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ANALYZING ANIMAL MOVEMENTS USING BROWNIAN BRIDGES

Jon S. Horne,[1] Edward O. Garton, Stephen M. Krone, and Jesse S. Lewis

University of Idaho, Department of Fish and Wildlife, Moscow, Idaho 83844 USA

Abstract. By studying animal movements, researchers can gain insight into many of the ecological characteristics and processes important for understanding population-level dynamics. We developed a Brownian bridge movement model (BBMM) for estimating the expected movement path of an animal, using discrete location data obtained at relatively short time intervals. The BBMM is based on the properties of a conditional random walk between successive pairs of locations, dependent on the time between locations, the distance between locations, and the Brownian motion variance that is related to the animal's mobility. We describe two critical developments that enable widespread use of the BBMM, including a derivation of the model when location data are measured with error and a maximum likelihood approach for estimating the Brownian motion variance. After the BBMM is fitted to location data, an estimate of the animal's probability of occurrence can be generated for an area during the time of observation. To illustrate potential applications, we provide three examples: estimating animal home ranges, estimating animal migration routes, and evaluating the influence of fine-scale resource selection on animal movement patterns.

Key words: Brownian bridge; home range; migration; random walk; resource selection; road crossings; stochastic process; utilization distribution.

Introduction

The causes and consequences of animal movements are of great interest to ecologists. In particular, by studying movements of individual animals, researchers have gained insight into population distributions (Turchin 1991), important resources (Birchfield and Deters 2005), dispersal strategies (Small and Rusch 1989), social interactions (Minta 1992), and general patterns of space use (Kenward et al. 2001). Critical to understanding these ecological characteristics and their subsequent effects on population dynamics are appropriate methods for quantifying and analyzing movement patterns of individual animals.

An animal's movements are defined by a continuous trajectory or path through space and time. Direct observation of this path may be the most powerful method for quantifying movement (Turchin 1998), but many organisms are not amenable to continuous observation. For these species, several alternative methods are often employed to collect locations at discrete intervals along the trajectory. Probably the most widely used of these methods is biotelemetry, a generic term incorporating all methods for remotely determining the location of an animal (Priede 1992). In particular, global positioning system (GPS) telemetry is increasingly being used to study animal movements because it provides researchers the opportunity to almost continuously follow the movements of individuals for extended periods of time and over great distances. Using these types of data, we describe a new model for estimating animal movements based on Brownian bridges.

A Brownian bridge is a continuous-time stochastic model of movement in which the probability of being in an area is conditioned on starting and ending locations, the elapsed time between those points, and the mobility or speed of movement. Use of Brownian bridges to depict animal movements was first proposed by Bullard (1999), who described their application in estimating animal home ranges. Recently, Calenge (2006) introduced software for performing the calculations described by Bullard. We further develop and extend Bullard's ideas for the general purpose of estimating the movement path of individual animals. In particular, we derive the BBMM when observed locations are measured with error and we develop a maximum likelihood approach for empirically estimating one of the key parameters of the BBMM, i.e., the variance term related to the animal's mobility. To demonstrate the breadth and utility of this model, we applied the BBMM to three common uses of movement data: (1) estimating animal home ranges, (2) determining migration routes, and (3) analyzing fine-scale resource selection.

The Brownian bridge movement model

An animal's movements define a path (i.e., trajectory), through an area, during a specified period of time from $t = 0$ to T_{total}. We assume that continuous observation of the animal is impossible, but n discrete locations along the trajectory are available. Our interest is in modeling an animal's utilization distribution (i.e., the relative frequency of use of a two-dimensional area $A \subset \mathbb{R}^2$) during

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[1] E-mail: jhorne@uidaho.edu

the period of observation [0, T_{total}]. Absent any a priori knowledge of movement patterns, it is natural to model such movement as a random walk or its continuous counterpart, Brownian motion (Turchin 1998). An animal's frequency of use in an area is estimated by treating each of the n locations along the trajectory as known or approximately known, and using the properties of a conditional random walk to model the expected movement path between each successive pair of locations. When Brownian motion is extended for this situation (i.e., conditioned on the beginning and ending locations of each pair), the corresponding stochastic process is called a Brownian bridge (Ross 1983).

Probability conditioned on starting and ending points

Let $Z_t^{a,b,T}$ denote the position of an animal at time $t \in [0, T]$ undertaking a random walk from positions a to b with known values $Z_0^{a,b,T} = a$ and $Z_T^{a,b,T} = b$ in $\mathbb{R}^2$. This process has a normal distribution $Z_t^{a,b,T} \sim \mathcal{N}(\mu(t), \sigma^2(t)\mathbf{I})$ at time $t \in [0, T]$, where

$$\mu(t) = a + \frac{t}{T}(b-a) \qquad \sigma^2(t) = \frac{t(T-t)}{T}\sigma_{\text{m}}^2.$$

Here, $\mathbf{I}$ is the 2×2 identity matrix and σ_{m}^2 is the diffusion coefficient related to the mobility of the animal. Thus, the expected position of an animal that moves randomly between a and b at any point in time from $t = 0$ to $t = T$ can be estimated by a normal distribution. The mean of this normal distribution moves from a to b proportional to the time between a and b [i.e., $\mu(t) = a + (b-a)t/T$], and the variance equals 0 when $t = 0$, increases up to the midpoint in time between a and b, and then decreases back down to 0 when $t = T$ [i.e., $\sigma^2(t) = \sigma_{\text{m}}^2 t(T-t)/T$]. For notational convenience, we write the bivariate $\mathcal{N}(\mu, \sigma^2\mathbf{I})$ density as

$$\varphi(z; \mu, \sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[\frac{-(z-\mu)^2}{2\sigma^2}\right]$$

where z is any location in $\mathbb{R}^2$. Using this notation, the probability density of a Brownian bridge with starting location a and ending location b, at any point in time from $t = 0$ to $t = T$, is

$$\hat{p}_t^{a,b,T}(a, z) = \varphi\Big(z; \mu(t), \sigma^2(t)\Big). \tag{1}$$

In tracking animal movements, biotelemetry error is a prominent feature of most techniques for obtaining locations (Millspaugh and Marzluff 2001). Therefore, we next consider a Brownian bridge that incorporates uncertainty in the starting and ending locations. To take this into account, we follow Bullard (1999) by letting the starting and ending locations be random, with probability density functions $f_a(x)$ and $f_b(y)$, respectively, where x and y are position variables (two-dimensional vectors) in $\mathbb{R}^2$. We use Z_t^T to denote a Brownian bridge with starting and ending locations that are random. Then, the probability of finding the animal in region A at time $t \in [0, T]$ is

$$\begin{aligned} P(Z_t^T \in A) &= \iint P(Z_t^{x,y,T} \in A) f_a(x) f_b(y)\,dx\,dy \\ &= \iint \left[\int_A \hat{p}_t^{x,y,T}(x, z)\,dz\right] f_a(x) f_b(y)\,dx\,dy. \end{aligned} \tag{2}$$

Expected occupation time in a region

To this point, we have described a Brownian bridge model that estimates the probability of the animal being in an area A at a specific time t in the interval [0, T]. However, our main objective of study involves the frequency of use of an area over the entire time of observation. In other words, as the animal moves from its starting position at time 0 to its ending position at time T, what is the fraction of time it is expected to spend in region A? To answer this, we first define the indicator function $1_A(x)$ that takes a value of 1 if x is in the region A and 0 otherwise. The random quantity

$$\int_0^T 1_A(Z_t^T)\,dt$$

known as the occupation time for the region A, gives the amount of time during the observation period that the animal spends in A. Dividing by T and taking the expected value (E), we get the expected fraction of time in A. As a function of the region A, this yields a probability measure. Our objective is to find the corresponding probability density function $h(z)$ such that

$$E\left[\frac{1}{T}\int_0^T 1_A(Z_t^T)\,dt\right] = \int_A h(z)\,dz.$$

Indeed,

$$\begin{aligned} &E\left[\frac{1}{T}\int_0^T 1_A(Z_t^T)\,dt\right] \\ &\quad = \frac{1}{T}\int_0^T P(Z_t^T \in A)\,dt \\ &\quad = \frac{1}{T}\int_0^T \left[\iiint_A \hat{p}_t^{x,y,T}(x, z) f_a(x) f_b(y)\,dz\,dx\,dy\right] dt \\ &\quad = \int_A \left[\frac{1}{T}\int_0^T \iint \hat{p}_t^{x,y,T}(x, z) f_a(x) f_b(y)\,dx\,dy\,dt\right] dz. \end{aligned} \tag{3}$$

Thus, the desired density function is given by

$$h(z) = \frac{1}{T}\int_0^T \iint \hat{p}_t^{x,y,T}(x, z) f_a(x) f_b(y)\,dx\,dy\,dt. \tag{4}$$

This equation depends on the density functions f_a and f_b of the initial and final positions of the Brownian bridge, as well as the variance σ_{m}^2 of the underlying Brownian motion. When the distribution of location errors, f_a and f_b, corresponds to circular normal distributions $\mathcal{N}(a, \delta_a^2\mathbf{I})$ and $\mathcal{N}(b, \delta_b^2\mathbf{I})$, respectively, Eq. 4 simplifies to:

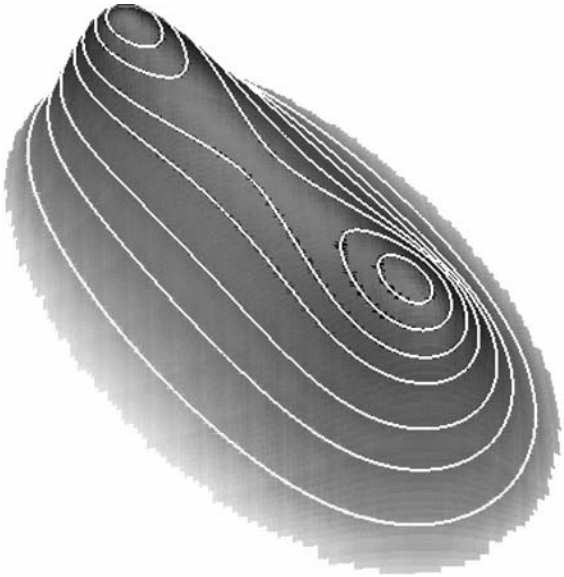

FIG. 1. Probability density for the fraction of time spent in different regions, constructed using the Brownian bridge movement model. Locations were 280 m and 20 min apart. The Brownian motion variance σ_m^2 was 642 m^2, and the standard deviation of normally distributed location error was 28.85 m. The two peaks in density correspond to the observed locations.

$$h(z) = \frac{1}{T}\int_0^T \varphi\Big(z; \mu(t), \sigma^2(t)\Big)dt \qquad (5)$$

where $\sigma^2(t) = T\alpha(1-\alpha)\sigma_m^2 + (1-\alpha)^2\,\delta_a^2 + \alpha^2\delta_b^2$, and $\alpha = t/T$. To avoid confusion of variance terms, note that the variance of location error is symbolized by δ^2. A derivation of Eq. 5 from Eq. 4 is provided in the Appendix. While the expression in Eq. 5 cannot be integrated, it can be approximated by discretizing time into arbitrarily small intervals of dt, which is the approach that we used. Using Eq. 5, an example of Brownian bridge probability density constructed between two locations that were 280 m and 20 min apart is shown in Fig. 1. For this example, the Brownian motion variance $\sigma_m^2 = 642$ m^2 and the standard deviation of telemetry error $\delta_a = \delta_b = 28.85$ m.

Model for multiple ($n > 2$) locations

We now describe the BBMM by considering the situation in which an animal's movements are monitored over an extended period of time, resulting in a series of space–time observations (Z_0, t_0), (Z_1, t_1), (Z, t_2), . . . , (Z_n, t_n) collected during $T_{total} = t_n - t_0$, where Z_i is the ith observed location and t_i is the time of that observation. We also assume normally distributed location errors; thus, the actual position of the animal at time t is modeled as a normal random variable $Z_i \sim \mathcal{N}(z_i, \delta_i^2\mathbf{I})$. Given the n observations during the time interval $[0, T_{total}]$, and accounting for location error as described, the density function for the fraction of time at z during $[0, T_{total}]$ is:

$$h(z) = \frac{1}{T_{total}}\sum_{i=0}^{n-1}\left\{\int_0^{T_i} \varphi\Big(z; \mu_i(t), \sigma_i^2(t)\Big)dt\right\} \qquad (6)$$

where $T_i = t_{i+1} - t_i$, $\mu_i(t) = z_i + \alpha_i(z_{i+1} - z_i)$, $\sigma_i^2(t) = T\alpha_i(1 - \alpha_i)\sigma_m^2 + (1-\alpha_i)^2\delta_i^2 + \alpha_i\delta_{i+1}^2$, and $\alpha_i = (t - t_i)(T_i)^{-1}$. To understand how the BBMM of Eq. 6 follows from the form of the density corresponding to two successive observations in Eq. 5, observe that the Brownian bridge probability density connecting each pair of locations is an estimate of the relative time spent in an area during the time interval between those locations. Thus, the part of the trajectory during $[T_i, T_{i+1}]$ should count as a fraction $(T_{i+1} - T_i)/T_{total}$ of the total. Weighting each integral from Eq. 5 by the appropriate fraction, and then adding, gives Eq. 6.

Parameter estimation

The BBMM is dependent on time-specific location data, the distribution of location errors and the Brownian motion variance parameter σ_m^2. For the model we described, the location error (e.g., from biotelemetry) is assumed to be normally distributed, with mean centered on the estimated location and variance either known or estimated via independent experiment. However, σ_m^2, which is related to the animal's mobility, is a feature of the particular animal under observation. An empirical estimate of σ_m^2 can be obtained from the location data used to construct the BBMM by assuming that the path connecting any two observed locations is a Brownian bridge. To estimate σ_m^2, assume that n is even and consider the independent Brownian bridges on the nonoverlapping time intervals $[t_0, t_2]$, $[t_2, t_4]$, $[t_4, t_6]$, . . . , $[t_{n-2}, t_n]$, while regarding the in-between observation times $t_1, t_3, t_5, \ldots, t_{n-1}$ as independent observations from these Brownian bridges (Fig. 2). Under the assumptions of the Brownian bridge model, this yields a sample of $n/2$ independent odd observations, $Z_1, Z_3, \ldots, Z_{n-1}$, that are normally distributed, $Z_i \sim \mathcal{N}(\mu_i(t_i), \sigma_i^2(t_i)I)$, 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 $T_i = t_{i+1} - t_{i-1}$. This allows us to construct the following likelihood function for odd

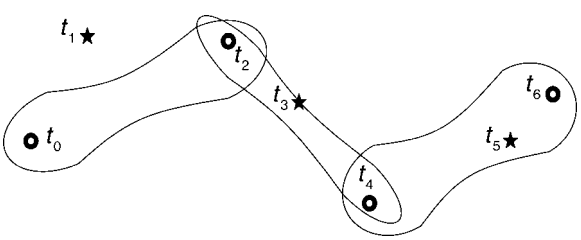

FIG. 2. Example of three Brownian bridges connecting even observations at time intervals $[t_0, t_2]$, $[t_2, t_4]$, and $[t_4, t_6]$. The in-between observations at times t_1, t_3, and t_5 are independent observations from these Brownian bridges and can be used to estimate the Brownian motion variance parameter.

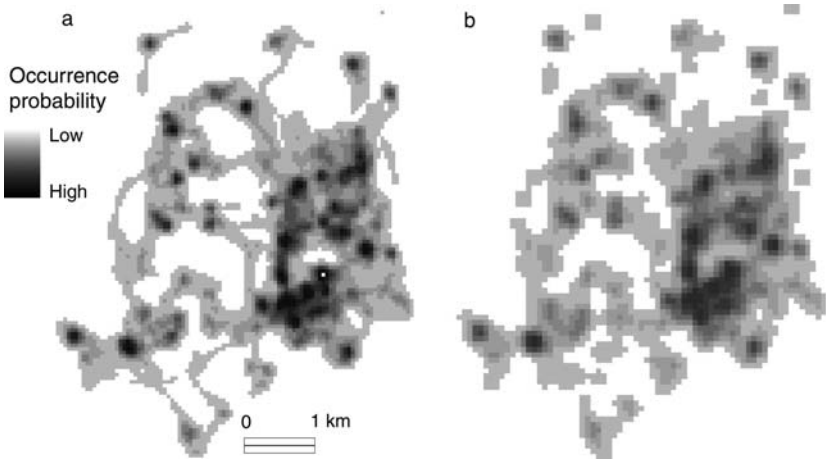

FIG. 3. Estimated home range (i.e., utilization distribution) of male black bear in northern Idaho, USA. The range in (a) is calculated using the Brownian bridge movement model with a variance parameter = 642.44. The range in (b) is calculated using a fixed kernel density estimate with a smoothing parameter = 76.95. In both panels, the outer contour represents the 99% contour.

locations:

$$L = \prod_{i=1}^{n-1} \frac{1}{2\pi\sigma_i^2(t_i)} \exp\left\{ \frac{-[Z_i - \mu_i(t_i)][Z_i - \mu_i(t_i)]^\top}{2\sigma_i^2(t_i)} \right\}. \quad (7)$$

Here $\top$ denotes transpose. If the standard deviation of telemetry error (δ) for each location is assumed to be known, then the Brownian motion variance σ_m^2 is the single unknown parameter and its maximum likelihood estimate can be obtained by numerically optimizing the likelihood function over values of σ_m^2. In effect, we are using the observed locations to find the value of σ_m^2 that best predicts the odd locations when a Brownian bridge is assumed between the even locations. For our examples, we used the Golden Section Search routine (Press et al. 1986) to accomplish this optimization.

Applications and Empirical Examples

Home range estimation

Since Burt (1943:351) formally defined home range as "...that area traversed by the individual in its normal activities of food gathering, mating, and caring for young," home range estimation has been a cornerstone of ecological inquiries. Building on Burt's original concept, several authors found home range estimation to be more tractable if an animal's space use is described as the probability that the animal occurred in an area during a specified period of time (i.e., utilization distribution; Jennrich and Turner 1969, Worton 1995). Because the BBMM estimates the probability that the animal occurred in an area over the analysis period, there is a direct application for estimating animal home ranges (Bullard 1999, Powell 2000).

As an example, we estimated the home range of a male black bear (*Ursus americanus*) in northern Idaho, USA, using the BBMM (see Supplement). Location data were collected in the summer of 2005 using Lotek 3300L GPS collars (Lotek, New Market, Ontario, Canada) programmed to store a location every 20 min. We determined mean location error by placing 18 collars in 48 test sites across the study area that represented a range of canopy cover and terrain obstruction. Collars were left at each test site for 24 hours, resulting in 72 attempted locations per test site. For each test site we calculated the standard deviation from the attempted locations and calculated a mean location error (δ) by averaging the standard deviations across the 48 test sites. The Brownian motion variance (σ_m^2) was estimated using the method of maximum likelihood described in the previous section. Using these parameters, an estimate of the utilization distribution was determined using the BBMM (i.e., Eq. 6). For comparison, we also estimated the home range using a fixed-kernel density with the smoothing parameter ($h = 76.95$) chosen using likelihood cross-validation (Horne and Garton 2006).

We used 1470 satellite telemetry locations, with most locations (85%) occurring at 20-min intervals. However, due to satellite acquisition failure, some (11%) were collected at 40-min intervals and the remainder (4%) were taken at intervals of >40 min, with none exceeding 120 min. Mean location error was $\hat{\delta} = 28.85$ and the estimated Brownian motion variance was $\hat{\sigma}_m^2 = 642.44$. Estimates of the utilization distribution were similar for the BBMM and the fixed-kernel method (Fig. 3). Both models suggested a complex distribution of space use, with multiple centers of activity as well as areas within the home range that receive little or no use. Indeed, there was 77% overlap in the areas represented by the 99% contours of the BBMM and the fixed-kernel estimate.

Although our example suggests that similar estimates of the utilization distribution may be obtained using the BBMM and kernel density estimates, it is important to realize some distinct differences in assumptions, both implicit and explicit, between the two models that may ultimately result in dissimilar estimates. From our black bear example, it is evident that areas of frequent use

were more likely to be "connected" via pathways using the BBMM as opposed to the kernel estimate. This is because the BBMM, having more of a mechanistic basis, estimates the utilization distribution by modeling the animal's expected movement path throughout an area over the period of observation. Uncertainty in the actual movement path is directly incorporated via the two ecologically based model parameters: the animal's mobility (i.e., σ_m^2) and measurable location error.

In contrast, kernel-smoothing techniques do not have a similar mechanistic basis. Instead, location data are assumed to represent a statistical sample from some underlying probability distribution, not the animal's movement path. Location data are smoothed to an "optimal" level in order to recover, as closely as possible, the true underlying distribution. The value of the smoothing parameter is usually chosen based on some type of statistical procedure designed to minimize the difference between the kernel estimate and the true distribution (Horne and Garton 2006), and kernel estimates are notoriously sensitive to these values. Although the smoothing employed by kernel estimates can be viewed as an indirect method for incorporating process and measurement error into estimates of the probability of occurrence, the connection is not as direct as the BBMM and there is no connection to ecological processes (Powell 2000).

Because of the differences in fundamental assumptions, the BBMM deals with the issues of serial correlation and unequal time intervals between locations in a much more straightforward manner. Unlike other probabilistic home range models, including kernel estimates, that assume temporal independence (Worton 1987), the BBMM assumes that locations are *not* independent and explicitly incorporates the time between locations into the model. In contrast, suggested methods for adapting kernel methods to serially correlated data with irregular sampling intervals require an additional user-defined parameter, beyond the spatial smoothing parameter, to control the amount of temporal weighting (Katajisto and Moilanen 2006). Although there are data-based techniques for choosing these parameters, even the proponents of these methods acknowledge that the choice of these parameters is "somewhat subjective" (Katajisto and Moilanen 2006:407). Using the BBMM to model home ranges removes this subjectivity by estimating the probability of occurrence based on observed animal movements and measurable location error.

Estimating migration routes

Most animals tend to remain in an area (i.e., home range) throughout their lives. However, for some, seasonal migrations to and from more permanent areas of use are a critical life history strategy necessary for population persistence (Baker 1978). For these species, identifying migration routes is an important component of ecological research and management and recent developments in satellite telemetry have enabled researchers to collect the location data needed to monitor animals during migration. When coupled with these data, the BBMM is well suited for describing migration routes probabilistically.

We used the BBMM to estimate the fall migration route of 11 female caribou (*Rangifer tarandus*) from the Nelchina Herd in south-central Alaska, USA, with data collected as part of an investigation of the influences of wildland fires on caribou habitat selection (Joly et al. 2003). Adult female caribou were fitted with telemetry collars that incorporated a GPS receiver and were programmed to calculate and store locations at 7-hour intervals. For this example, we used location data collected during 9–31 October 2000. Because we did not have an independent estimate of location error for these data, we used the same estimate that we used for the black bear data (i.e., $\delta = 28.85$ m). We estimated a unique Brownian motion variance for each caribou individual using the method of maximum likelihood described previously. We estimated each individual's probability of occurrence along the migration route using the BBMM. As an estimate of the population-level migration route, we calculated a mean probability of occurrence across the 11 individuals that were monitored.

The number of telemetry locations per individual ranged from 55 to 79, with most (92%) being collected at 7-hour intervals. However, due to satellite acquisition failure, some (6%) were collected at 14-hour intervals and the remainder (2%) were taken at intervals >14 hours, with none exceeding 31 hours. Estimates of the Brownian motion variance for individual caribou ranged from 13 008 to 29 256 m^2, with a mean of 22 804 m^2. Mean probability of occurrence across the 11 individuals suggested high selectivity in choosing a migration route to minimize travel across the steep terrain characterizing the Alaska Range (Fig. 4).

Although several probabilistic models are available for describing space use of animals occupying a home range (Kernohan et al. 2001), there are no similar techniques to describe space use of animals during migration or dispersal. The BBMM is well suited for describing these processes by modeling the uncertainty in the movement path between observed locations along the migration route. When coupled with location data collected at relatively short time intervals, the BBMM enables researchers to effectively identify important characteristics of migration routes, such as stopover sites (Mehlman et al. 2005), movement corridors (Berger 2004), and migratory landscape and habitat features (Skagen et al. 2005).

Resource selection

The previous two examples demonstrated the applicability of the BBMM for describing animal movements and space use. In this section, we demonstrate how estimates of the movement path can be used to analyze

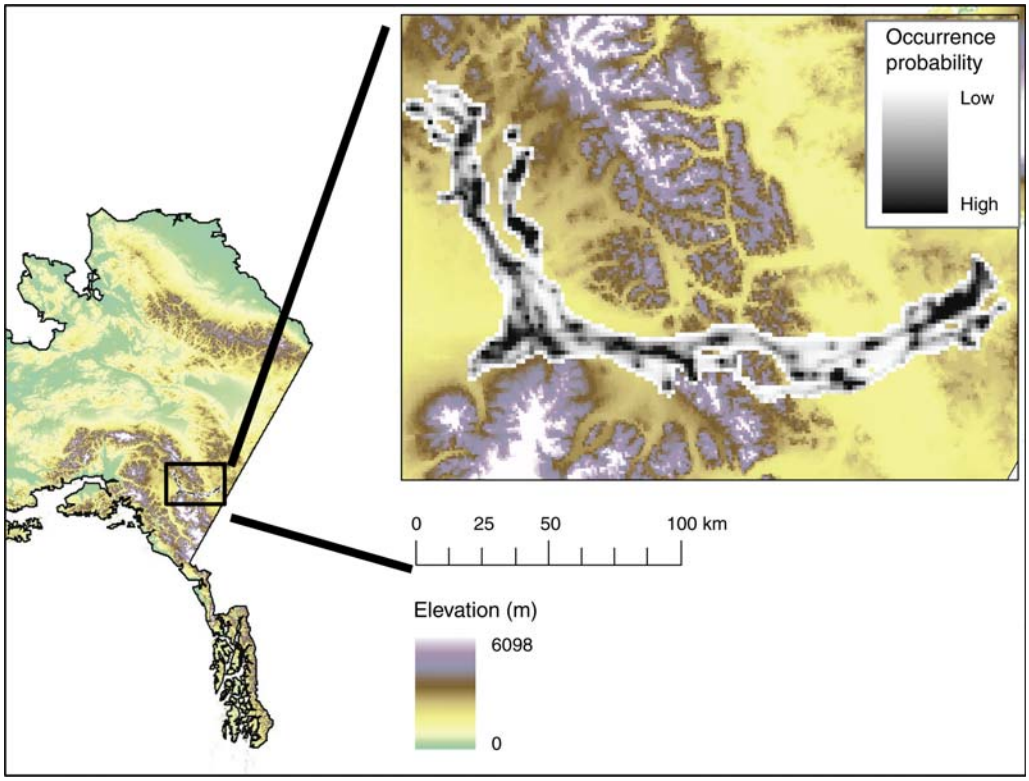

FIG. 4. Estimated fall migration route of 11 caribou in south-central Alaska, USA, in relation to elevation. Probability of occurrence was estimated using the Brownian bridge movement model cumulative probability contour.

fine-scale patterns of resource selection. In particular, we use the BBMM to investigate environmental attributes that make certain sections of highways likely places for animal crossings (see Plate 1).

Because heavily used roads have been shown to increase habitat fragmentation, many highway projects include road structures (e.g., overpasses and underpasses) designed to increase road permeability (Clevenger and Waltho 2000). An essential component of determining where to place these structures is information on where animals currently cross and what environmental characteristics are associated with likely crossing points. Here we show how the BBMM can be used to identify places along the highway where animals frequently cross by estimating the probability of occurrence along the road. These probabilities can then be regressed against environmental covariates to determine characteristics associated with likely crossing points.

For this example, we used 1046 satellite locations collected on a female black bear whose home range spanned Highway 95 in northern Idaho. Location data were collected, and BBMM parameters were estimated, using the same protocol as described in the previous section on home range analysis. To identify sections of the highway frequently used for crossing, we first selected all pairs of consecutive locations that occurred on opposite sides of the highway. We then defined areas along the highway as 50×50 m grid cells and estimated the relative frequency of use of each grid cell using the BBMM.

To investigate characteristics associated with likely crossing points, we regressed the probability at each grid cell on three spatially explicit environmental variables. The first variable depicted the amount of human disturbance (or development) near each grid cell (HumDev), the second described the amount of canopy cover (CanCov), and the third measured the distance to water (DistWat). We used a linear model (as per Marzluff et al. 2004) to determine the relative influence of each environmental variable on the probability of crossing. The importance of each variable j in explaining the variation of probabilities was determined using standardized partial regression coefficients (Zar 1984, Marzluff et al. 2004).

Estimates of the probability of occurrence in each grid cell suggested that certain sections of the highway were substantially more likely to be used for crossing than others (Fig. 5). The least squares fit of our linear model indicated that a significant amount of the variation ($R^2 = 0.57$) in the probability of crossing the highway was explained by the amount of developed area, distance to water, and mean canopy cover. As indicated by the standardized regression coefficients, the proportion of human development was the most significant variable in determining likely crossing points (Table 1).

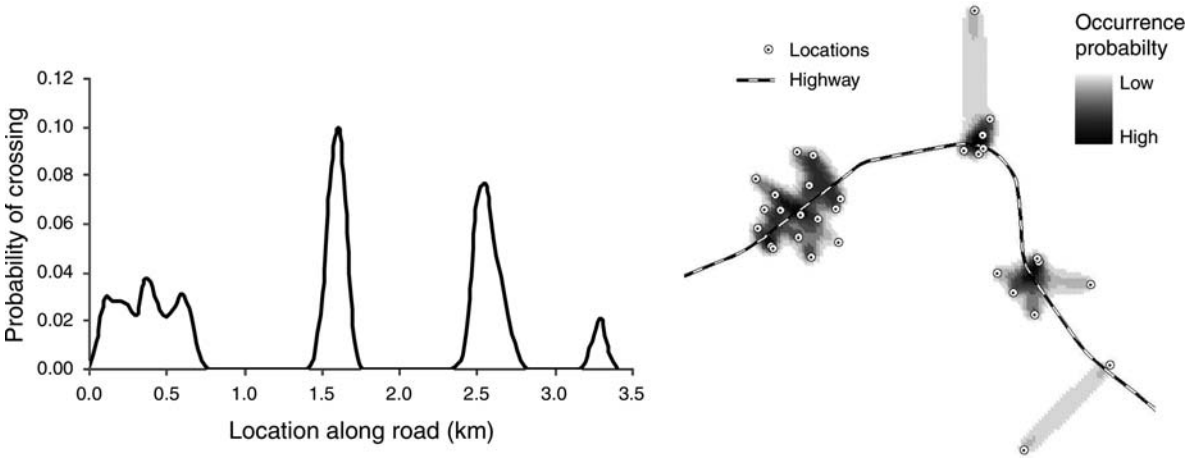

FIG. 5. Probability of a female black bear crossing along a 3.5-km stretch of Highway 95 in northern Idaho.

By using the BBMM to estimate likely crossing points and regressing these probabilities against environmental characteristics, we were able to predict the probability of a female black bear crossing along Highway 95 as a function of environmental variables. Our approach generally followed the method for analyzing resource selection developed by Marzluff et al. (2004). However, instead of using a kernel density to estimate the probability of use, we used the BBMM. This allowed for investigation of relatively fine-scale movement and selection patterns and allowed us to use only the paired locations of a known highway crossing.

DISCUSSION

Although biotelemetry has become increasingly prominent in ecological studies (Kenward 2001), methods for quantifying animal trajectories based on discrete locations, until recently, had not progressed much beyond connecting the locations with a straight line (Pace 2001). However, recognizing the need for more sophisticated models to analyze these data, there has been a surge of recent work to develop state–space models for analyzing and predicting animal movements (e.g., Jonsen et al. 2003, 2005, Morales et al. 2004, Flemming et al. 2006). We view the BBMM as complementary to these process-based models. One key difference in our approach is a greater focus on estimation, as opposed to prediction. The BBMM is useful for estimating space use of individual animals by melding location data collected on each individual with conditional random walk models.

Technological advances (e.g., satellite telemetry) are fostering a trend toward collecting location data at increasingly smaller time intervals on an ever-growing number of species; the BBMM offers a new approach to describe and analyze animal movements using these types of data. By treating movements between observed locations probabilistically, researchers are able to quantify the uncertainty in estimating the actual path caused by key factors such as the distance between observed locations, the time interval between locations, the measurement error in observed locations, and the mobility of the animal under investigation.

The BBMM has several important applications to the study of animal populations. First, because the BBMM was explicitly created to analyze location data that are collected at relatively short time intervals, space use of individuals can now be described in detail previously unavailable to researchers. By applying BBMM to estimate the movement path of individuals, researchers are able to more precisely identify the probability of an area being utilized. Secondly, despite location error being a well-known component of biotelemetry studies (White and Garrott 1990:46), a direct avenue for incorporating this error into estimates of space use is lacking (Powell 2000). This ability to account for

TABLE 1. Parameter estimates for the linear model explaining variation in log-transformed probability of occurrence values for a female black bear along a highway in northern Idaho, USA.

Variable	Standardized parameter estimate	Parameter estimate	SE	t	P
HumDev	−0.717	−20.8	2.59	−8.01	<0.001
DistWat	0.010	0.01	0.01	1.07	0.290
CanCov	0.001	0.10	9.35	0.01	0.992

Note: Variables are amount of human disturbance (human development), distance to water, and canopy cover.

PLATE 1. Female black bear with cubs crossing a road in southern Alaska. Photo credit. J. S. Lewis.

location error will become increasingly important as technological advances continue to shrink the time between locations and location error becomes the ultimate limit on the accuracy of estimating animal movements. Lastly, the ability to describe long-distance movements (e.g., migration routes) probabilistically represents a significant improvement over methods that simply connect locations using straight lines (e.g., Stokes et al. 1998, Saher and Schmiegelow 2004).

Assumptions and future directions

The BBMM is based on the properties of a conditional random walk between locations. Although it is certain that most animals do not move in a truly random fashion, using a model based on stochastic movement can still be justified (Turchin 1998). In the absence of any other information on how an animal moved from one location to another, a Brownian bridge can serve as a useful approximation or null model of the actual movement process. However, violating the assumption of random movement between pairs of locations may become much more prominent as the time interval between locations increases. For example, when using the Brownian bridge model to estimate the home range of an animal, the assumption of random movement between locations will become progressively unrealistic as the time interval between locations increases. In this situation, animal movements between locations separated by long time intervals are more likely to reflect a biased random walk (i.e., toward the home range center) than a simple random walk between locations.

The previous discussion brings up an important question regarding data requirements for the BBMM to be useful. In particular, what is the maximum time interval between locations? Unfortunately, there is no single answer that will apply to all situations. Instead, the BBMM will be able to identify the movement path with progressively less confidence as the time interval increases (Fig. 6). However, in addition to the time interval between locations, the amount of uncertainty is also dependent on the amount of location error and an

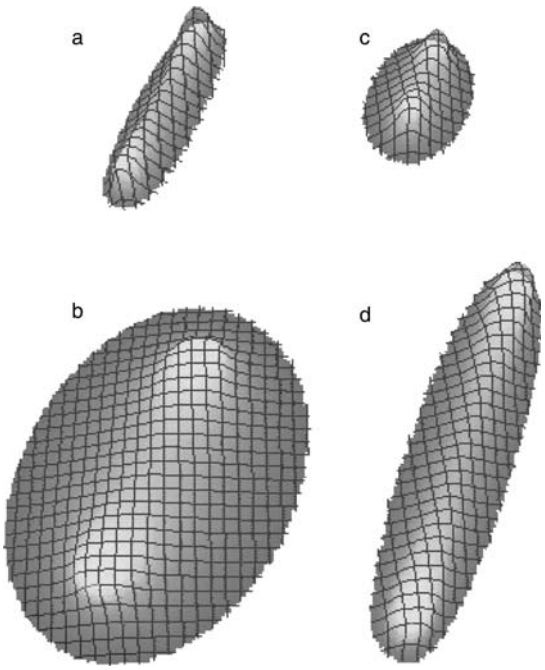

FIG. 6. Probability densities of four pairs of location separated by varying time intervals and distances, constructed using the Brownian bridge movement model. Probability densities in (a) and (b) were constructed from two pairs of locations separated by the same distance (550 m) but different time intervals: (a) 20 min; (b) 240 min. Probability densities in (c) and (d) were constructed from two pairs of locations separated by the same amount of time (40 min) but different distances: (c) 275 m; (d) 925 m.

animal's mobility, which will necessarily be specific to the particular individual under investigation. For example, given two sets of consecutive locations from animals with differing mobility, but otherwise separated by the same time and distance, the utilization distribution for the more mobile animal will be flatter (i.e., less certain of the movement path) than that for the less mobile animal. Thus, until future work establishes these relationships, we recommend that researchers critically evaluate whether the assumption of a conditioned random walk with constant movement rate holds for the time intervals contained within their location data.

We chose to model animal movement based on continuous time and space because the resulting distributions have the advantage of being amenable to direct calculations. However, we recognize that real animal movement is more exactly portrayed as a discrete process, with animals taking straight-line steps or movements of length λ and time between steps τ. Using a diffusion-based process like Brownian motion to approximate a stochastic process that might be discrete in time and/or space is similar in spirit to using a normal distribution to approximate a sum or average of discrete random variables when the central limit theorem applies. For example, the distribution of a two-dimensional discrete random walk at time t can be approximated by the Gaussian distribution with variance $\sigma^2 = 4\lambda^2/2\tau$ if the "time of observation t is much greater than the duration time τ of each random step, and the scale of observation x is much greater than the length λ of each random step" (Okubo 1980:10). In other words, the approximation is useful when the animal takes a large number of steps during the time interval between locations.

For all of our examples, we assumed that the distribution of location error was circular normal and used a single estimate of the variance. Although the assumption of normally distributed errors is appropriate for GPS telemetry (J. S. Horne, *personal observation*), this may not hold for locations collected using other satellite systems (Vincent et al. 2002). Future work should seek to derive other versions of the BBMM when location errors are nonnormally distributed. We used a single variance for all locations to simplify calculations. However, if researchers have reason to believe that each location has a unique error (see Lewis et al. 2007), this easily can be incorporated into the BBMM. Similarly, we simplified calculations by using a single estimate of the Brownian motion variance parameter for all pairs of locations. However, because this parameter is related to the mobility of the animal, it would be reasonable to consider different variances for different behaviors. For example, Morales et al. (2004) used characteristics of observed paths (i.e., turning angles and movement distances) and Jonsen et al. (2005) used state–space models to identify different movement states of animals (e.g., encamped vs. exploratory). If researchers can a priori identify these periods, separate variance parameters could be estimated for each period. These different estimates could then be incorporated into the BBMM to more accurately depict animal movements.

The resulting probability distribution of the movement path based on the BBMM is dependent on several factors, including the distance between observed locations both in space and time, the error associated with each observed location, and the animal's mobility. From the standpoint of initially setting up a telemetry study, it is important to realize that one of these factors can be manipulated by the researcher (i.e., time interval between locations). By decreasing the amount of time between successive locations, the uncertainty of the actual path can be reduced (Fig. 6). As the time interval increases, there is less and less certainty of the actual path and this uncertainty is reflected in a flatter probability distribution between observed locations. Future work will need to investigate differing time intervals and their effect on estimates of space use using the BBMM.

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Literature Cited

Baker, R. R. 1978. The evolutionary ecology of animal migration. Holmes and Meier, New York, New York, USA.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18:320–331.

Birchfield, G. L., and J. E. Deters. 2005. Movement paths of displaced northern green frogs (*Rana clamitans melanota*). Southeastern Naturalist 4:63–76.

Bullard, F. 1999. Estimating the home range of an animal: a Brownian bridge approach. Thesis. University of North Carolina, Chapel Hill, North Carolina, USA.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Clevenger, A. P., and N. Waltho. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology 14:47–56.

Flemming, J. E. M., C. A. Field, M. C. James, I. D. Jonsen, and R. A. Myers. 2006. How well can animals navigate? Estimating the circle of confusion from tracking data. Environmetrics 17:351–362.

Horne, J. S., and E. O. Garton. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70:641–648.

Jennrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22:227–237.

Joly, K., B. W. Dale, W. B. Collins, and L. G. Adams. 2003. Winter habitat use by female caribou in relation to wildland fires in interior Alaska. Canadian Journal of Zoology 81: 1192–1201.

Jonsen, I. D., J. M. Flemming, and R. A. Myers. 2005. Robust state–space modeling of animal movement data. Ecology 86: 2874–2880.

Jonsen, I. D., R. A. Myers, and J. M. Flemming. 2003. Meta-analysis of animal movement using state–space models. Ecology 84:3055–3063.

Katajisto, J., and A. Moilanen. 2006. Kernel-based home range method for data with irregular sampling intervals. Ecological Modelling 194:405–413.

Kenward, R. E. 2001. Historical and practical perspectives. Pages 3–12 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Kenward, R. E., S. S. Walls, and K. H. Hodder. 2001. Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. Journal of Animal Ecology 70:1–13.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, New York, New York, USA.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effects of habitat on GPS collar performance using data screening to reduce location error. Journal of Applied Ecology 44:663–671.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85:1411–1427.

Mehlman, D. W., S. E. Mabey, D. N. Ewert, C. Duncan, B. Abel, D. Cimprich, R. D. Sutter, and M. Woodrey. 2005. Conserving stopover sites for forest-dwelling migratory landbirds. Auk 122:1281–1290.

Millspaugh, J. J., and J. M. Marzluff. 2001. Radio-tracking and animal populations: past trends and future needs. Pages 189–206 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Minta, S. C. 1992. Tests of spatial and temporal interaction among animals. Ecological Applications 2:178–188.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85:2436–2445.

Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, New York, New York, USA.

Pace, R. M., III. 2001. Estimating and visualizing movement paths from radio-tracking data. Pages 189–206 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling. 1986. Numerical recipes: The art of scientific computing. Cambridge University Press, Cambridge, UK.

Priede, I. G. 1992. Wildlife telemetry. Pages 3–25 *in* I. G. Priede and S. M. Swift, editors. Wildlife telemetry: remote monitoring and tracking of animals. Ellis Hardwood, West Sussex, UK.

Ross, S. M. 1983. Stochastic processes. John Wiley, New York, New York, USA.

Saher, D. J., and F. K. A. Schmiegelow. 2004. Movement pathways and habitat selection by woodland caribou during spring migration. Rangifer 16:143–154.

Skagen, S. K., J. F. Kelly, C. van Riper III, R. L. Hutto, D. M. Finch, D. J. Krueper, and C. P. Melcher. 2005. Geography of spring landbird migration through riparian habitats in southwestern North America. Condor 107:212–227.

Small, R. J., and D. H. Rusch. 1989. The natal dispersal of Ruffed Grouse. Auk 106:72–79.

Stokes, D. L., P. D. Boersma, and L. S. Davis. 1998. Satellite tracking of Magellanic Penguin migration. Condor 100:376–381.

Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72:1253–1266.

Turchin, P. 1998. Quantitative analysis of movement. Sinauer Associates, Sunderland, Massachusetts, USA.

Vincent, C., B. J. McConnell, V. Ridoux, and M. A. Fedak. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. Marine Mammal Science 18:156–166.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecological Modeling 38:277–298.

Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794–800.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

APPENDIX

Derivation of Brownian bridge probability distribution when location errors are normally distributed (*Ecological Archives* E088-142-A1).

SUPPLEMENT

Visual Basic source code containing the algorithms described in this paper (*Ecological Archives* E088-142-S1).