

MECHANISTIC HOME RANGE MODELS AND RESOURCE SELECTION ANALYSIS: A RECONCILIATION AND UNIFICATION

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Abstract. In the three decades since its introduction, resource selection analysis (RSA) has become a widespread method for analyzing spatial patterns of animal relocations obtained from telemetry studies. Recently, mechanistic home range models have been proposed as an alternative framework for studying patterns of animal space-use. In contrast to RSA models, mechanistic home range models are derived from underlying mechanistic descriptions of individual movement behavior and yield spatially explicit predictions for patterns of animal space-use. In addition, their mechanistic underpinning means that, unlike RSA, mechanistic home range models can also be used to predict changes in space-use following perturbation. In this paper, we develop a formal reconciliation between these two methods of home range analysis, showing how differences in the habitat preferences of individuals give rise to spatially explicit patterns of space-use. The resulting unified framework combines the simplicity of resource selection analysis with the spatially explicit and predictive capabilities of mechanistic home range models.

Key words: home range analysis; mechanistic home range models; resource selection analysis; RSA; spatially explicit space-use.

INTRODUCTION

Since its introduction in the 1980s, resource selection analysis (RSA) has become a widespread method for identifying underlying environmental correlates of animal space-use patterns (Manly 1974, Johnson 1980). In contrast to earlier descriptive methods of home range analysis, such as the minimum convex polygon, bivariate normal, and kernel methods that simply summarize observed spatial patterns of relocations (for reviews, see Macdonald 1980, Worton 1987, Kernohan et al. 2001), conventional RSA uses a spatially implicit frequentist approach to identify habitats that are used disproportionately in relation to their occurrence.

Ratios of habitat utilization relative to habitat availability provide a simple estimate of habitat selection (Fig. 1). More commonly, however, resource selection models are specified in terms of the probability P_j of obtaining a relocation in a given habitat type j :

$$P_j = \frac{A_j w_j}{\sum_{k=1}^{n_{\text{hab}}} A_k w_k} \quad (1)$$

where w_j is the selective value of habitat j relative to other habitats ($j=1 \dots n_{\text{hab}}$, where n_{hab} is the number of habitat types) and A_j is the availability of habitat j on the landscape. The collection of resource selection values

for all habitats within a landscape $\{w_j\}$ ($j=1 \dots n_{\text{hab}}$) is known as the resource selection function (Manly et al. 1993). Eq. 1 is generally preferred over simpler ratio-based estimates of habitat selectivity because of its improved statistical properties, having smaller variance and being less subject to bias (Arthur et al. 1996).

As results from numerous studies have shown, RSA can be used successfully to identify associations between animal space-use and habitat types as well as other forms of environmental heterogeneity, such as topography and resource availability, yielding insight into the underlying causes of animal space-use (for reviews, see Manly et al. 1993, Boyce and McDonald 1999, Cooper and Millsaugh 2001, Erickson et al. 2001).

More recently, mechanistic home range models have been proposed as an alternative framework for analyzing patterns of animal home ranges (Moorcroft and Lewis 2006, Moorcroft et al. 2006). In contrast to the spatially implicit, frequentist nature of RSA models such as Eq. 1, mechanistic home range models develop spatially explicit predictions for patterns of animal space-use, by, in the words of Millsaugh and Marzluff (2001), “modeling the movement process.” Mathematically, this involves characterizing the fine-scale movement behavior of individuals as a stochastic movement process that is defined in terms of a redistribution kernel $k(\mathbf{x}, \mathbf{x}', \tau, t)$, where $k(\mathbf{x}, \mathbf{x}', \tau, t) d\mathbf{x}$ specifies the probability of an animal located at \mathbf{x}' at time t moving to a location between location \mathbf{x} and $\mathbf{x} + d\mathbf{x}$ in the time interval τ .

Relevant behavioral and ecological factors influencing the movement of individuals can be incorporated into

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the redistribution kernel that defines the fine-scale stochastic movement process. For example, in a recent analysis of coyote home ranges in Yellowstone, Moorcroft et al. (2006) developed a “prey availability plus conspecific avoidance” (PA + CA) mechanistic home range model in which individuals exhibit: (1) an avoidance response to encounters with foreign scent marks (Fig. 2a, b), (2) an over-marking response to encounters with foreign scent marks, and (3) a foraging response to prey availability in which individuals decrease their mean step length in response to small-mammal abundance (Fig. 2a, c).

From this description of fine-scale movement behavior, it is then possible to derive probability density functions for the expected spatial pattern of home ranges that result from individuals moving on a landscape according to the underlying rules of movement. For example, in the case of the mechanistic home range model used by Moorcroft et al. (2006) to analyze coyote movements, the stochastic foraging response and responses to scent marks yield the following equations for the expected steady-state pattern of space-use:

$$\begin{aligned} \frac{\partial u^{(i)}(\mathbf{x}, t)}{\partial t} &= -\nabla \cdot [e^{-\alpha h(\mathbf{x})} \nabla u^{(i)}] \\ &+ \nabla \cdot \left[e^{-\alpha h(\mathbf{x})} \beta(\mathbf{x}) \vec{\mathbf{x}}_i u^{(i)} \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)} \right] \\ &- \nabla \cdot [e^{-\alpha h(\mathbf{x})} u^{(i)} \nabla h] = 0 \end{aligned} \quad (2)$$

where $\nabla = (\partial/\partial x, \partial/\partial y)$, and the three bracketed terms on the right-hand side of the equation, in order, represent random motion, scent-mark avoidance, and directed movement toward areas of high resource density; and

$$\frac{dp^{(i)}(\mathbf{x}, t)}{dt} = u^{(i)} \left[1 + m \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)} \right] - p^{(i)} \quad (3)$$

where the right-hand side of Eq. 3 represents the difference between scent-mark deposition and scent-mark decay. In Eqs. 2 and 3, $u^{(i)}(\mathbf{x}, t)$ is the expected space-use of individuals in pack i , $p^{(i)}(\mathbf{x}, t)$ is the scent-mark density of individuals in pack i , $h(\mathbf{x})$ is the spatial distribution of prey availability, and $\vec{\mathbf{x}}_i$ is a vector indicating the direction of the individual’s home range center from its current position. The coefficients α and β of the space-use equation (Eq. 2) reflect the underlying characteristics of individual movement behavior. Specifically, $\alpha = 2\rho_1$, where ρ_1 is the mean step length of the individual, and β reflects the strength of the avoidance response to foreign scent marks (Fig. 2b, c). The parameter m of the scent-marking equation (Eq. 3) governs the strength of the over-marking response of individuals (i.e., the rate at which individuals increase their rate of scent marking following encounters with foreign scent marks relative to the background rate of marking of individuals). Fig. 3 shows the fit of the PA +

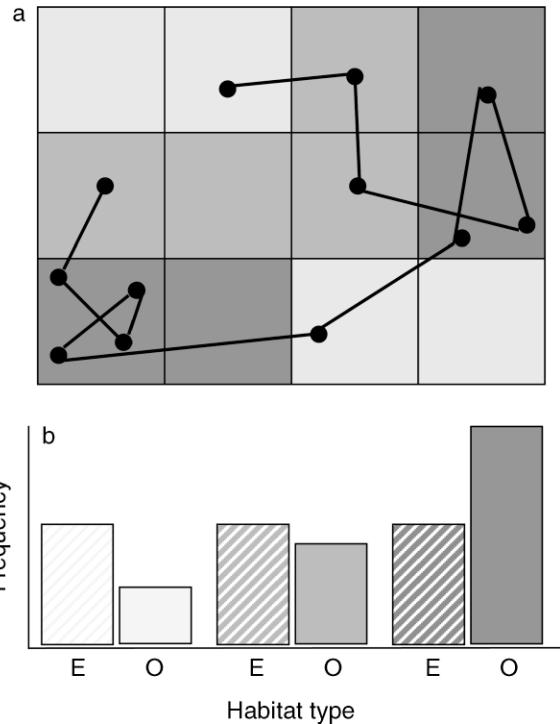


FIG. 1. Schematic illustrating the resource selection analysis (RSA) approach to analyzing patterns of animal space-use. (a) Shaded squares represent an idealized landscape comprising three equally abundant habitat types. Black lines represent the movement trajectory of an individual as it traverses the landscape, with points representing fixed-interval relocations of the individual. Because the three habitat types that comprise the landscape plotted in panel (a) are equally abundant, in the absence of preference, equal numbers of relocations would be expected to be obtained in each habitat, as indicated by the hatched bars in panel (b). The actual observed distribution of relocations, indicated by the solid bars in panel (b), shows that the individual exhibits a preference for the dark gray habitat type.

CA space-use equations to the observed spatial distribution of relocations of five adjacent coyote packs in Yellowstone National Park home ranges. As the figure illustrates, the model captures the influences of resource availability and the presence of neighboring groups on the patterns of space-use within the region.

Mechanistic home range models address several limitations of RSA. First, as the fit of the PA + CA model shown in Fig. 3 illustrates, in addition to incorporating the effects of underlying landscape heterogeneities such as prey density, mechanistic home range models can also incorporate the influence of conspecifics that can significantly influence patterns of animal space-use. Second, a critical step in any RSA is to define the region within a landscape that constitutes available habitat. The spatially implicit, frequentist nature of conventional RSA models such as Eq. 1 means that all areas within the predefined region defined as “available habitat” are assumed to be equally accessible to individuals. On real landscapes, the patchy

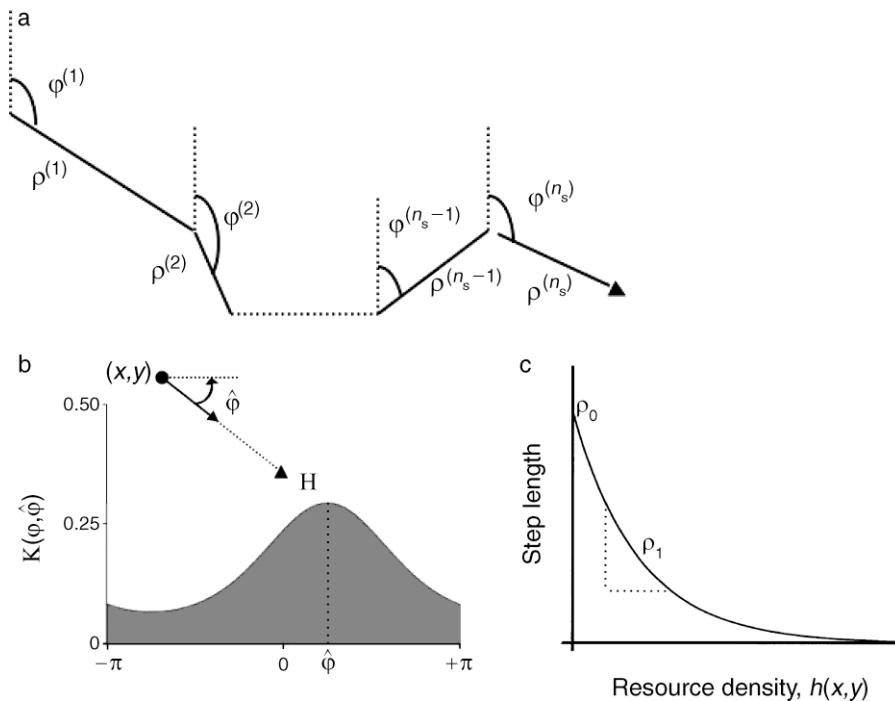


FIG. 2. (a) Schematic illustrating the model of individual movement behavior underlying mechanistic home range models. The movement trajectory of individuals is characterized as a stochastic movement process, defined in terms of sequences of movements ($i = 1 \dots n_s$) [where n_s is the total number of steps] of distance $\rho^{(i)}$ and direction $\varphi^{(i)}$, drawn from statistical distributions of these quantities that are influenced by relevant factors affecting the movement behavior of individuals. Superscripts in parentheses indicate the step sequence. (b, c) Movement responses incorporated in the PA + CA (prey availability plus conspecific avoidance) mechanistic home range model used by Moorcroft et al. (2006) to characterize coyote home range patterns in Yellowstone. (b) Individuals display a conspecific avoidance response, in which encounters with foreign scent marks give rise to a nonuniform distribution of movement directions $K(\varphi)$, with individuals preferentially moving toward the center of their home range (H), whose direction from their current position is indicated by the angle $\hat{\varphi}$. The magnitude of the avoidance response is governed by the density of foreign scent marks encountered and the value of an avoidance parameter β . (c) Consistent with observations of carnivore movement behavior, increasing prey availability causes the mean step length of individuals to decrease; ρ_0 is the mean distance between successive relocations in the absence of resources and ρ_1 governs the rate at which the mean step length of individuals decreases with increasing resource density, $h(x, y)$. The figure is from Moorcroft and Lewis (2006).

spatial distribution of habitats and resources such as that seen in Fig. 3, means that individuals are frequently required to traverse less favorable habitats in order to move between preferred areas. In conventional RSA, the time that individuals spend traversing unfavorable habitat registers as a degree of selection for the unfavorable habitat type (i.e., a nonzero probability that the individual chooses the unfavorable habitat at its next move) rather than as a constraint imposed by the spatial distribution of habitats on the landscape. In contrast, the mechanistic and spatially explicit nature of mechanistic home range models avoids the need to define available habitat, a priori, because the underlying model of individual movement behavior (Fig. 2) determines the likelihood and feasibility of an individual moving to a particular location, given its current position. Thus, by explicitly modeling the process of individual-level movement, mechanistic home range models naturally capture the influence of spatial constraints on patterns of space-use by individuals. Finally, their mechanistic nature means that mechanistic

home range models can be used to predict patterns of space-use following perturbation. For example, Moorcroft et al. (2006) showed that their PA + CA model correctly captured the shifts in patterns of space-use that occurred following the loss of one of the packs in the study region. For further discussion of these issues, see Moorcroft et al. (2006) and Moorcroft and Lewis (2006).

Such considerations imply that resource selection analysis (RSA) and mechanistic home range models constitute two distinct frameworks for analyzing patterns of animal space-use. However, as we will show, some recent developments now permit a formal reconciliation and unification of these two seemingly disparate methods for analyzing patterns of animal space-use.

The first important development toward reconciling mechanistic home range models and RSA came in an analysis of polar bear relocations by Arthur et al. (1996), who argued that, rather than assuming a fixed measure of habitat availability across the entire study region, a more appropriate measure was the availability habitats

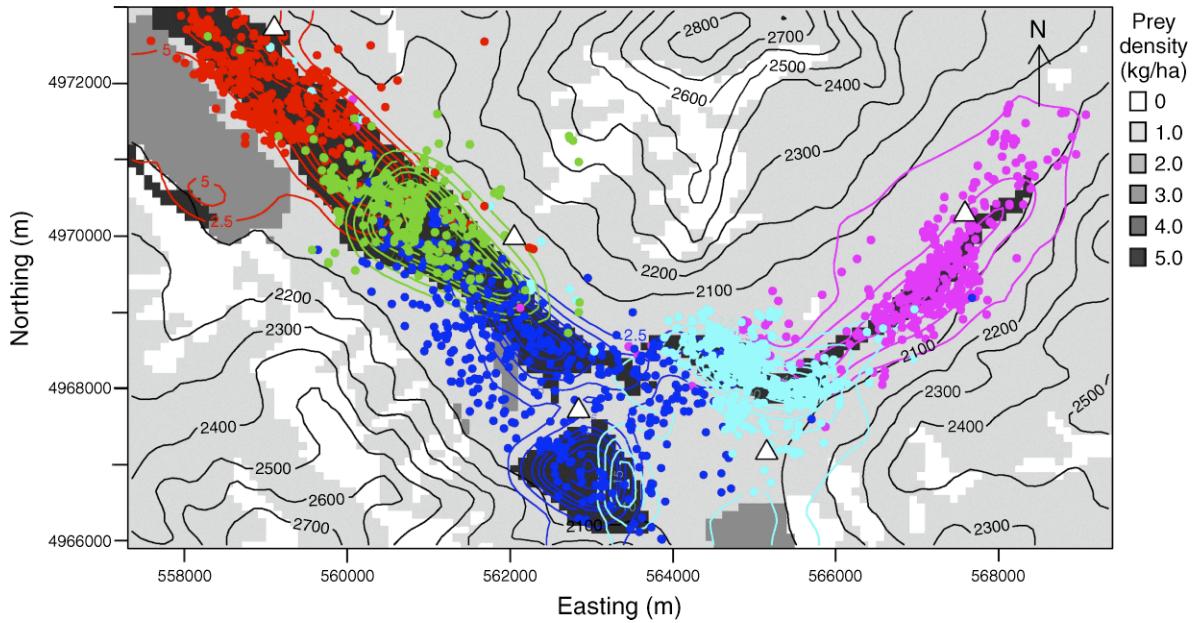


FIG. 3. Colored contour lines showing fit of the prey availability plus conspecific avoidance (PA + CA) home range model (Eqs. 2 and 3) to relocations (solid circles) obtained from five adjacent coyote packs in Lamar Valley Yellowstone National Park. The home range centers for each of the packs are also shown (open triangles), and the gray-scale background indicates small-mammal prey density in the different habitat types. Elevation contour lines (black) are in m.a.s.l. The Akaike Information Criterion (AIC) score for the PA + CA home range model indicates that it gives a substantially improved goodness of fit to the observed spatial distribution of relocations compared to both an alternate model consisting of conspecific avoidance alone ($\Delta AIC = 1299.6$) and an alternate model incorporating conspecific avoidance plus an avoidance response to steep terrain ($\Delta AIC = 456.9$). The figure is redrawn from Moorcroft et al. (2006).

within a circle centered on the individual’s current location, with radius R corresponding to the maximum distance that the individual was likely to travel in the time between successive relocations. They incorporated this into an RSA model by using a modified version of Eq. 1, in which habitat availability varies between relocations:

$$P_{ij} = \frac{A_{ij}w_j}{\sum_{k=1}^{n_{hab}} A_{ik}w_k} \quad (4)$$

where P_{ij} is the probability of choosing habitat j for the i th move, w_j is the habitat selection parameter for habitat j , and A_{ij} is the proportional availability of habitat j associated with relocation i , calculated as the fraction of the area within distance R of location i that is of type j .

The second development came in a paper by Rhodes et al. (2005), who proposed an extension of the approach of Arthur et al. (1996) to defining available habitat. Eq. 4 incorporates spatial variation in habitat availability; however, like Eq. 1, it is written in terms of the probability of observing a relocation of a given habitat type. Rhodes et al. (2005) recast the model of Arthur et al. (Eq. 4) in terms of the probability of an individual moving from location, given location a , to a subsequent location b :

$$P(a \rightarrow b) = \frac{\phi(a, b) \sum_{j=1}^{n_{hab}} w_j I(b, j)}{\sum_{j=1}^{n_{hab}} w_j \int_{I(c, j)=1} \phi(a, c) dc} \quad (5)$$

where $I(b, j)$ is an indicator function that takes the value 1 when location b is of type j and 0 otherwise, and $\phi(a, b)$ is given by

$$\phi(a, b) = \begin{cases} \frac{1}{\pi R^2} & \text{if } r_{ab} \leq R \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

where r_{ab} is the distance between locations a and b , and R is the maximum distance an individual is likely to travel between successive relocations, which defines the area of available habitat at location a .

The motivation of Rhodes et al. (2005) for casting the model of Arthur et al. (1996) into the form of Eq. 5 was twofold. First, they argued for a different functional form for $\phi(a, b)$ than Eq. 6, namely an exponential distribution $\phi(a, b) = \lambda \exp(-\lambda r_{ab}) / 2\pi r_{ab}$. Second, they introduced distance from the center of the individual’s home range as a spatial covariate of the resource selection parameter; that is, w_j becomes a function $w_j(x)$. Rhodes et al. (2005) termed this a “spatially explicit habitat selection model” to reflect the spatially

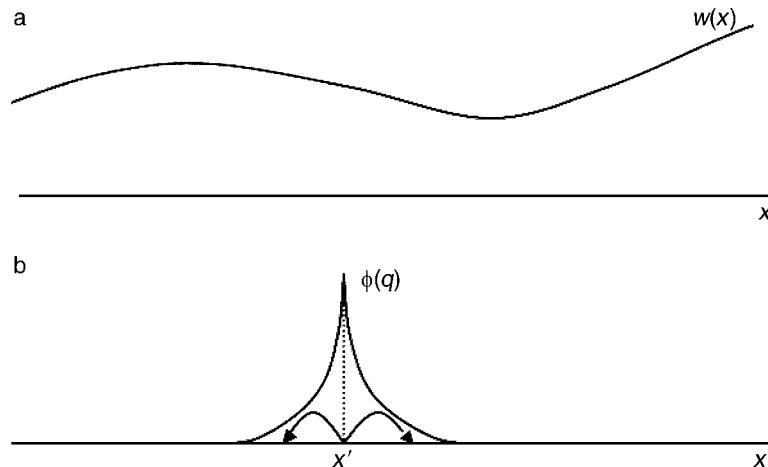


FIG. 4. Schematic illustrating a simple resource-selection-based mechanistic home range model for an animal moving in a single space dimension. Panel (a) shows the spatially dependent resource selection function $w(x)$. Panel (b) shows the individual's distribution of movement distances $\phi(q)$, where q is the displacement between the individual's current location x' and its subsequent location x .

varying resource selection coefficient. Note, however, that, unlike mechanistic home range models, resource selection models such as Eq. 5 do not directly yield predictions for actual patterns of space-use by individuals.

Switching from a model defined in terms of the probability of observing a relocation in a given habitat type to a model defined in terms of the probability of an individual moving between its current location and its subsequent location has, however, a third important consequence: Eq. 5, unlike Eq. 4, constitutes a redistribution kernel for the fine-scale movement behavior of individuals. In other words, RSA models of the form of Eq. 5 are, in effect, "modeling the movement process." This observation implies that it should be possible to establish a formal connection between RSA models of the form of Eq. 5 and corresponding mechanistic home range models. We will consider a simple pedagogical example demonstrating that this is indeed the case.

ANALYSIS

Consider an individual living on a one-dimensional landscape whose relative preference for different habitats can be expressed by a resource selection function $w(x)$ (Fig. 4a). Suppose further that, in the absence of habitat preference (i.e., $w(x)$ is constant), the individual moves to the right or left of its current position during time interval τ , with a distribution of displacements $\phi_\tau(q)$, where $q = x - x'$ is the displacement between the individual's current location x' and its subsequent location x (Fig. 4b). Note that, in contrast to Moorcroft et al. (2006), where the fine-scale movement behavior in two dimensions is described in terms of a sequence of movements of length ρ_τ and direction ϕ_τ ($i = 1 \dots n_s$) (where n_s is the number [sequence] of steps; see Fig. 2), here we describe the fine-scale movement behavior of an individual moving in a single space dimension in terms

of a sequence of displacements q_τ ($i = 1 \dots n_s$) that have both a magnitude and a sign. Because $\phi_\tau(q)$ is a probability density function, $\int_{-\infty}^{\infty} \phi_\tau(q) dq = 1$.

The probability density of the individual moving to location x from its initial location x' , during time interval τ , in this landscape with varying preference is then given by our model redistribution kernel:

$$P(x' \rightarrow x) = k_\tau(x, x') = \frac{\phi(x - x')w(x)}{\int_{-\infty}^{\infty} \phi(x'' - x')w(x'') dx''}. \quad (7)$$

Note that Eq. 7 has the same form as Eq. 5, with

$$w(x) = \sum_{j=1}^{n_{\text{hab}}} w_j I(x, j).$$

Note that the probability of moving from x' to x in the absence of habitat preference is determined only by the difference between x and x' and that the preference function w is evaluated at the location to which the individual moves, rather than its current location. In this example, we assume that an individual's redistribution kernel does not vary in time, and thus the dependency on time t can be dropped.

Defining $u(x, t) dx$ as the probability that the individual is located between x and $x + dx$ at time t , we can write an equation that summarizes all the possible ways that an individual located at x' can arrive within the interval $(x, x + dx)$ at time $t + \tau$:

$$u(x, t + \tau) = \int_{-\infty}^{\infty} k_\tau(x, x')u(x', t) dx'. \quad (8)$$

Eq. 8 is converted into an equation for the expected pattern of space-use by the individual by expanding the right-hand side using a Taylor series and then considering the limit as $\tau \rightarrow 0$, yielding the following

advection–diffusion equation:

$$\frac{\partial u(x, t)}{\partial t} = -\frac{\partial}{\partial x} [c(x)u(x, t)] + \frac{\partial^2}{\partial x^2} [d(x)u(x, t)] \quad (9)$$

where the advection and diffusion coefficients, $c(x)$ and $d(x)$, respectively, are given by

$$c(x) = \lim_{\tau \rightarrow 0} \frac{1}{\tau} \int_{-\infty}^{\infty} (x - x') k_{\tau}(x, x') dx' \quad (10a)$$

and

$$d(x) = \lim_{\tau \rightarrow 0} \frac{1}{2\tau} \int_{-\infty}^{\infty} (x - x')^2 k_{\tau}(x, x') dx'. \quad (10b)$$

Details of the derivation can be found in the Appendix. Because $u(x, t)$ is a probability density function, the normalization

$$\int_{\Omega} u(x, t) dx = 1 \quad (11)$$

where Ω is the region over which the individual is able to move, is preserved for all future times t .

Inserting Eq. 7 into Eqs. 10a, b (see Appendix) yields the following equations for the coefficients d and c :

$$c(x) = \lim_{\tau \rightarrow 0} \frac{M_2(\tau)}{\tau} \frac{w_x(x)}{w(x)} \quad (12a)$$

$$d(x) = \lim_{\tau \rightarrow 0} \frac{M_2(\tau)}{2\tau} \quad (12b)$$

where the second moment is $M_2(\tau) = \int p^2 \phi_{\tau}(x) dx$ and $w_x = dw/dx$.

Thus we see that a simple, spatially explicit resource-selection model yields an advection–diffusion equation (Eq. 9) for the expected location of an individual. Note that while the advection term (Eq. 12a) varies in space, the magnitude of the diffusion coefficient (Eq. 12b) is constant.

Inserting Eqs. 12a, b into Eq. 9, we can derive an approximation for the expected steady-state pattern of space-use $u^*(x) = \lim_{t \rightarrow \infty} u(x, t)$. The result for the case of a smooth continuous preference function $w(x)$ is

$$u^*(x) = \frac{1}{W_0} w(x)^2 \quad (13)$$

with the normalization constant $W_0 = \int_{\Omega} w(x)^2 dx$. The details of the derivation are given in the Appendix. In other words, the steady-state pattern of space-use by an individual is given by the normalized square of its resource selection function $w(x)$.

Fig. 5a shows a plot of Eq. 13 and a numerical solution of Eqs. 7 and 8 for the case of an individual that, in the absence of habitat preference, moves with an exponential distribution of step lengths and with an equal probability of moving in either direction. Mathematically, this is equivalent to an individual with a Laplace distribution of displacement distances q .

As can be seen in Fig. 5a, Eq. 13 captures the pattern of space-use arising from the underlying habitat preferences of the individual.

Eq. 13 is an approximation that technically holds only when variation in $w(x)$ is at spatial scales that are large relative to the characteristic width of the individual’s distribution of displacements $\phi_{\tau}(q)$. Fig. 5b shows a case in which the individual’s resource selection function is discontinuous. In this case, Eq. 13 does not accurately capture the pattern of space-use in the region of the discontinuity; however, the errors are localized, and thus Eq. 13 still reasonably describes the overall pattern of space-use.

DISCUSSION

The analysis presented here demonstrates that resource selection models of the form of Eq. 5 proposed by Rhodes et al. (2005) constitute an underlying stochastic movement process, and thus can be used to formulate corresponding mechanistic home range models that predict the expected patterns of space-use resulting from the underlying habitat preferences. As we would expect, increasing preference for a given habitat type (higher $w(x)$) gives rise to increasing space-use in the preferred habitats relative to the less preferred habitats (Fig. 5).

What is surprising, however, is that the relative intensity of space-use by an individual at a given location is governed by the square of its preference function for that location. Although Eq. 13 is an approximation that technically holds only when the preference function varies on spatial scales larger than the individual’s redistribution kernel, as seen in Fig. 5b, it still captures the overall pattern space of space-use even when an individual’s resource selection function changes rapidly in space. The mathematical explanation for this nonintuitive result is that the equilibrium pattern of space-use $u^*(x)$ is governed by the relative strength of the advection term relative to magnitude of the diffusion term, the squared term arising because of the factor of 2 in the denominator of the diffusion coefficient Eq. 12b (see Appendix for further details).

A somewhat more biological explanation is as follows. When viewed in terms of individual movement behavior, resource selection models of the form of Eq. 5 reflect a specific assumption about how environmental factors such as habitat type influence an animal’s movement: the influence of habitat preference occurs by generating a differential probability of an individual moving in a given movement direction. The resulting bias in the individual’s distribution of movement directions gives rise to the positive advection term (Eq. 12a), whose sign and magnitude is governed by the relative gradient in the animal’s resource selection function, with preferential movement toward preferred habitat types. It is this preferential movement up gradients of habitat preference relative to the random component of the individual’s motion (represented by the diffusion term) that

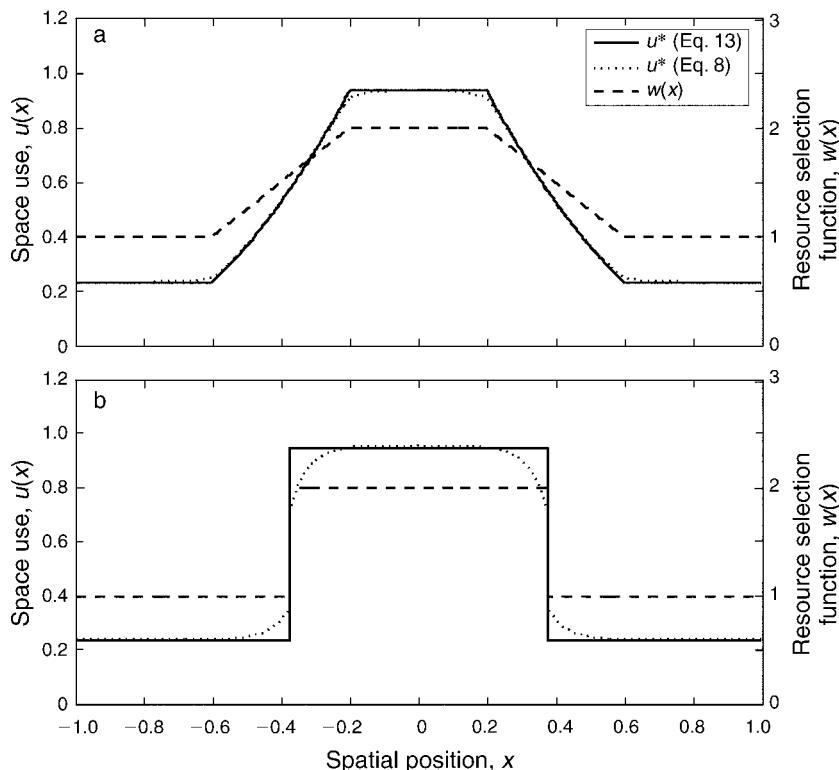


FIG. 5. Patterns of space-use arising for an individual with a resource selection function that is (a) piecewise continuous or (b) discontinuous, and who moves to the left or right with equal probability with an exponential distribution of step lengths in the absence of habitat preference [i.e., $\phi_s(q) = (1/2l) \exp(-|q|/l)$, with $l = 0.05$ for the example shown]. In both (a) and (b), the resource selection function $w(x)$ (dashed line), the predicted steady-state pattern of space-use $u^*(x)$ given by Eq. 13 (solid line), and $u^*(x)$ calculated by a numerical steady-state solution of Eq. 8 (dotted line) are plotted. When $w(x)$ is piecewise continuous (panel a), the solution of Eq. 13 closely approximates the steady-state pattern of space-use. When $w(x)$ is discontinuous (panel b), the solution of Eq. 13 fails to capture the pattern of space-use in the neighborhood of the discontinuities but still gives a reasonable match to the overall pattern of space-use.

determines the individual's equilibrium pattern of space-use $u^*(x)$.

In mechanistic home range models, environmental and biological factors affecting an individual's movement behavior can influence not just its distribution of movement directions, but also its distribution of movement distances. For example, in the PA + CA model used by Moorcroft et al. (2006) to analyze coyote home range patterns in Yellowstone (see *Introduction*), encounters with foreign scent marks alter an individual's distribution of movement directions (Fig. 2b). However, consistent with observations of coyote foraging responses (Laundre and Keller 1981), prey availability does not influence an individual's distribution of movement directions, but instead influences its distribution of movement distances. Specifically, the mean step length of individuals declines as an exponential function of the prey availability encountered (Fig. 2c). These two qualitatively different forms of movement response give rise to different terms in the equations for expected patterns of space-use: conspecific avoidance response gives rise to an advective term, directed movement

toward the home range center, whereas the foraging response gives rise to a spatially varying diffusion term (see Eq. 2). The influence of spatial variation in step length on patterns of space-use has been explored by a number of authors, including Okubo (1980), Kareiva and Odell (1987), and Turchin (1991, 1998).

The above discussion implies that current (RSA) models embody one aspect of how animals can respond to factors affecting their movement, namely, by changing their distribution of movement directions. Changes in an animal's distribution of movement distances, such as the foraging response in the PA + CA model of Moorcroft et al. (2006), constitute a second mechanism by which animals respond to their environment, one that is not represented in resource selection models such as Eq. 5. These two qualitatively different forms of movement response (preferential movement in particular directions and spatial variation in mean-squared displacement) together determine the relative intensity of space-use in different areas.

Finally, although the example considered here of an individual moving on a one-dimensional landscape is

clearly idealized, previous analyses (Moorcroft and Lewis 2006) suggest that the reconciliation between a model of resource selection and a corresponding mechanistic home range model demonstrated here will also apply in the more biologically relevant case of individuals moving on two-dimensional landscapes consisting of multiple habitat types. In the long term, this ability to translate resource-selection-based analyses of patterns of animal relocations into corresponding mechanistic home range models offers the promise of a unified framework for analyzing patterns of animal space-use.

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APPENDIX

Derivation of the Fokker-Planck equation for space-use (*Ecological Archives* E089-067-A1).