

Theory of home range estimation from displacement measurements of animal populations

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Abstract

A theory is provided for the estimation of home ranges of animals from displacement measurement procedures. The theoretical tool used is the Fokker–Planck equation, its characteristic quantities being the diffusion constant which describes the motion of the animals, and the attractive potential which addresses their tendency to live in restricted regions, e.g., near their burrows. The measurement technique is shown to correspond to the calculation of a certain kind of mean square displacement of the animals relevant to the specific probing window in space corresponding to the region of observation. The output of the theory is a sigmoid curve of the observable mean square displacement as a function of the ratio of distances characteristic of the home range and the measurement window, along with an explicit prescription to extract the home range from observations. Applications of the theory to rodent movement in Panama and New Mexico are pointed out. An analysis is given of the sensitivity of our theory to the choice of the confining potential via the use of various representative cases. A comparison is provided between home range size inferred from our method and from other procedures employed in the literature. Consequences of home range overlap are also discussed.

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1. Introduction

The use of space by animals is the result of a combination of internal factors, such as the physiology and morphology of the animal, and external factors such as the environment. It is well known that mammals, in order to conduct their daily activity, occupy only part of their available environment: the so-called home range (Burt, 1943). A recent study on the scaling of home range size as function of animal body mass or metabolic rate (Jetz et al., 2004) shows that the home range dimensions are a trade-off between two ingredients: the necessity for harvesting resources and the detection and response to intrusion. On one hand, the home range has to

be large enough to meet energy requirements; on the other, it has to be small enough for the resident to be protected from intrusions of same-species foraging neighbours (Buskirk, 2004). The importance of learning about home ranges stems not only from the intellectual need to understand animal movement (Okubo, 1980), but also from the practical value in the determination of the size of the home range: it is intimately related to a variety of ecological phenomena ranging from social organization to mating behaviour and disease transmission (Wolff, 1997; Yates et al., 2002; Parmenter and MacMahon, 1983; Abramson and Kenkre, 2002; Abramson et al., 2003; Kenkre, 2003, 2004; Kenkre et al., 2004). There is already a body of biological literature on home ranges and related animal movements (Okubo, 1980; Murray, 1993). It is useful to build upon that literature to provide a comprehensive mathematical description of the dynamics of ecological systems.

Given the spatial probability density for an individual, the home range size has been typically defined as the

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contour that contains a fixed percentage (usually 95%) of the total volume under the distribution (Jennrich and Turner, 1969; Ford and Krumme, 1979). Home range size can be estimated from data of recorded locations over a sufficiently large period of time. These data can be obtained through a variety of methods including radio tracking and live trapping. Different techniques have been proposed for estimating home range size from location data of *single* animals (see e.g. the review by Worton (1987)). The various approaches can be divided into three categories. In the first, estimates are made using the peripheral points of the location data. In the second, the data are fitted to a pre-assumed probability distribution. In the third, the probability distribution is determined only from the statistical properties of the data (such as the one proposed by Anderson (1982)). The first method gives the maximum extent of the animal's range while the other two methods give a profile of the probability density inside the home range.

In order to obtain reasonable accuracy, all three procedures have the requirement that the number of locations recorded for each animal be large (Ford and Krumme, 1979). Unless unusual efforts are made during the field sampling, the number of locations for each individual is typically not very large (e.g. Mares et al., 1980; Bergstrom, 1988). On the other hand, the number of individuals is typically quite large. Home range estimation from location data of *many* individuals, therefore, avoids such problems (Ford and Krumme, 1979): the positions are averaged over all the animals recorded.

The purpose of the present paper is to develop a theoretical model which gives a simple prescription for the extraction of home range parameters from location data of animal population inside a limited region of space. Such a limited window of observation represents, in the case of radiotelemetry, simply the region over which the tracking is performed; in the case of mark-recapture observations it represents the size of the trapping array, in which an animal is captured, tagged and then recorded every time it is recaptured (Parmenter et al., 2003). It is well known that the former method is preferable by far because of the absence of the need to account for animal–trap interaction. Our theoretical procedure applies directly to radiotelemetry observations but can also be used for trapping observations if additional assumptions can be reasonably made concerning animal–trap interactions.

In the model we suggest, the motion of each animal is represented by diffusion in a confining potential, the latter representing the attraction of the animal to the home-place, the burrow. The potential has a characteristic width associated with the size of the home range, which we call L . The underlying equation in our approach is the Fokker–Planck equation for the probability distribution for each individual (Okubo, 1980; Risken, 1989). The stationary solution of this Fokker–Planck equation is used to calculate the infinite-time limit of the mean square displacement saturation value of all the individuals as

function of L . Comparison with the measured mean square displacement allows then the determination of the home range size, expressed here in units of length. The home range size has been typically denoted in the literature in term of an area. The relation to our description is simply that the area is given by the product of L for the two directions. Application of our procedure to rodent measurements in Panama and in New Mexico may be found in Giuggioli et al. (2004), Abramson et al. (2004) where our model in its simplest form has been successfully used to extract not only home range sizes but also diffusion constants from measurements of rodent populations.

The practical output of our present theoretical procedure is a saturation curve for the observed mean square displacement as a function of L/G , the ratio of the home range to G , a length that is characteristic of the size of the observation window. We predict a sigmoid shape for the saturation curve. An immediate consequence is that, for the greatest accuracy in the measurement of the home range, the observation window should be of the order of the home range. For certain potentials it is possible to write down simple analytical expressions for the saturation curve. For others the curve is obtained through numerical integration. Our theory also addresses the distribution of home ranges according to habitat, equivalently home range overlap, a quantity independently accessible through allometric scaling arguments (Jetz et al., 2004).

The paper is organized as follows. The general problem of calculating the average mean square displacement for a population of individuals, each one living in its own home range, and observed only inside a spatially limited window, is addressed in Section 2. The sensitivity of the saturation curve to the choice of the confining potential is studied in Section 3 through various representative cases. The case of a non-uniform distribution of home ranges and considerations for experimentally determining the average inter-home distance (related to the home range overlap) is the subject of Section 4. The comparison between home range size inferred from our method and the so-called convex polygon method, usually employed in the literature, forms Section 5, and conclusions are in Section 6.

2. Mean square displacement in a probing window: general considerations

In order to model the motion of an animal living in its home range, it is necessary to describe two tendencies of the animal: to move in a restricted region, including in some cases biased motion towards its burrow which provides it with food and safety, and to execute a roaming motion superposed on that restricted or biased motion. To incorporate these two features in our description we use a Fokker–Planck equation for the probability distribution $\mathcal{P}(x, t)$

$$\frac{\partial \mathcal{P}(x, t)}{\partial t} = \frac{\partial}{\partial x} \left[\frac{dU(x)}{dx} \mathcal{P}(x, t) \right] + D \frac{\partial^2 \mathcal{P}(x, t)}{\partial x^2}, \quad (1)$$

wherein D is the diffusion coefficient of the animal and $U(x)$ is the potential in which the animal is forced to roam. The potential $U(x)$ is a representation of the bias or reduced randomness associated with the walk. A pure random walk as in a simple diffusive process has $U(x) = 0$. When $U(x) \neq 0$ we identify its characteristic length with the home range size L . For a clear demonstration of how biotic random walks in continuous time in a confining potential may lead to a Fokker–Planck equation, we refer the reader to Okubo and Grünbaum (see Okubo, 1980, p. 144).

The two-dimensional counterpart of Eq. (1), written in polar coordinates, is

$$\frac{\partial \mathcal{P}(r, \phi, t)}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left[r \left(\frac{\partial U(r, \phi)}{\partial r} \mathcal{P}(r, \phi, t) + D \frac{\partial \mathcal{P}(r, \phi, t)}{\partial r} \right) \right] + \frac{1}{r^2} \frac{\partial}{\partial r} \left[\frac{\partial U(r, \phi)}{\partial \phi} \mathcal{P}(r, \phi, t) + D \frac{\partial \mathcal{P}(r, \phi, t)}{\partial \phi} \right]. \tag{2}$$

The description provided by Eq. (2) would be appropriate for a wide range of animal motion contexts including those that involve non-circular home ranges which would correspond to ϕ -dependent $U(r, \phi)$. The third dimension is very rarely required but can be easily incorporated. All the essential concepts are, however, easily represented through the description provided by the one-dimensional version. Therefore, we restrict ourselves in the present paper to Eq. (1). It is straightforward to generalize all considerations to higher dimensions if required.

The overall characteristics of the motion can be obtained by calculating just the moments of the distribution $\mathcal{P}(x, t)$ rather than the full $\mathcal{P}(x, t)$ which entails an integration of the probability. In a typical experiment a probing window is used, i.e., the animal is observed only inside a limited region of space. The integration to calculate the moments is then performed only over the probing window. The second moment of $\mathcal{P}(x, t)$, i.e., the mean square displacement, is given by

$$\langle \Delta x^2(t) \rangle = \frac{\int_{-G/2}^{G/2} dx (x - x_0)^2 \mathcal{P}_{x_0}(x, t)}{\int_{-G/2}^{G/2} dx \mathcal{P}_{x_0}(x, t)}, \tag{3}$$

where G is the dimension of the window and x_0 is the position of the animal at time $t = 0$. Because initially each animal can be anywhere inside G , the numerator and denominator of Eq. (3) have to be averaged over all the possible initial positions inside the window. We then have, for the average,

$$\langle \langle \Delta x^2(t) \rangle \rangle = \frac{\int_{-G/2}^{G/2} dx_0 \int_{-G/2}^{G/2} dx (x - x_0)^2 \mathcal{P}_{x_c, x_0}(x, 0) \mathcal{P}_{x_c, x_0}(x, t)}{\int_{-G/2}^{G/2} dx_0 \int_{-G/2}^{G/2} dx \mathcal{P}_{x_c, x_0}(x, 0) \mathcal{P}_{x_c, x_0}(x, t)}. \tag{4}$$

We have introduced here the label x_c to represent the burrow position of each animal. Eq. (4) is the contribution to the mean square displacement of an animal whose burrow is at x_c . A further average over the distribution of

burrow positions is necessary. If this distribution is denoted by $\rho(x_c)$, the observed mean square displacement within the window of size G is given by

$$\overline{\Delta x^2(t)} = \frac{\int_{-\infty}^{\infty} dx_c \rho(x_c) \int_{-G/2}^{G/2} dx_0 \int_{-G/2}^{G/2} dx (x - x_0)^2 \mathcal{P}_{x_c, x_0}(x, 0) \mathcal{P}_{x_c, x_0}(x, t)}{\int_{-\infty}^{\infty} dx_c \rho(x_c) \int_{-G/2}^{G/2} dx_0 \int_{-G/2}^{G/2} dx \mathcal{P}_{x_c, x_0}(x, 0) \mathcal{P}_{x_c, x_0}(x, t)}. \tag{5}$$

Short-time measurements of $\overline{\Delta x^2(t)}$ can be used (Giuggioli et al., 2004; Abramson et al., 2004) to obtain the diffusion constant D . In the present paper we are interested only in the home ranges, consequently in the infinite time limit of Eq. (5) which requires only the steady state solution, and corresponds to observations of positions that can be regarded as uncorrelated in time.

Analytic solutions of the Fokker–Planck equation for all times are known only for very few cases of $U(x)$. However, steady state solutions are known for any potential explicitly in terms of an integral (Risken, 1989; Kuś and Kenkre, 1992; Parris et al., 2001)

$$\mathcal{P}_{x_c, x_0}(x, t \rightarrow +\infty) = \frac{e^{-U(x-x_c)/D}}{\int_{-\infty}^{\infty} dx' e^{-U(x')/D}}. \tag{6}$$

Eq. (5) for $t \rightarrow \infty$ can, thus, be written as

$$\overline{\Delta x_{ss}^2} = \frac{\int_{-\infty}^{\infty} dx_c \rho(x_c) \int_{-G/2}^{G/2} dx_0 \int_{-G/2}^{G/2} dx (x - x_0)^2 e^{-\frac{U(x_0-x_c)+U(x-x_c)}{D}}}{\int_{-\infty}^{\infty} dx_c \rho(x_c) \int_{-G/2}^{G/2} dx_0 \int_{-G/2}^{G/2} dx e^{-\frac{U(x_0-x_c)+U(x-x_c)}{D}}}, \tag{7}$$

and further reexpressed in terms of quantities related to moments of the steady state probability density, equivalently of $\exp[-U(x)/D]$:

$$\overline{\Delta x_{ss}^2} = 2 \left\{ \int_{-\infty}^{\infty} dx_c \rho(x_c) \left[\left(\int_{-G/2-x_c}^{G/2-x_c} dx e^{-\frac{U(x)}{D}} \right) \times \left(\int_{-G/2-x_c}^{G/2-x_c} dx x^2 e^{-\frac{U(x)}{D}} \right) - \left(\int_{-G/2-x_c}^{G/2-x_c} dx x e^{-\frac{U(x)}{D}} \right)^2 \right] \right\} \times \left\{ \int_{-\infty}^{\infty} dx_c \rho(x_c) \left[\left(\int_{-G/2-x_c}^{G/2-x_c} dx e^{-\frac{U(x)}{D}} \right)^2 \right] \right\}^{-1}. \tag{8}$$

Expression (7) can be reduced further if the burrow distribution $\rho(x_c)$ is uniform in space. We obtain

$$\overline{\Delta x_{ss}^2} = \frac{G \int_{-G}^G dy y^2 g(y) - (\int_{-G}^G dy y^3 g(y) - \int_{-G}^0 dy y^3 g(y))}{G \int_{-G}^G dy g(y) - (\int_{-G}^G dy y g(y) - \int_{-G}^0 dy y g(y))}, \tag{9}$$

where $g(y)$ is the convolution of $\exp[-U(x)/D]$ with itself:

$$g(y) = \int_{-\infty}^{\infty} dx_c e^{-\frac{U[x_c]+U[x_c-y]}{D}}. \tag{10}$$

If the potential $U(x)$ remains finite for all finite values of x , $g(y) = g(-y)$, and it is possible to write a simpler

form of Eq. (9):

$$\overline{\Delta x_{ss}^2} = \frac{\int_0^G dy (G-y)y^2 g(y)}{\int_0^G dy (G-y)g(y)}. \tag{11}$$

Clearly, the observation window of width G can be interpreted as a probe into the system whose characteristic width is L . The mean square displacement depends on the relative magnitude of L and G of the probe. In the limit of an infinitely large probe, $(\overline{\Delta x_{ss}^2})^{1/2}$ measures simply the characteristic length of the system. It is thus natural to define the home range length L for arbitrary potentials as the square root of the limit $G \rightarrow \infty$ of Eq. (9),

$$L = \sqrt{\frac{\int_{-\infty}^{+\infty} dy y^2 g(y)}{\int_{-\infty}^{+\infty} dy g(y)}}, \tag{12}$$

when such a limit exists. If the probe is very small compared to the home range width, the observation window will measure a quantity associated with the width of the grid. In fact $g(y)$ becomes a constant in the limit $L \rightarrow \infty$ and Eq. (11) gives $G^2/6$ for the mean square displacement.¹

In a recent article, one of the present authors (Kenkre, 2005) has given an alternate formulation in terms of the Fourier transform of the steady state probability distribution (6). It has been shown there that the mean square displacement is given simply in terms of Fourier-space integrals of the product of the square of the sine function (which carries information about the probe) with, respectively, the square, and the derivative of the square, of the transform of the steady state probabilities (which carry information about the home ranges). Alternative expressions equivalent to Eqs. (9) and (12), respectively, are given in Kenkre (2005) as

$$\overline{\Delta x_{ss}^2} = -\frac{\int_{-\infty}^{\infty} dk \frac{\partial^2 \hat{P}^2(k)}{\partial k^2} \frac{[1 - \cos(Gk)]}{k^2}}{\int_{-\infty}^{\infty} dk \hat{P}^2(k) \frac{[1 - \cos(Gk)]}{k^2}} \tag{13}$$

and

$$L^2 = -2 \left. \frac{\partial^2 \hat{P}(k)}{\partial k^2} \right|_{k=0} = 2 \frac{\int_0^{+\infty} dy y^2 e^{-\frac{U(y)}{D}}}{\int_0^{+\infty} dy e^{-\frac{U(y)}{D}}}, \tag{14}$$

where $\hat{P}(k)$ is the Fourier transform of $\exp[-U(x)/D]$.

Clearly, a dimensionless quantity of crucial importance to the analysis is the ratio ζ of the home range to the observational probe length G :

$$\zeta = L/G. \tag{15}$$

In the next section we study the functional dependence of the saturation curve on this quantity ζ with attention to the

effects of the details of the confining potential, assuming that $\rho(x_c)$ is a constant.

3. Dependence on the details of the confining potential

The precise shape of the confining potential $U(x)$ obviously depends on the detail of animal movement, such as habitat and distance between neighbours. Since this detail is largely unavailable, it is important to determine the sensitivity of the deduced value of the home range size L to the choice of $U(x)$. It is clear that, when plotted as a function of ζ (see Eq. (15)), the mean square displacement $\overline{\Delta x_{ss}^2}$ for each potential starts out as L^2 when $\zeta \rightarrow 0$ and saturates to $G^2/6$ when $\zeta \rightarrow \infty$.

Extensive studies we have carried out with different potentials have made it clear that the curvature at the bottom and the steepness with which $U(x)$ becomes infinite both play a role in shaping the saturation curve of $\overline{\Delta x_{ss}^2}$. More precisely, the rise of $\overline{\Delta x_{ss}^2}$ is controlled by the steepness of the potential when $x/L \gg 1$: the steeper the rise to infinity of the potential, the smaller the value of ζ for which the saturation curve grows faster than the L^2 dependence at $L = 0$. In addition, the curvature of $U(x)$ for $x/L \ll 1$ determines the way $\overline{\Delta x_{ss}^2}$ approaches the value $G^2/6$: the larger the curvature, the slower it approaches the asymptote $G^2/6$. In Fig. 1 we show this dependence by comparing four characteristic potentials: a box potential, a harmonic potential and two types of logarithmic potentials.

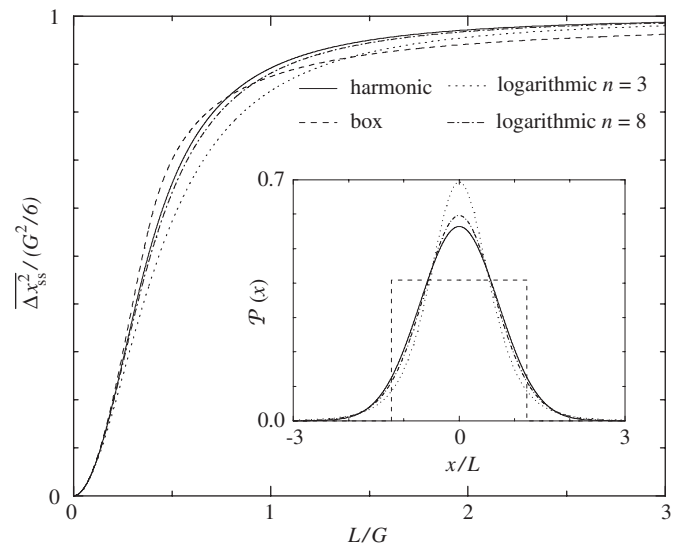


Fig. 1. Mean square displacement at saturation for four different potentials: a box potential (dashed line), a harmonic potential (solid line), and two logarithmic potentials (see text for definition) one with $n = 3$ (dotted line) and the other with $n = 8$ (dash-dotted line). The inset shows the corresponding stationary distributions $\mathcal{P}(x)$ as obtained from Eq. (6) by putting $x_c = 0$.

¹While definition (12) of the home range L is the most natural, alternate definitions are possible as used, e.g., in Abramson et al. (2004).

3.1. Box and harmonic potentials

The box potential has the steepest rise among the four curves in Fig. 1, since it diverges at a finite distance. Observe also that it is the slowest to reach $G^2/6$, being the one with the smallest curvature (zero) close to the origin. Such a potential has been considered in our previous work (Giuggioli et al., 2004; Abramson et al., 2004) for extracting home range sizes from mark-recapture data for two different rodent populations. In those investigations the saturation curve was numerically simulated. However, it is possible to calculate analytically all the integrals in Eq. (8) by selecting judiciously the limit of integration for the variable x_c as function of the relative dimension of the box width and the probe width. The resulting expression in terms of ζ is given by

$$\frac{\overline{\Delta x_{ss}^2}}{G^2/6} = \begin{cases} \frac{18\zeta^2}{5} \frac{(5 - 3\sqrt{6}\zeta)}{(3 - \sqrt{6}\zeta)} & \text{for } \zeta < \sqrt{6}, \\ \frac{3}{5} \frac{(3 - 5\sqrt{6}\zeta)}{(1 - 3\sqrt{6}\zeta)} & \text{for } \zeta > \sqrt{6}. \end{cases} \quad (16)$$

The limiting behaviour is that $\overline{\Delta x_{ss}^2} \simeq L^2$ for small ζ and $\overline{\Delta x_{ss}^2} \simeq G^2/6 - 4/(15\sqrt{6}\zeta)$ for large ζ .

The harmonic potential has been used in one of our previous studies (Abramson et al., 2004) for extracting the home range size for the deer mouse, *Peromyscus maniculatus*, in New Mexico. It was shown in that work that the distribution of displacements is found directly from observations to be approximately Gaussian. This finding suggests the use of a harmonic potential with $U(x) = D(x/L)^2$. Since the domain where $U(x)$ is not zero extends over the entire real axis, it is convenient to calculate the convolution in Eq. (10) which gives $g(y) = L\sqrt{\pi/2} \exp[-y^2/(2L^2)]$. Integrating Eq. (11) gives the mean square displacement at saturation as

$$\frac{\overline{\Delta x_{ss}^2}}{G^2/6} = 6\zeta^2 \left\{ 1 + \frac{\sinh[(1/2\zeta)^2]}{\sinh[(1/2\zeta)^2] - \frac{1}{2\zeta} \sqrt{\frac{\pi}{2}} e^{(1/2\zeta)^2} \operatorname{erf}\left(\frac{1}{\sqrt{2}\zeta}\right)} \right\}, \quad (17)$$

with $\overline{\Delta x_{ss}^2} \simeq L^2$ when $\zeta \ll 1$ and $\overline{\Delta x_{ss}^2} \simeq G^2/6[1 - (7/120\zeta^2)]$ when $\zeta \gg 1$. The intersection in Fig. 1 between the harmonic potential curve (solid) and the box potential curve (dashed) becomes evident here given that the former approaches $G^2/6$ linearly while the latter approaches it quadratically as $\zeta \rightarrow \infty$.

3.2. Logarithmic potentials

As an example of $U(x)$, whose corresponding steady state distribution given by Eq. (6) decays to zero slower (algebraically) than in the box or the harmonic case, we

consider a family of potentials of the form

$$U(x) = D \ln \left\{ 1 + \frac{x^2}{(\kappa_n L)^2} \right\}^n, \quad (18)$$

with $\kappa_n = \sqrt{n - 3/2}$ and $n \geq 2$. These potentials have a quadratic dependence when $x/L \ll 1$ and a logarithmic dependence for $x/L \gg 1$ such that $\mathcal{P}(x) \simeq x^{-2n}$ as $|x| \rightarrow \infty$. It is straightforward to check that expression (18) is consistent with definition (12) of the home range L for any value of n . In the limit of $n \rightarrow +\infty$ Eq. (18) reduces to the harmonic case. We have studied, in particular, the cases from $n = 2$ to 8 and have obtained analytical expressions for the mean square displacement. We do not display them here because they do not add to the understanding. In Fig. 1 we show the cases $n = 3$ and 8. Already for $n = 8$ the saturation curve for the logarithmic and the harmonic cases are very close to each other. The inset of Fig. 1 shows the origin of such similarities by comparing the corresponding steady state probability distributions $\mathcal{P}(x)$.

As mentioned above, the $\mathcal{P}(x)$ associated with the logarithmic potentials possesses long tails. Probability distributions with long tails can be appropriate when the motion of the animal cannot be represented by a simple random walk. More complex types of walk may occur if the walker awaits for very long times between jumps, or if the jumps are of very large distance. Long-tailed $\mathcal{P}(x)$ are characterized by the feature that certain moments of the distribution become infinite. If all the moments beyond the first are infinite, Eq. (12) is no longer applicable for defining the home range width. A qualitatively different behaviour is expected for large values of G . To illustrate this situation, we consider the potential

$$U(x) = D \ln \left(1 + \frac{x^2}{\sigma^2} \right) \quad (19)$$

whose corresponding $\mathcal{P}(x)$ is the Cauchy distribution (Lemons, 2002) $\mathcal{P}(x) = (1 + (x/\sigma)^2)^{-1}/\pi$. Also for this case the mean square displacement can be obtained analytically and it is given by

$$\frac{\overline{\Delta x_{ss}^2}}{G^2/6} = 6 \left[\frac{\xi}{\tan^{-1}\left(\frac{1}{2\xi}\right) - \xi \ln\left(1 + \frac{1}{(2\xi)^2}\right)} - 4\xi^2 \right], \quad (20)$$

where $\xi = \sigma/G$. As $\xi \rightarrow 0$, $\overline{\Delta x_{ss}^2}/(G^2/6) \simeq (12/\pi)\sigma/G$ in Eq. (20). A linear growth of the saturation curve emerges, as depicted in Fig. 2. Notice that L , as defined by Eq. (12), does not exist for this potential. The home range is therefore defined as the characteristic length σ , the ratio ξ being the counterpart of ζ of Eq. (15). This different qualitative behaviour with respect to the previously analysed cases could be exploited for determining the characteristics of the animal walks by making various measurements with large grid size. A sufficient number of these measurements would allow one to discern if the

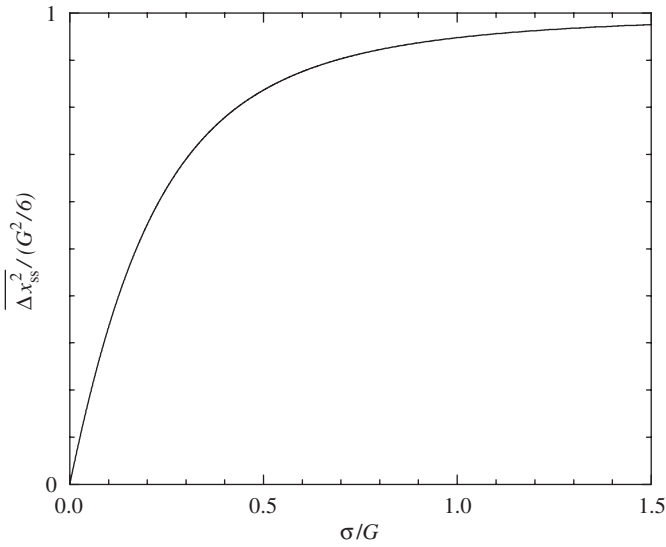


Fig. 2. Mean square displacement at saturation for the potential $U(x) = D \ln(1 + (x/\sigma)^2)$. Compared to the potentials depicted in Fig. 1, here $U(x)$ grows to infinity qualitatively slower. The corresponding distribution $\mathcal{P}(x)$ does not possess a finite second moment. The long-tailed distribution changes drastically the behaviour of $\overline{\Delta x_{ss}^2}$ when very large observation window sizes are used. The growth of the saturation curve for small σ/G is linear and not quadratic.

saturation curve is growing quadratically (as in the examples of Fig. 1) or linearly (as in Fig. 2).

The examples of this section illustrate that the choice of $U(x)$ in any application of the present theory should be assessed in each case, based, for example, on a priori knowledge of the specific animal behaviour. The different potentials shown here give an overview of the possible qualitative behaviours of the mean square displacement at saturation.

4. Inhomogeneous distribution of home ranges: the case of a periodic arrangement

The results obtained in Section 2, from Eq. (9) onward, and the examples developed in Section 3, assume a continuous and homogeneous distribution of burrow location x_c . A more realistic situation invokes the home ranges arranged in a non-continuous manner, the centres of adjacent ranges (the burrow locations) separated by some characteristic distance a . In this section we show an example of how this feature may be incorporated in our analysis and how, in principle, a can be deduced from displacement measurements.

Let us suppose for simplicity that the home ranges are distributed in a periodic array, with a being the distance between nearest neighbours. The mean square displacement, measured within a window of linear size G , is now a function of a and L , besides depending parametrically on G . As in Section 2, G can be used to rescale the two coordinates a and L . The function $\overline{\Delta x_{ss}^2} / (G^2/6) = f(L/G, a/G)$ is universal and does not depend on the size of the observation window. We show a contour plot of this

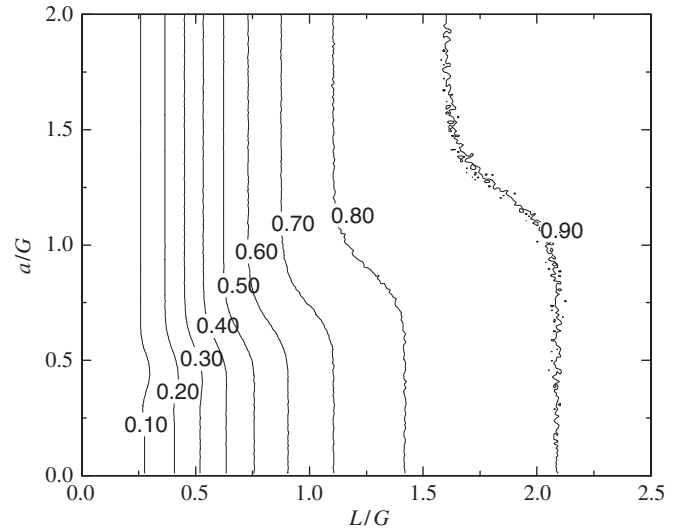


Fig. 3. Contour plot of the normalized mean square displacement, $\overline{\Delta x_{ss}^2} / (G^2/6)$, as a function of the normalized home range size, L/G and the normalized inter-home distance, a/G . The lines are the result of simulations of the harmonic model (Gaussian occupation of space). The fluctuations in the lines are an artifact of the construction of the contours from discrete simulations.

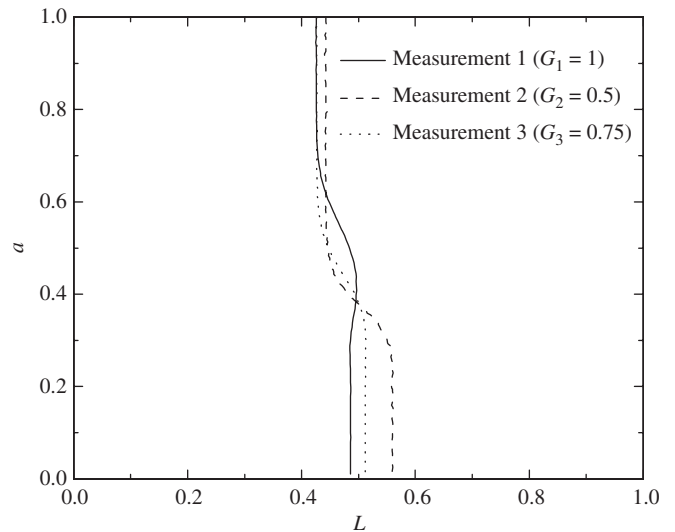


Fig. 4. Graphical explanation of the procedure to determine home range overlap via a hypothetical measurement. Both L and a can be determined by taking three measurements of the same population, using three windows, of sizes G_1 , G_2 and G_3 . The measured mean square displacements are supposed to be $\overline{\Delta x_1^2} = 0.045$, $\overline{\Delta x_2^2} = 0.029$, and $\overline{\Delta x_3^2} = 0.041$. The corresponding contours intersect at $L = 0.5$, $a = 0.375$, providing these values as a result. Both a and L are displayed in units of G (arbitrary linear units).

function in Fig. 3, as calculated by numerical simulation of the harmonic model (Gaussian probability distributions). At $a = 0$, the shape of the surface coincides with the curve calculated in Eq. (17). The contours of equal mean square displacement are nearly vertical lines in this plot, indicating that the dependence on the inter-home distance a is very weak (in particular for small values of the normalized mean

square displacement), except for a region well defined in a , where the contours shift from one value of L to another. This feature will certainly be of relevance if an experiment is designed in order to measure both a and L , since the uncertainty on a will tend to be large.

In general, given that the function $\overline{\Delta x_{ss}^2}$ is nonlinear in both its variables a/G and L/G , two or more measurements are necessary to determine the home range size and the inter-home distance. In Fig. 4 we show a hypothetical situation in which three measurements are supposed to be taken on the same population, using three windows sizes, $G_1 = 1$, $G_2 = G_1/2$ and $G_3 = 3G_1/4$. The results of the measurement are curves of constant $\overline{\Delta x_{ss}^2}$ in the plane (L, a) . With three measurements, $\overline{\Delta x_1^2}$, $\overline{\Delta x_2^2}$ and $\overline{\Delta x_3^2}$, three curves are obtained, and the model predicts:

$$\overline{\Delta x_1^2}/(G_1^2/6) = f(L/G_1, a/G_1),$$

$$\overline{\Delta x_2^2}/(G_2^2/6) = f(L/G_2, a/G_2),$$

$$\overline{\Delta x_3^2}/(G_3^2/6) = f(L/G_3, a/G_3). \tag{21}$$

This is a system of three (nonlinear) equations with two unknowns, L and a , and its solution can be found as the intersection of three curves. These curves are shown in Fig. 4, displaying an intersection very near $L = 0.5$, $a = 0.375$ (within the accuracy of the fluctuations of the contours). The curves were obtained from the normalized function, shown in Fig. 3, using the appropriate contours. As mentioned above, the weak dependence on a may hinder its determination by the present method. It is clear that the choice of the appropriate values of the window sizes is critical to obtain the best results. This must be done specifically for each situation, with the help of an informed guess of the range where both a and L lie. Regardless of this practical difficulty, the procedure we describe provides a method for an immediate measurement of an important quantity that is hard to obtain by other means. Additionally, if the population is not well characterized by a typical inter-home distance, as we suppose here (for example, if the inter-home distance is bimodal due to gender differences or other polymorphism), the model can be immediately modified to incorporate those features.

Moreover, the inter-home distance is closely related to the overlap of home ranges (or to the exclusivity of space use). See Fig. 5 for an illustration of three typical situations. The home ranges of three neighbouring animals, A , B , and C , are displayed as arrows, schematically representing the extent of the area occupied by 95% of the norm of $\mathcal{P}(x)$, as usually defined (Worton, 1987). When $a = L/2$, the first neighbours, B and C , of A have their home ranges situated at the border of A 's home range. Then, A does not have exclusive use of any part of its own home range (overlap equal 100%). On the other extreme, when $a = L$, the home ranges of B and C are completely outside A 's. In consequence, the exclusivity of A is 100% (home range overlap 0%). This value of exclusivity,

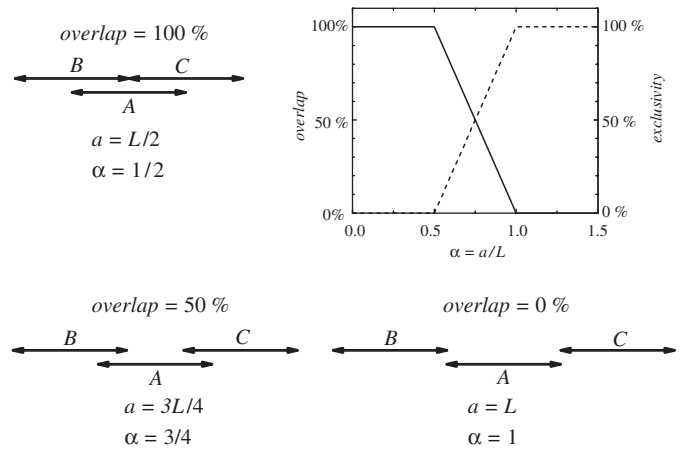


Fig. 5. Illustration of home range overlap situations, and the variables characterizing them. The schematic diagram shows three cases: 100%, 50%, and 0% overlap, with arrows representing the extent of the home range of three neighbouring animals, A , B and C . The plot shows the relation between the overlap, the exclusivity of space use, and the normalized inter-home distance $\alpha = a/L$.

certainly, is maintained for any value of $a > L$. An intermediate situation, in which the exclusivity of animal A is equal to 50% (as well as its overlap with the neighbours) is also shown.

The exclusivity of space use has recently been found to obey an allometric scaling relation with the animal mass by Jetz et al. (2004). The present theory provides a method to determine both the home range size and the home range overlap, and thus to verify the scaling of these and related magnitudes (West et al., 1997; Banavar et al., 1999).

5. Comparison with convex polygon calculations

Home range sizes have been often deduced from the measurement of the so-called minimum convex polygon of an animal position. Although this procedure suffers from a number of drawbacks (Worton, 1987), it is used rather widely. Among its drawbacks it is easy to recognize at least a logical and a methodological one. The surveyed perimeter provides no information about the use of space inside it, effectively encompassing areas that may be inaccessible to the animal, or potentially huge areas of very low frequency of utilization. The methodological one is the fact that the measured area converges very slowly to the actual home range, and as such the observation of a few tens of positions provides a very bad estimation. Both kinds of flaws have been recognized in the literature before (see Worton (1987) and references therein), and suggestions have been made to compensate for them. These proposals, such as discarding some fraction of the extreme positions from a set of observations to compensate for the first, or to join the perimetral points in a fashion different from the minimum convex polygon, are surely arbitrary. Furthermore, methodologically, they are obviously subject to uncontrollable errors.

In the following we illustrate how the calculation of the mean square displacement we have given in the present paper provides a rapidly converging measurement of the home range size. This is an additional advantage when displacements of animals belonging to a population are more readily accessible than repeated measurements of the position of individual animals. For the sake of the illustration, we will consider that the probability of space use of an animal is a bivariate Gaussian distribution of variance σ :

$$\mathcal{P}(x, y) = \frac{1}{2\pi\sigma^2} e^{-\frac{x^2+y^2}{2\sigma^2}}. \quad (22)$$

We consider this symmetric distribution for simplicity, but the discussion applies equally to a distribution with anisotropic σ . Moreover, the conclusions are equivalent for more general distributions, including those with a finite cut-off.

If we define the home range of the animal whose space use distribution is described by Eq. (22) as the area A that contains the 95% of \mathcal{P} (Worton, 1987), a simple integration gives

$$A = \pi R^2 = 2\pi\sigma^2(-\ln 0.05) \approx 18.8\sigma^2. \quad (23)$$

This the quantity that we intend to measure by both methods. In Fig. 6 we show the area of the minimum convex polygon defined by a set of N points drawn at random with a bivariate Gaussian distribution of $\sigma = 1$. Observe, firstly, that the area grows unboundedly as the number of observations grows, since \mathcal{P} is unbounded. More relevant from the practical point of view is the fact that the growth is very slowly, and that the area A

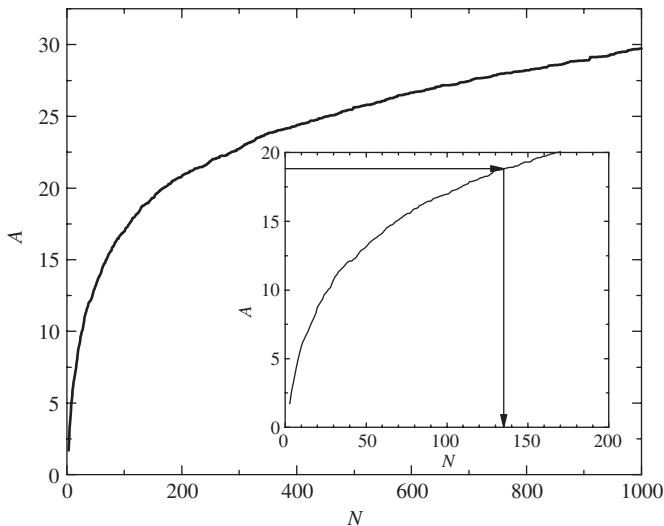


Fig. 6. Area A enclosed by the minimum convex polygon corresponding to a set of random points with Gaussian distribution in the plane, as a function of N , the number of points of the set. The line shows the average of 50 independent realizations. The inset shows a detail of the same function, with arrows showing the necessary number of points to obtain a good measurement of the home range, defined as the 95% of the space occupation which, for $\sigma = 1$, and $A \approx 18.8$, is $N = 135$ points. The variance σ has arbitrary units of length, and A those of length squared.

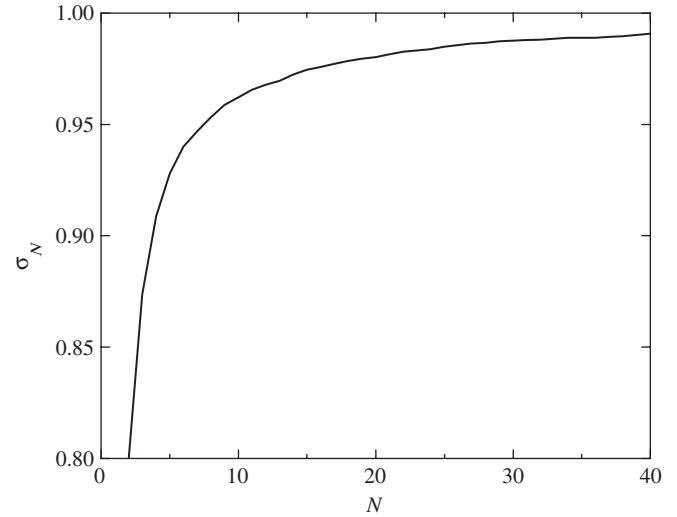


Fig. 7. Measurement of the variance of a bivariate Gaussian distribution ($\sigma = 1$), as a function of the number of displacements used for the estimate. The curve shows an average based on 104 realizations.

(obtained with 95% rule and marked in Fig. 6 with an arrow) is achieved after the observation contains, on average, 135 points (see the inset of Fig. 6).

Now consider that one wants to determine A by measuring *displacements*, instead of positions. The relevant quantity to be estimated is the variance σ , immediately derived from the home range size L , accessible through our present theory explained in Section 2. Expression (23) gives then the home range area. Fig. 7 shows that the measurement of the variance, σ_N , for a finite set of N observations, converges very rapidly to the actual value (which is 1 in this case), when the number of observations is increased. Indeed, with just 10 observations of the displacement the variance can be estimated with an accuracy greater than 95%. Ten displacements correspond to just 11 positions of a single animal, if taken at intervals long enough that they are uncorrelated, or 10 displacements of different animals for which an average distribution would be found.

In summary, the mean square displacement provides a faster convergence to the area of the home range than the construction of the convex polygon. In addition, the estimation of the distribution \mathcal{P} (unimodal in this case, but easily generalizable) by that method provides information about the use of the home range, which is inaccessible to the convex polygon procedure.

6. Conclusions

The determination of home range dimensions and spatial overlap of two neighbouring home ranges from field observation is a subject of great interest for the understanding of animal motion. We have provided here a general theory to extract such demographic parameters on the basis of the measurement of displacements of individual animals in a population.

The most common techniques for gathering information of home range size employ trapping of animals and radiotelemetry observations. It is well known that radiotelemetry methods constitute by far the superior procedure. Our theory in the present paper has been constructed with the specific goal of interpreting data obtained from *either* type of observation. To use it with trapping observations, a further assumption that trapping introduces only a negligible effect on animal movement needs to be made. Such an assumption is generally questionable, and in a specific situation may or may not be valid. On the other hand no further assumption needs to be made to use our procedure for radiotelemetry observations.

The motion of an animal inside its own home range has been modeled by a Fokker–Planck (1), i.e. by diffusion in a confining potential $U(x)$. While the equations considered are, for simplicity, one-dimensional, extension to higher dimensions is straightforward and unnecessary for practical purposes.

Even though the precise determination of the home range size L depends on the choice of the potential $U(x)$, the general sigmoid shape of the saturation curve in our theory indicates that the difference in the results is not substantial if the window size is chosen such that $L < G$. Eventually, the choice of the right potential is to be determined for each given case, on the basis of biological information of the animal population under study. We have shown that, for those situations in which the second moment of the distribution $\mathcal{P}(x) = \exp(-U(x)/D)$ is not finite, the saturation curve for large G grows linearly with the home range length rather than quadratically as in more conventional potentials (box or harmonic). Such cases may arise when the animal motion is not simple but involve a more complicated random walk such as a Lévy walk or flight (Morales et al., 2004). This means that our theory may be used, in principle, to determine whether the animal population is performing a Gaussian random walk or a more complicated walk. By measuring the mean square displacement at saturation with different values of the probe length G (sufficiently larger than L) it might be possible to determine if the saturation curve grows quadratically or linearly.

The obtained parameters that characterize the average use of space, when obtained via displacement observations and their interpretation with our present theory, converge rapidly to the expected values. We have shown in Section 5 that this is not the case in the application of the traditional minimum convex polygon method.

The other important demographic parameter that can be extracted within the framework developed here is the inter-home characteristic distance of the animals, called a in the present paper. Such a length is simply related to the mean overlap (or the mean exclusivity of space usage). We have outlined a procedure to extract this parameter quantitatively and provided a general way to verify directly the scaling of home range overlap as function of body mass.

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