the σ_m^2 values from low (blue) to high (red). A portion of these maps are highlighted to demonstrate the more confined estimation of rest sites by the dBBMM using a grey scale indicating high UD estimations. (c) The distribution of σ_m^2 as a function of the time of the day with higher values indicating more irregular movement.

irregular) and low during the day (inactive animal and/or regular paths; see Fig. 3). These results highlight that a flexible σ_m^2 estimation can not only be used for calculating a UD, but can also indicate changes in the behavioural state of an individual. In addition to the clear influence of the time of the day, the movement pattern of the fisher also varied between different environments. A Kruskal–Wallis test showed a significant change in σ_m^2 between different land use types used at night ($P < 0.001$, d.f. = 6, $\chi^2 = 107.9$) with the animal showing a considerably lower σ_m^2 (more directed, regular and small scale movements) in mixed ($\sigma_m^2 = 325.5$) and evergreen forest ($\sigma_m^2 = 841.2$) versus the overall mean ($\sigma_m^2 = 1582.0$).

Discussion

Our method for dynamically estimating σ_m^2 for Brownian bridges provides two major advances. First, it improves on the estimation of the UD of the Brownian bridge movement models for behaviourally heterogeneous animal tracks by relaxing the assumption of a fixed σ_m^2 . Second, the variation of σ_m^2 along a trajectory provides insight into variation in animal behaviour. Our method makes it possible to analyse entire tracks that include different behavioural types. Simulations showed that there is a significant increase in the ability of the UD to predict other locations as soon as there is some behavioural change or irregular sampling. The values for the cross-validation index showing this are not very high because they are an average increase per location. Given the high variation in σ_m^2 found in real tracks, the dBBMM produces improved UD. Previous studies worked around the problem of behavioural heterogeneity by subsetting trajectories using expert knowledge (e.g. nonmigratory or migratory parts of the animal track Sawyer *et al.* 2009; Farmer *et al.* 2010; Sawyer & Kauffman 2011). In contrast to expert knowledge, a method that is demanding and often difficult to replicate between experts, the dBBMM allows for the efficient, objective, and repeatable analysis of a large number of complex tracks. The dBBMM would also work for situations where the range of behaviour is unknown and therefore can not be identified by experts. The advantages of automated analyses of behaviourally complex tracks by the dBBMM are apparent in view of the increasing number of animals being tracked for ecological and environmental health studies and the ever improving temporal and spatial resolution of the trajectories owing to technical advances.

Despite the potential to account for differences in movement patterns and reducing the necessary preparation and

tion (Fig. 4). Estimating σ_m^2 of the fisher with the described method further revealed a very clear circadian activity, where σ_m^2 was high during the night (animal is active and the path

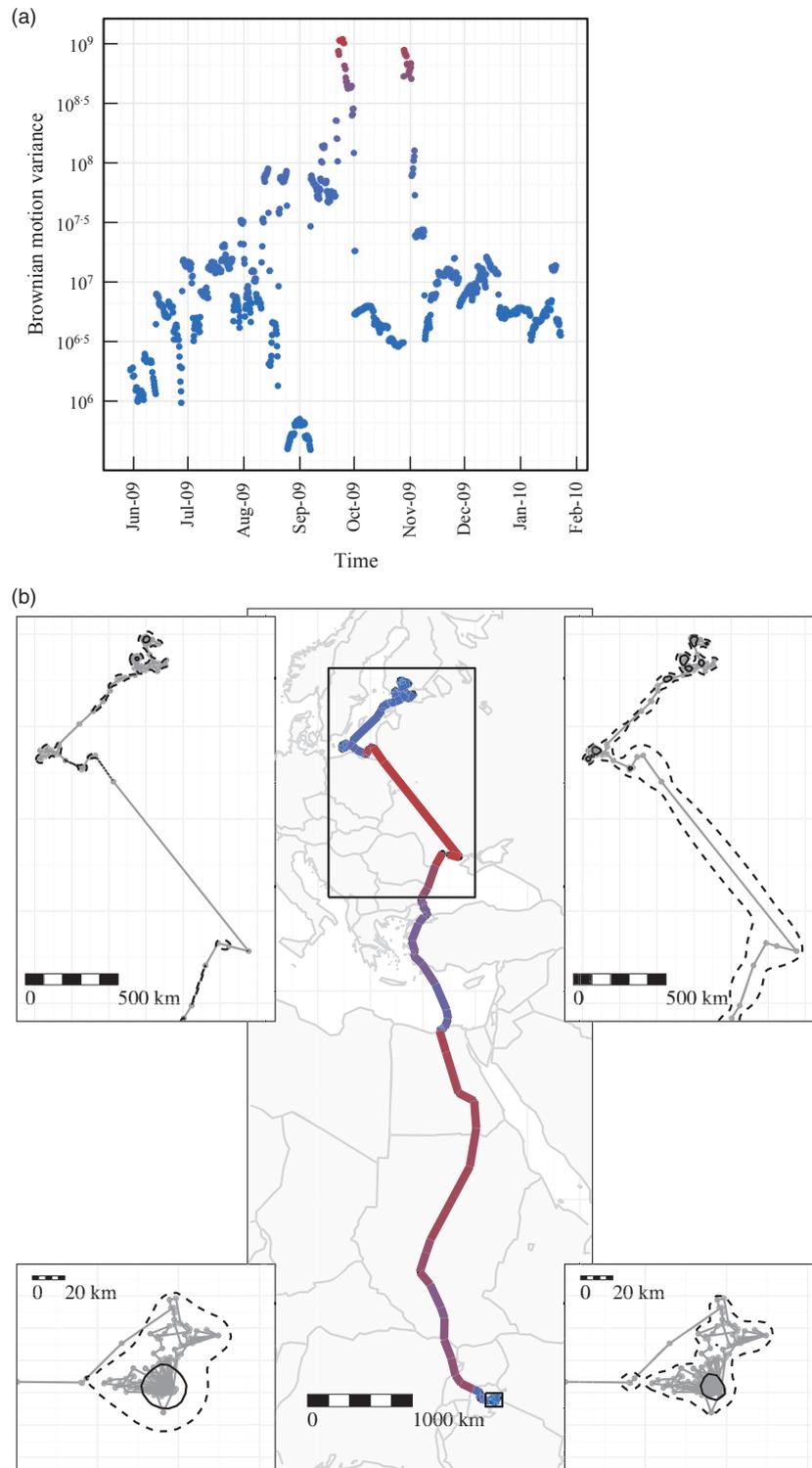


Fig. 4. The track of a lesser black-backed gull (*Larus fuscus*) migrating from Finland to lake Victoria in Africa. The colour of the path (b) indicates σ_m^2 and corresponds with (a). The variance in the σ_m^2 during the season (a) has clear spikes around the migration period. Plotting the first part of the trajectory more closely shows the difference in the high confidence that the fixed Brownian bridge (upper left inset) puts on a narrow corridor, in contrast to the dynamic Brownian bridge (upper right inset). At the end of the track, a varying σ_m^2 also better describes the UD at the wintering grounds around lake Victoria. The black lines indicate the 50 and 95% contours of the utilization distribution, the grey line the track of the gull.

segmentation of long trajectories, our extension of the Brownian bridge method still requires user interaction. The choice of margin and window sizes should be based on bio-

logically relevant measures of behavioural change (see also Gurarie, Andrews & Laidre 2009). However, we can provide guidelines as to how these measures could be deter-

mined sensibly. For example, larger windows lead to more stable estimates of σ_m^2 , decreasing the likelihood of detecting weak or spurious changes. Larger margins provide more power to identify breakpoints. To detect diurnal changes in the behaviour of an animal tracked with one positional fix every half hour, the window size should be near, but < 24 . It is important to note that regardless of the choice for the sizes of margins and window size the dBBMM generally outperformed the classical approach. In our analyses, over a range of possible margin window size combinations, margins of 9–11 locations and window sizes of around 30 seemed to perform best. Finally, in cases of uncertainty or for exploratory purposes, an alternative computer intensive approach such as the one we used above for the fisher track based on cross-validation can be used (implemented in the dBBMM R code).

UTILIZATION DISTRIBUTION

Because nearly all animal tracks show some level of behavioural change, the dBBMM approach should provide more realistic UD than traditional estimates of space use. As illustrated by our analysis of the fisher resting sites, a fixed σ_m^2 value can lead to unnecessarily large errors in parts of the trajectory where the actual σ_m^2 value is in fact low. But, as illustrated by our example of the migrating gull, using a dynamic σ_m^2 also prevented false confidence in the UD in areas where the actual σ_m^2 should be higher. Larger variation in σ_m^2 because of different behaviours will lead to a larger difference in the UD derived from the BBMM versus the dBBMM. This is reflected in the lower volume of intersection for the gull in contrast to the fisher, which shows that the UDs of the gull are more dissimilar.

Underestimating σ_m^2 results in a problematic bias for conservation planning. For example, identifying places for road crossing facilities or determining corridors connecting populations, based on an underestimate of σ_m^2 would lead to the identification of too small a stretch than actually necessary for the conservation measures to be effective. The corridor between the northwestern and southeastern parts of the fisher home range (Fig. 3) could be one example. This error can become even larger if the animal shows more distinct movements such as migrations.

The latest generation of GPS loggers are able to acquire information more efficiently by making the GPS fix schedule dependent on activity, battery status, time of the day, or location. These novel technological developments make our approach a useful improvement. Such novel tags lead to poor predictions of the UD if the dynamics in determining the position of the animal are not taken into account. Using Brownian bridges cannot fully avoid a potential inaccuracy caused by the changes in fix frequency. Compared to other UD methods, the BBMM is less sensitive to irregular sampling because it takes the time differences between locations into account. However, consistent differences in the number of locations obtained either because of changes in behaviour or indirectly because of temporal or spatial coincidence

between specific behaviour and specific locations still will influence the UD estimate obtained from traditional BBMM. This is because the σ_m^2 estimate will be biased towards stretches with many locations, while that is not necessarily representative for the whole tracking period. Dynamic Brownian bridges can mitigate this source of inaccuracy, because they allow σ_m^2 to vary along a trajectory and thus the estimates of UD to be less influenced by the differences in behaviour.

BROWNIAN MOTION VARIANCE AS A MEASURE OF BEHAVIOURAL STATE

Using σ_m^2 as a measure for behavioural state has the advantage of being one-dimensional while still detecting changes in both turning angles and speed, and/or step length. This measure is insensitive to changes in fix frequency in the case of pure Brownian motion. The one dimensionality of σ_m^2 being an advantage for statistical purposes, also has clear limitations. Because it is a unidimensional measure, it can only separate a limited amount of behaviours. Thus, two relatively different tracks, for example a twisted track and a track highly varying in speed could produce similar σ_m^2 values, but these differences would be easily identifiable using other methods. Changes in the scale of movement and frequently missed fixes when the movement is not Brownian can lead to changes in σ_m^2 . This diversity of nonmutually exclusive potential influences make it necessary to be careful with the interpretation of changes in σ_m^2 . One example is the migrating gull where one could expect σ_m^2 to drop because of more regular strait movements during migration. But in fact the opposite happens, because the scale of the movement increases from local to continental. In cases where more details about the exact nature of the changes is required state–space models or BCPA may be more powerful for identifying specific differences in movement (Patterson *et al.* 2008; Gurarie, Andrews & Laidre 2009). Nonetheless, owing to its simplicity we see great potential for σ_m^2 in identifying behavioural states within animal trajectories.

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