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Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions

PAUL R. MOORCROFT*

Harvard University, Department of Organismic and Evolutionary Biology, 22 Divinity Avenue, Cambridge, MA 02138, USA

* Correspondent: paul_moorcroft@harvard.edu

The coming of age of global positioning system telemetry, in conjunction with recent theoretical innovations for formulating quantitative descriptions of how different ecological forces and behavioral mechanisms shape patterns of animal space use, has led to renewed interest and insight into animal home-range patterns. This renaissance is likely to continue as a result of ongoing synergies between these empirical and theoretical advances. In this article I review key developments that have occurred over the past decade that are furthering our understanding of the ecology of animal home ranges. I then outline what I perceive as important future directions for furthering our ability to understand and predict mammalian home-range patterns. Interesting directions for future research include improved insights into the environmental and social context of animal movement decisions and resulting patterns of space use; quantifying the role of memory in animal movement decisions; and examining the relevance of these advances in our understanding of animal movement behavior and space use to questions concerning the demography and abundance of animal populations.

Key words: animal movement, biotelemetry, environmental covariates, foraging behavior, global positioning system telemetry, habitat selection, home ranges, mechanistic home-range models, memory, population demography

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Two interrelated questions that are often asked about species of management or conservation interest are: how is the spatial distribution of animals on a landscape likely to change as a result of changes in the environment? And how will this, in turn, affect the demography and abundance of the animal? Such questions regarding the distribution and abundance of animals in space and time are longstanding and lie at the heart of wildlife ecology. Being able to provide meaningful answers to these questions is becoming increasingly important, however, as the impact of humans on the planet's ecosystems intensifies due to continuing habitat transformation, resource exploitation, and human-induced climate change. Here I review recent progress in measurements and analysis methods relevant to understanding mammalian home-range patterns. I then outline what I see as the next key steps for improving the ability to provide relevant scientific answers to ecologists and wildlife biologists about how mammalian home-range patterns and the resulting spatial distributions of animal populations are likely to change as environments change. Finally, I discuss the relevance of these advances in understanding animal home-range patterns for answering questions regarding the 2nd related issue: the abundance of animal populations on current and future landscapes.

Mammals do not tend to move at random, but instead restrict their movements to particular areas (Seton 1909). This phenomenon underlies the concept of an animal's home range, defined by Burt (1943, p. 351) as "that area traversed by an individual in its normal activities of food gathering, mating, and caring for the young." As a result, understanding the key factors underlying animal home-range patterns is therefore crucial to understanding how patterns of mammalian space use will respond to changes in the environment. Prior to the 1950s, information on home ranges came from either direct behavioral observations of animal movements, spatially distributed trapping of animals over a period of time, or by following animal tracks on snow-covered landscapes. The advent of radiotelemetry in the 1950s ushered in a new era of animal home-range analysis, enabling researchers to document systemically the patterns of space use by animals. Radiotelemetry was subsequently widely adopted in animal ecology and wildlife studies (see Macdonald et al. [1980] and Millsbaugh and Marzluff [2001] for reviews).



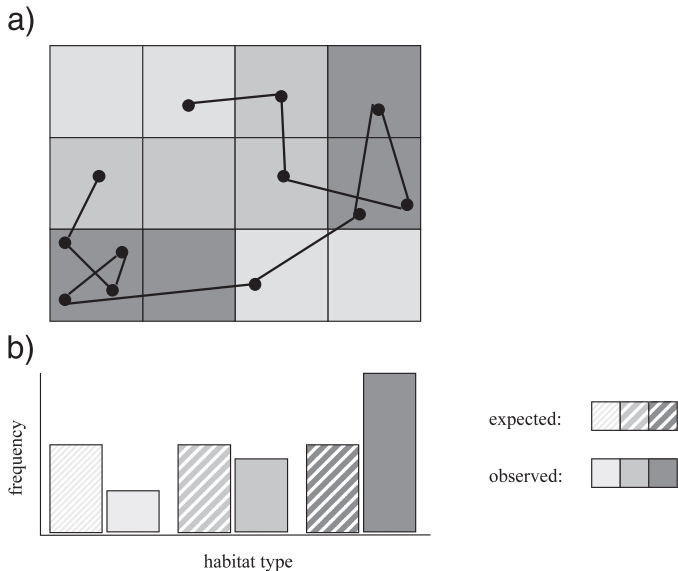


FIG. 1.—Schematic illustrating the resource selection analysis (RSA) approach to analyzing patterns of animal space use. a) Shaded squares represent an idealized landscape composed of 3 equally abundant habitat types. Black lines represent the movement trajectory of an individual as it traverses the landscape with points representing fixed-interval relocations of the individual. b) Histogram showing the observed and predicted frequency of relocations in the 3 habitat types. Because the 3 habitat types that compose 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 distribution of relocations, indicated by the solid bars in panel b) shows that the individual exhibits a preference for the dark gray habitat type.

The widespread adoption of radiotelemetry, in turn, spurred the development of methods for analyzing radiotelemetry data. In particular, a variety of density estimation methods for analyzing telemetry data were developed, including the bivariate normal, harmonic mean, kernel, and nearest-neighbor convex hull (Getz and Wilmsers 2004) home-range models (see Kernohan et al. [2001], Macdonald [1980], and Worton [1987] for reviews). These statistical methods convert spatial patterns of telemetry relocations into useful summary estimates and descriptors of home-range size, shape, and intensity of use.

A 2nd important milestone in the study of animal home ranges was the introduction of resource selection analysis (RSA) during the 1980s. In contrast to the descriptive statistical methods of home-range analysis that simply summarize observed spatial patterns of animal relocations, RSA seeks to identify key habitats or resources by analyzing the frequency at which habitats are used relative to some measure of their availability on a landscape (Fig. 1). RSAs can be conducted at a variety of spatial scales; however, here I focus on RSAs conducted at scale of individual home ranges, that is, so-called 3rd-order selection (sensu Johnson [1980] and Thomas and Taylor [1990]). Results from numerous studies have shown how the RSA approach can be used to identify associations between animal home ranges and particular land-cover types,

and other aspects of environmental heterogeneity, such as topography, resource availability, or habitat edges (see Boyce and McDonald [1999], Cooper and Millsbaugh [2001], Erickson et al. [2001], and Manly et al. [1993] for reviews).

Mechanistic home-range analysis has been advanced as an alternative framework for analyzing animal home ranges (Moorcroft and Lewis 2006; Moorcroft et al. 1999). In contrast to conventional RSAs that are spatially implicit in nature (the RSA equations, in effect, assume that animals choose between habitats in a manner analogous to choosing different colored balls from a container, i.e., without regard to spatial proximity of habitat types [see Moorcroft and Barnett {2008} and Moorcroft and Lewis {2006} for further discussion of this issue]), mechanistic home-range models develop spatially explicit predictions for patterns of animal space use by modeling the process of individual movement (Millsbaugh and Marzluff 2001). The origins of these models lie in the mathematical analysis of correlated random walks (Kareiva and Shigesada 1983; Okubo 1980; Skellam 1951; Turchin 1998) that characterize the fine-scale movement behavior of individuals via a so-called redistribution kernel, which specifies probability of an animal moving from any given location to any other location in a specified time interval (Fig. 2A). In addition to the effects of habitat or resources considered in RSA, other behavioral and ecological factors influencing the movements of individuals can be incorporated into the redistribution kernel that defines the stochastic fine-scale movement process. For example, in a recent analysis of coyote (*Canis latrans*) home ranges in Yellowstone National Park, Moorcroft et al. (2006), building on earlier work by Holgate (1971), Okubo (1980), and Lewis and Murray (1993), developed a “prey availability plus conspecific avoidance” mechanistic home-range model in which individuals exhibit a foraging response to prey availability in which individuals decreased their mean step length in response to small mammal abundance, an avoidance response to encounters with foreign scent marks, and an over-marking response to encounters with foreign scent marks. From the mathematical description of fine-scale movement behavior, it is then possible to derive probability density functions for the expected spatial pattern of home ranges that results from individuals moving on a landscape according to these underlying rules of movement. Fig. 2B shows the fit of the “prey availability plus conspecific avoidance” mechanistic home-range model to the observed spatial distribution of radiotelemetry relocations of 5 adjacent coyote packs in Yellowstone National Park (Moorcroft et al. 2006; see also Moorcroft and Lewis 2006). As Fig. 2B illustrates, the model captures the influences of both resource availability and the presence of neighboring groups on the coyote home ranges within the region. Note that in linking the scent-mark and foraging responses of individuals to their resulting patterns of home ranges, mechanistic home-range models are, in some sense, implicitly linking 3rd-order selection (how an animal utilizes the different habitats in its home range) with 4th-order selection (the way in which the animal uses each of the

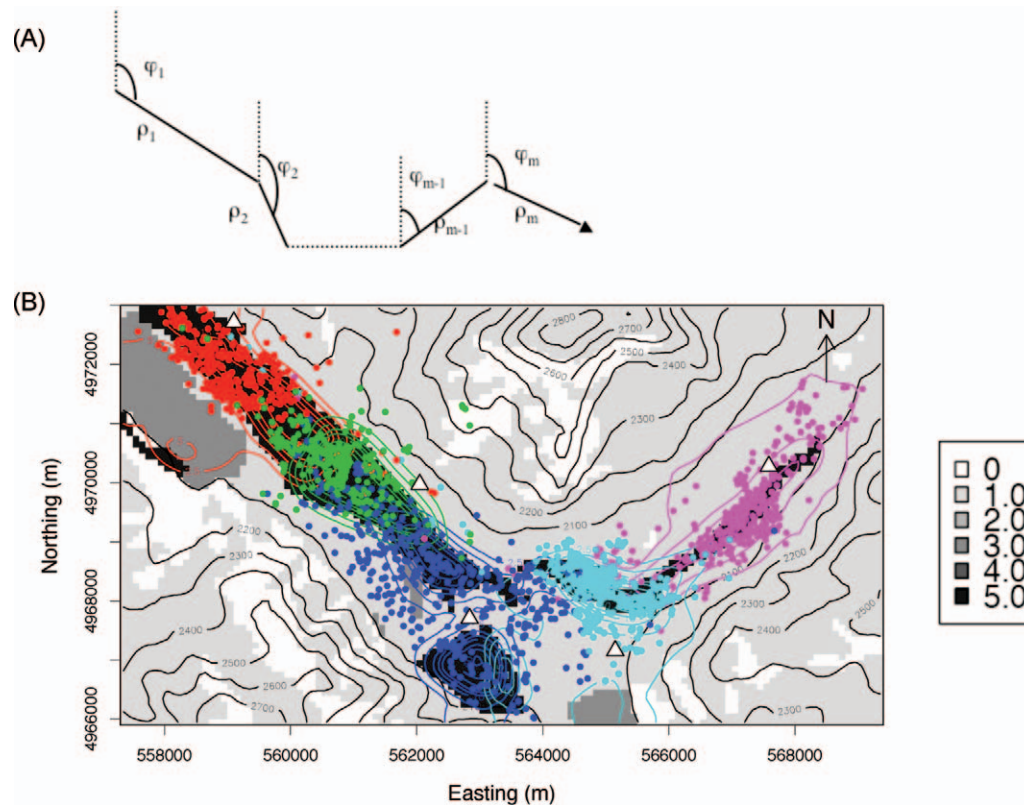


FIG. 2.—A) Schematic illustrating the underlying model of individual movement behavior that underpins a mechanistic home-range model. The movement trajectory of individuals is characterized as a stochastic movement process, defined in terms of sequences of movements between successive relocations ($i = 1, \dots, m$) of distance ρ_i and directions φ_i drawn from statistical distributions of these quantities that are influenced by relevant factors affecting the movement behavior of individuals. B) Colored contour lines showing fit of a mechanistic home-range model to relocations (filled circles) obtained from 5 adjacent coyote packs in Lamar Valley Yellowstone National Park. As described in the text, the PA+CA (prey availability and conspecific avoidance) mechanistic home-range model used in this study incorporates a foraging response to small mammal prey availability plus a conspecific avoidance response to the scent marks of individuals in neighboring packs. Also shown are the home-range centers for each of the packs (triangles), and the grayscale background indicates small mammal prey density (kg/ha) across the landscape (Moorcroft and Lewis 2006).

different habitats). For a discussion of orders of selection, see Johnson (1980).

RECENT DEVELOPMENTS

Global positioning system telemetry.—One of the most significant developments in studies of animal home ranges has been the recent coming of age of global positioning system (GPS)–based telemetry. Satellite-based telemetry systems began appearing in the 1970s. The 1st systems, such as ARGOS, used Doppler shift to identify an animal's spatial position. However, since the 1990s, this technology has been increasingly combined with, or replaced by, GPS-based telemetry systems that have higher positional accuracy (Tomkiewicz et al. 2010). GPS-based telemetry systems were initially only suitable for deployment on large terrestrial and marine vertebrates (e.g., Ballard et al. 1995; Bethke et al. 1996; Priede and French 1991; Rempel et al. 1995), but over the subsequent 2 decades, advances in GPS-based telemetry systems have enabled their deployment on species of ever-smaller body sizes such as white-tailed deer (*Odocoileus*

virginianus—Merrill et al. 1998), coyotes (Windberg et al. 1997), and more recently, Japanese macaques (*Macaca fuscata*—Sprague et al. 2004), and lynxes (*Lynx lynx* and *Lynx canadensis*—Burdett et al. 2007; Krofel et al. 2006). It takes several years of pilot and evaluation studies before GPS-based telemetry becomes an operational technology suitable for addressing particular scientific or management questions for a species. For moose (*Alces alces*), the transition from pilot and evaluation studies (e.g., Moen et al. 1996; Rempel et al. 1995) into an operational technology suitable for addressing particular scientific or management questions (e.g., Dussault et al. 2004, 2005a, 2005b) took almost a decade. As GPS telemetry continues to mature, however, the transition between technology evaluation studies and operational deployment is getting shorter. For example, for elk (*Cervus elaphus*), evaluation studies of GPS telemetry were conducted in 2001 (e.g., Biggs et al. 2001; Rumble et al. 2001), and only a few years later were beginning to be used to answer scientific questions regarding elk movement (e.g., Boyce et al. 2003; Rumble et al. 2005). Thus, although GPS-telemetry systems

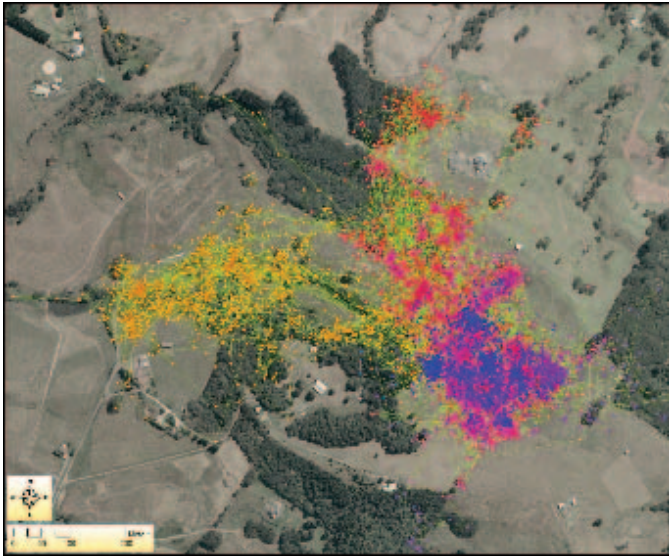


FIG. 3.—Example of a global positioning system–telemetry data set collected by T. Dennis and colleagues on brushtail possums. The data set consists of more than 140,000 relocations collected at 5- to 15-min intervals over a 2-year period. The figure shows 13,000 relocations of for a single individual and the color indicates the time of relocation (T. Dennis, University of Auckland, pers. comm.).

have existed for 2 decades, I would argue that only in the past 5 years has their scientific potential begun to be realized.

Now that GPS telemetry is becoming a mainstream technique for studying patterns of animal movement, it is providing a wealth of new information on patterns of animal space use and movement behavior. One of its most obvious benefits is the sheer volume of data that each collar yields. For example, the radiotelemetry data set used by Moorcroft et al. (2006) in the analysis of coyote home ranges shown in Fig. 2 consisted of approximately 2,000 relocations, whereas modern GPS-telemetry data sets are typically 10 to 100 times larger. For example, Fig. 3 shows a GPS-telemetry data set composed of 140,000 locations of 29 brushtail possums (*Trichosurus vulpecula*) collected at 5- to 15-min intervals, recently collected by T. Dennis, University of Auckland, and colleagues (pers. comm.).

As the data set shown in Fig. 3 exemplifies, the increase in data volume in GPS telemetry is primarily due to an increase in the temporal frequency with which relocations are obtained. This increased frequency of sampling does come at cost, however: the short battery life and high price of GPS-telemetry collars means that GPS-telemetry studies typically have a shorter duration, and collars placed on fewer numbers of individuals compared to radiotelemetry collars.

The increased sampling frequency in GPS-telemetry studies compared to conventional radiotelemetry has yielded more detailed and spatially resolved description of an animal's pattern of space use (although see Fieberg and Börger [2012]). One reflection of this has been the increased temporal resolution of RSAs; in particular, the move toward so-called step-selection RSA in which resource selection is examined on

a per-step, or, more accurately, relocation-to-relocation, basis. Further details on step-selection RSA can be found in the section below. This has resulted in a considerable increase in statistical power to detect the signatures of factors affecting fine-scale movements of individuals, and resulting insights into factors influencing movement behavior. For example, whereas Boyce et al.'s (2003) analysis of elk resource selection in Yellowstone National Park used radiotelemetry measurements separated by 10- to 14-day intervals, the subsequent analyses of Forester et al. (Forester 2005; Forester et al. 2007) used GPS-telemetry data collected at 5-h intervals. Both studies included common landscape covariates, such as cover type and topography; however, the higher frequency of relocations in the analyses of Forester et al. (Forester 2005; Forester et al. 2007) also enabled the identification of a clear crepuscular pattern of elk movement, and distance to forest edge and distance to roads as additional explanatory covariates for patterns of elk space use.

Advances in analysis methods.—Conventional RSA uses ratios of habitat utilization to create an aggregate measure of habitat availability in order to identify habitats that animals use disproportionately relative to their occurrence on a landscape. Concurrent with the rise of GPS telemetry has been a shift toward step-selection RSA methods that assess animal habitat preferences at the scale of successive relocations. This trend began with a ground-breaking analysis of patterns of polar bear (*Ursus maritimus*) habitat use by Arthur et al. (1996), who argued that habitat availability should not be treated as a constant, but should vary in relation to the current location of an individual. Accordingly, in their analysis, Arthur et al. (1996) used a circle around the animal's current location, the radius of which corresponded to the maximum distance the animal could travel in the time interval between relocations, to define a measure of habitat availability that was specific for each relocation in the data set. This step-selection methodology is well suited to the increased temporal frequency of GPS-telemetry data, and accordingly has been widely adopted in analyses of GPS-telemetry measurements. The estimates of habitat availability used in step-selection studies also are becoming increasingly sophisticated, and often now account for the probability of an animal moving a given distance within the sample interval. As I discuss later in this article, habitat availability also depends on what an animal remembers (see also Spencer 2012).

A 2nd important methodological advance linked to the rise of GPS telemetry has been the incorporation of an animal's state into analyses of animal movement behavior. Whereas RSA approaches have shown that landscape attributes significantly influence animal movement decisions, focal studies have shown that the movements of animals are also strongly influenced by their internal physiological and behavioral states, such as hunger (e.g., Jung and Koong 1985), thirst (e.g., Senft et al. 1987), and fear (e.g., Mitchell and Lima 2002; Zollner and Lima 2005). The significance of an animal's internal physiological and behavioral state on its patterns of fine-scale movements has been inferred in 2 recent

analyses of elk GPS-telemetry data. Morales et al. (2004), building on earlier work by Johnson et al. (2002), showed that state-based movement models, in which individuals switched probabilistically between a series of behavioral states that are associated with different distributions of step lengths or turning angles, provided a better fit to the observed patterns of fine-scale movement than models in which an animal's fine-scale movement behavior was invariant. Similarly, Forester et al. (2007) showed that the movements of individual elk were significantly influenced both by current landscape attributes and the landscape attributes associated with previous relocations, implying the existence of 1 or more internal state variables that individuals used to track the history of places that they had previously visited.

Biotelemetry.—Although the analyses of Morales et al. (2004) and Forester et al. (2007) described above illustrate how the existence of different movement states for animals can be inferred from telemetry relocations, these approaches, are, in essence, inferring process from pattern, which as noted by Pielou (1977), is an inherently difficult exercise. For these reasons, obtaining direct measurements of the external conditions and physiological and behavioral condition of animals as they move is highly desirable for improving our understanding the underlying impacts of physiological and behavioral states on animal movement behavior. Beginning in the 1960s, researchers have deployed devices on free-living animals that are designed to provide information on the animal's physiological condition (e.g., heart rate, breathing rate, wingbeat frequency, and head position), as well as information on the external environment (e.g., air temperature and water temperature or depth). Such techniques are often referred to as either "biologging" or "biotelemetry" (Cooke et al. 2004; Ropert-Coudert and Wilson 2005; Ropert-Coudert et al. 2010). Biotelemetry techniques were pioneered in the marine realm (e.g., Kooyman 1965) where direct animal observation is difficult, and they have provided important insights into the ecology of marine mammals and birds. Recent advances in electronics have led to the development of a wide variety of biosensors, including ones to measure food intake (via gut temperature, gut pH, or esophagus temperature sensors), energy expenditure (via heartbeat or wingbeat frequency sensors), and foraging behavior (via timed video-capture or sensors to detect head position [Ropert-Coudert and Wilson 2005]).

Integrating resource selection and mechanistic analyses of home-range patterns.—As discussed earlier, the spatially implicit nature of conventional RSA contrasts with the spatially explicit nature of mechanistic home-range analysis, and thus these two methods of analysis appear to constitute alternate frameworks for analyzing patterns of animal space use (Moorcroft and Lewis 2006). However, subsequent developments in RSA have enabled a reconciliation between RSA and mechanistic home-range models. Rhodes et al. (2005) recast the resource selection equation of Arthur et al. (1996) in terms of the probability of an animal moving from its current location to any subsequent location within the circle defining

habitat availability for each relocation. Their motivation for doing so was to argue for a measure of habitat availability that took into account the fact that the probability of moving a given distance within the relocation time interval was likely to be a decreasing function of the distance moved. Moorcroft and Barnett (Barnett and Moorcroft 2008; Moorcroft and Barnett 2008) then showed that when written in this form, the equations used by Arthur et al. (1996) and Rhodes et al. (2005) in their RSAs constituted redistribution kernels. This result means that RSA equations can be used to derive a corresponding mechanistic movement model, yielding spatially explicit predictions for the pattern of space use that results from the animal moving around a landscape with a given set of habitat preferences. The analyses of Moorcroft and Barnett (Barnett and Moorcroft 2008; Moorcroft and Barnett 2008) showed that, surprisingly, when an animal's habitat preferences are spatially localized (i.e., preferences are governed by local availability), the relative intensity of its space use at a given location is equal to the square of its preference for that location (Moorcroft and Barnett 2008) but, as the spatial scale of animal's habitat preference increases, the intensity of space use becomes proportional to its preference (Barnett and Moorcroft 2008).

The role of memory in animal movement behavior.—A key issue for developing quantitative predictions of mammalian space use is formulating mathematical descriptions of the mechanisms responsible for the formation and maintenance of characteristic home ranges for animals. In mathematical terms, the formation of home range requires the existence of some form of centralizing tendency in the movement behavior of animals that localizes their movements to a particular portion of the landscape. Although the existence and significance of these behaviors for patterns of animal space use has been known for decades within ecology and wildlife biology, the ability to formulate compact mathematical representations of the process of home-range formation and maintenance is relatively new. In the mechanistic home-range models developed by Holgate (1971), Okubo (1980), Lewis and Murray (1993), and Moorcroft et al. (2006), this centralizing tendency arose from a bias in the movements of individuals toward a prescribed home-range center. Such formulations are arguably reasonable for species that have clear, identifiable centers of attraction, such as the den sites of carnivores. However, in mammal groups, such as ungulates and primates, that lack a well-defined center of attraction, other mechanisms must be responsible for the centralizing tendency of individuals and their resulting home ranges.

An important area of recent theoretical development with regard to the issue of home-range formation has been incorporating the effect of memory on animal movement behavior. In classical random walk models of animal movement (e.g., Okubo 1980; Patlak 1953; Turchin 1991, 1998), the movements of individuals are unaffected by their history of previously visited locations. Note that some classical random-walk formulations (e.g., Patlak 1953) incorporate autocorrelation between successive movement directions, but

this does not usually result in any spatial localization. However, in many mammals, it is clear that the movements of individuals are influenced not only by their current environment, but also by their history of past movements (Powell 2000; see also Mitchell and Powell [2012] and Spencer [2012]). As highlighted in recent reviews (e.g., Börger et al. 2008; Smouse et al. 2010), the role of memory is a key issue in understanding the formation and maintenance of animal home ranges in many mammalian species. Indeed, it has been argued that an animal's cognitive map of its environment constitutes and defines its home range (Powell 2000; Powell and Mitchell 2012; Spencer 2012). In an early paper, Siniff and Jessen (1969) proposed a home-range simulation model in which individuals biased their movements toward locations that they had previously visited. More recently, Tan et al. (2001, 2002), building on earlier work by Sapozhnikov (1994, 1998) and Dalziel et al. (2008), have analyzed the behavior of so-called "self-attracting" random walks in which individuals display an increased probability of moving toward previously visited locations. Their analyses showed that movement models of this kind result in individuals developing quasi-stable home ranges: over short timescales, the movements of an individual are largely confined to some characteristic area (i.e., a home range), whereas on longer timescales the center of the individual's home range drifts randomly around the landscape. Van Moorter et al. (2009) recently proposed an alternative formulation of animal memory in which an individual displays both an avoidance response to recently visited resource patches, and an attractive response toward resource patches that have been visited sometime in the past. Their simulations indicated that both components of this movement process are necessary for the production of stable home ranges for individuals. Home-range models also have been proposed in the context of Levy flight models of animal movement, in which the probability distribution of movement distances exhibited by an animal is "fat-tailed" (leptokurtic—Gautestad and Mysterud 2006; Smouse et al. 2010). Spatial memory also has been incorporated into optimal foraging models to determine its impacts on the movement of individuals between resource patches and the conditions under which spatial memory gives rise to home ranges (see Spencer 2012).

FUTURE DIRECTIONS

Global positioning system telemetry.—Analyses of animal habitat selection using hourly-to-daily scale GPS-telemetry data, such as that by Forester et al. (2007), are undoubtedly advancing our understanding of the factors influencing fine-scale movement behavior of animals. This trend is likely to continue for some time as more GPS collars are deployed and the resulting data sets are analyzed. As data sets accumulate for more species with differing and diverse ecologies, the prospects for developing generalizations about the nature of mammalian home ranges and home-range movement behavior will increase.

Although GPS telemetry is now delivering large volumes of data on animal home-range movements, it is not without limitations (Hebblewhite and Haydon 2010). First, because of the constraints on battery longevity, the high cost of GPS collars, and the relatively high failure rate of deployed collars, the duration and number of animals with active collars is often lower than in telemetry studies using conventional radiocollars. As a result, the ability to reliably characterize generalized differences in the movement behavior of individuals of ages, or sexes, and differences between years is often limited. Second, although GPS telemetry typically provides higher temporal resolution than either radiotelemetry or ARGOS-based telemetry, it does not yield the complete path of an individual through its environment (such as that obtained through tracking studies), and thus the accuracy of the implied animal movement trajectories of animals arising from relocations remains a concern, particularly when collars are programmed to deliver relatively infrequent relocations in order to preserve battery life. Third, a key issue in any ecological study is the extent to which information collected at a given temporal and spatial scale is relevant to other scales (Levin 1992). In this context, an important and, as yet, unanswered issue is the extent to which the improvements in our understanding of the fine-scale movement behavior of animals made possible by GPS-telemetry data will inform the ability of ecologists and wildlife biologists to understand and predict the long-term, large-scale patterns of space use by animals. Hebblewhite and Haydon (2010) detailed the benefits and limitations of GPS telemetry.

Environmental covariates.—Another critical factor determining the value of GPS-telemetry data is the availability of corresponding information about the animal's environment as it moves across a given landscape. A key source of information on landscape characteristics has been the increasing availability of data layers derived from remote sensing. Explanatory variables used in resource selection studies have typically used simple categorical classifications of land-cover types (e.g., Johnson 1980; Manly et al. 1993). Whereas some more recent studies have included more relevant information about the environment, such as estimates of forage productivity derived from measures of vegetation greenness (Carroll et al. 2001; Mueller et al. 2008; Ryan et al. 2006), the majority of analyses still use "off-the-shelf" land-cover classifications that may be weakly related to the actual habitat requirements of the species being studied, and the temporal resolution of the land-cover classification may not be well matched to the rate at which the relevant attributes of the habitat change over time. Thus, the exploitation of remote-sensing data for explanatory environmental variables in studies of animal home ranges is still in its infancy.

One significant hurdle has been that virtually all of the remote-sensing data products used in analyses of animal space use have been derived from optical remote-sensing data, consisting of reflectance values in the visible and near-infrared wavelengths for each spatial location. Optical remote-sensing measurements can be used to discriminate basic land-cover

classes and to calculate estimates of vegetation greenness, but are unable to measure directly other landscape characteristics important for animals, such as structure of forest canopies, or the presence of downed logs in forest understory. Ongoing developments in active remote-sensing methods—so called because they involve the transmission of signal and measurement of the return signal—offer a promising source of additional information about the landscapes that animals inhabit. For example, light detection and ranging (lidar), can provide measurements of forest canopy height and vertical canopy structure (Dubayah and Drake 2000; Hyde et al. 2006), and radio detection and ranging (radar) can provide measurements of aboveground biomass and basal area, and measurements of moisture levels in the canopy and in the soil (Fransson et al. 2000; Quiñones and Hoekman 2004; Saatchi et al. 2007; Treuhaft et al. 2003; Treuhaft and Siqueira 2000). Another significant development is the increasing availability of remotely sensed imaging spectrometry, which yields a continuous reflectance spectrum for each pixel rather than reflectance values in a few specific wavelengths. The principal advantage of imaging spectrometry (also known as hyperspectral remote sensing) over conventional optical remote sensing is its increased ability to discriminate vegetation types including, in some cases, the ability to detect the presence of particular species of plants that have distinctive reflectance spectra (e.g., Asner et al. 2008; Lewis et al. 2001; Vane and Goetz 1993). Although the benefits of these new forms of data remains to be seen, it seems likely that the most promising new data sets in the near term will be ones coming from airborne deployed instruments that can provide information on habitat structure and composition at meter and submeter scales rather than the coarser-resolution data sets that come from instruments deployed on satellite platforms Kampe et al. (2010).

The 2nd significant hurdle in generating environmental covariates has been the technical and biological expertise necessary to translate the raw remote-sensing data into meaningful ecological information for a given species of interest, such as food availability, cover from predators, or nest or den-site availability. Although the tools and methodologies for doing this have become cheaper and easier to use, it still requires a significant investment to learn how to analyze and process remote-sensing measurements, and also, in many cases, significant expense to purchase the necessary imagery. As a result, the use of remote-sensing imagery in analyses of animal space-use patterns has largely been confined to the use of standard data products, such as basic habitat classifications, vegetation indexes, and estimates of percent cover. In some cases, these have been combined with field sampling to develop custom maps for particular species, for example, the coyote small mammal biomass shown in Fig. 2, and the forage maps for elk in Yellowstone National Park (Anderson et al. 2008; Forester et al. 2007). However, I argue here that exploiting the full richness of environmental information available from remote sensing to understand animal spatial distribution better will require moving beyond standard remote-sensing data products such as general land-cover

classifications. Many species are known to have particular ecological requirements, and, thus, what is needed is for animal ecologists and wildlife biologists to develop customized data layers that measure key habitat attributes for the species of interest, rather than simply relying on the generalized landscape attributes available in standard remote-sensing data products.

Biotelemetry.—Improved understanding of the connections between an animal's movements, other components of its behavior such as foraging, and its physiological condition will be an important bridge to link the movement ecology of animals with the demography of animal populations. Commercial telemetry devices for marine animals now typically include sensors for measuring temperature, depth, and saltwater immersion; however, the rate of adoption in telemetry studies of terrestrial mammals has been relatively slow (Ropert-Coudert and Wilson 2005): telemetry collars for terrestrial animals typically have only a basic activity sensor to indicate whether an animal is moving or not, although some newer GPS- and ARGOS-based telemetry collars also contain a temperature and activity sensor.

The principal limitations on the use of biotelemetry are 2-fold. First, the cost of the units limits the number of units deployed on animals, resulting in small sample sizes. Second, the increased battery consumption arising from powering the various sensors limits the duration of a biotelemetry collar deployment (Cagnacci et al. 2010). Thus, whereas the trend toward increasing use of biotelemetry will likely continue, it seems likely that the constraints imposed by sensor cost and the negative impacts of additional sensors on collar battery life will mean that, for the time being at least, the use of biotelemetry sensors will be confined to targeted studies involving small numbers of animals. One interesting area for potential future growth is crossover technologies from human biotelemetry. For example, a number of biomedical companies are developing minimally invasive implantable biosensors for long-term measurement of blood glucose levels in humans (Newman and Turner 2005). Because such sensors are usually tested on animal subjects before being approved for human use, similar sensors could be deployed easily on wild animal subjects. An interesting study relevant to assessing the value of such approaches is an ongoing study of polar bear movement behavior (Durner et al. 2011) in which internal temperature and activity sensors are being used to relate foraging behavior of the bears to resulting animal condition.

Another growing area is deployment of sensors that provide information on an animal's social environment. The social context in which animals live affects patterns of space use in many animal populations (Rubenstein and Wrangham 1986). Until recently, obtaining such information required detailed observational studies of focal animal subjects. The social environment of animals can be estimated using conventional and GPS-based telemetry systems (e.g., Haydon et al. 2008); however, the accuracy of the information regarding the social environment is limited due to the number of collars deployed,

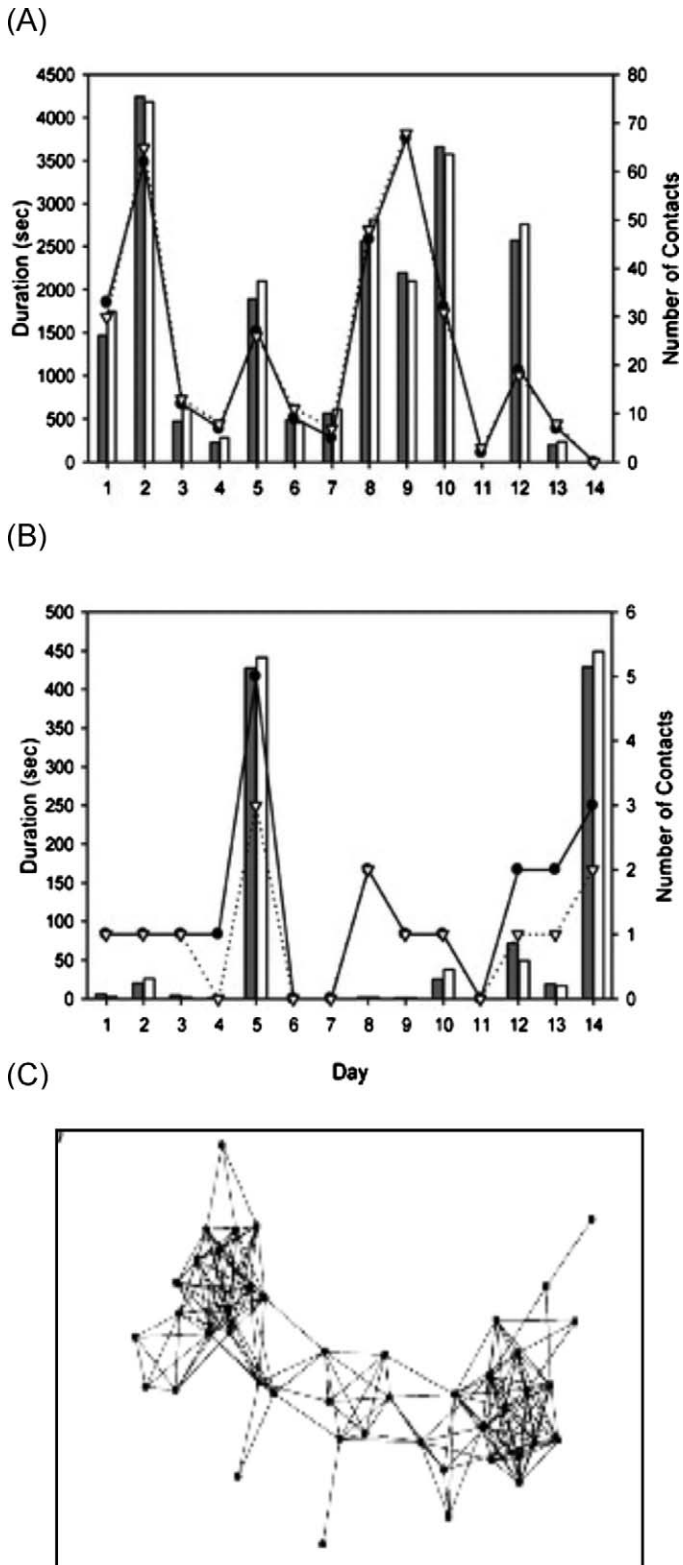


FIG. 4.—A and B) Total number and daily duration (in seconds) of contacts recorded by proximity detectors during a 2-week period in summer 2004 for 2 pairs of raccoons in northeastern Illinois. The vertical bars indicate the total duration of contacts for both members of each pair, while the open triangles and closed circles show total number of contacts for both members of each pair. C) Visualization of the social environment of red deer on the island of Rum, Scotland. The closed

and the temporal frequency and spatial accuracy of the relocations (Prange et al. 2006).

One promising approach to the study of animal social environments is the deployment of proximity tags. As their name implies, these can be attached to an animal and then used to detect the presence of other tagged animals within a given distance of the individual. A number of pilot studies have evaluated proximity tag technology in several species, including brushtail possums (Douglas et al. 2006; Ji et al. 2005), raccoons (*Procyon lotor*—Prange et al. 2006), and lions (*Panthera leo*—Tambling and Belton 2009). Fig. 4 shows the contrasting patterns in the frequency and duration of contacts between 2 pairs of raccoons collected by Prange and colleagues (2006). Thus far, studies using proximity tags have focused on estimating animal-to-animal contact rates, a key factor influencing rates of disease transmission (Douglas et al. 2006; Ji et al. 2005; Prange et al. 2006), and patterns of mating behavior (e.g., Douglas et al. 2006). More generally, however, proximity tag measurements such as those shown in Fig. 4 offer a new source of measurements for understanding the social environment in which animals live and move, and thus the promise of new insights into patterns of group formation, relatedness, and social cohesion in ungulates, primates, and social carnivores (e.g., Tambling and Belton 2009), and into impacts of these social interactions on movement decisions of individuals.

As with GPS telemetry, the ability to gain insight into animal social structure from proximity tag deployments will require new methods of analysis. Alongside the methodological advances in analyzing animal home ranges that have occurred over the past decade have been methodological advances in the analysis of animal social structure. In particular, social network analysis (SNA), a branch of graph theory that characterizes social groups as networks of nodes connected by social ties, is providing a theoretical framework for understanding the patterns of association seen in Figs. 4A and 4B. Social network analysis has been used over several decades in the social sciences to study human social interactions (e.g., Wasserman and Faust 1994), but is now being applied to the study of animal interactions (see Coleing [2009], Croft et al. [2008], and Wey et al. [2008] for reviews). For example, Fig. 4C shows an example of a network graph that reveals the group structure of a population of red deer (*Cervus elaphus*) in Scotland. An important long-term challenge will be integrating these approaches used to quantify patterns of animal grouping



circles indicate different individuals and the lines between pairs of closed circles indicate when the 2 individuals were observed in the same group 6 or more times during the 26 census observation periods. The network plot indicates the existence of groups of individuals that interact strongly with one another, but interact weakly with individuals in other groups. Panels A and B are from Prange et al. (2006) and panel C is from Croft et al. (2008).

that ignore the effects of spatial position, with the kinds of spatially explicit approaches used to study the dynamics of animal movement and space use described earlier (although see Eftimie et al. [2004], Gueron and Levin [1993], and Turchin [1998]).

Making mechanistic home-range analysis easier and simpler.—Although conceptually simple, the process of translating individual-based models of animal movement behavior into corresponding predictions for the resulting expected pattern of space use is, in practice, quite challenging. The simplest approach, directly simulating the underlying stochastic movement process on a computer, requires programming expertise, and, even with modern computers, is computationally expensive, requiring multiple simulations of the underlying stochastic movement model. The alternative approach, of formulating partial differential equations (PDEs) that approximate the outcome of the underlying movement process (e.g. Moorcroft et al. 2006), is computationally more efficient, which makes model fitting easier and offers the possibility of mathematical insight into the connection between underlying movement behavior of individuals and resulting patterns of space use. However, the partial differential equation–based approach requires familiarity with formulating and solving systems of differential equations that is not part of the training of most ecologists and wildlife biologists. As with RSA, broadening the use of mechanistic movement models in studies of animal movement is likely to require the development of more user-friendly software that simplifies the process of formulating mechanistic movement models for animals and fitting them to observational data sets.

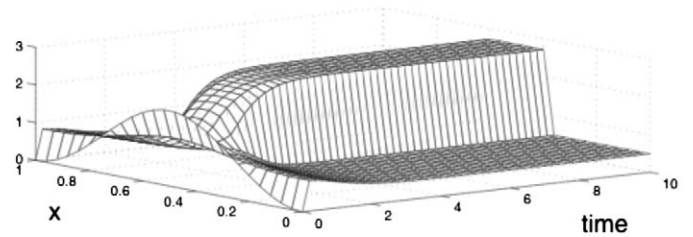
The roles of memory in observed home-range patterns.—As noted earlier, there has been considerable progress on developing mathematical understanding of how memory may influence the movement behavior of animals and their resulting patterns of space use. However, because memory is, for the most part, a latent process, that is, a process whose impacts we observe, but are unable to measure directly (except in controlled laboratory settings), understanding the roles that memories play in determining actual animal spatial distributions is inherently challenging.

By way of example, suppose an animal moves along a 1-dimensional landscape, and in the absence of memory it moves at random with mean squared displacement D_0 . Suppose further that the animal’s probability of moving per unit time decreases as a function of its familiarity with a given area, whereas its familiarity with a given area increases as a function of its utilization and its existing familiarity with the area, and familiarity decays over time. These assumptions yield the following equations for the expected space use $u(x,t)$ and its familiarity $f(x,t)$ with each location x at time t :

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2} [D(x,t)u(x,t)], \tag{1}$$

where

Pattern of space use $u(x,t)$



Familiarity $f(x,t)$

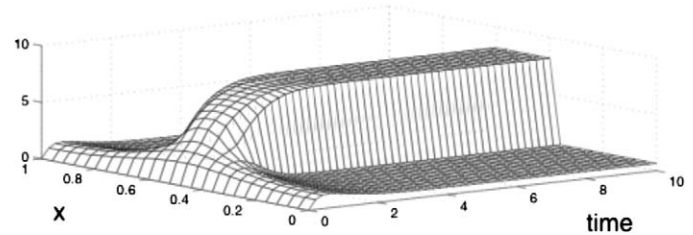


FIG. 5.—Solution of equations 1 and 2 in 1 space dimension (x) showing the formation of a characteristic home range $u(x,t)$ for an individual that arises due to the animal developing familiarity $f(x,t)$ with the landscape as it moves.

$$D(x,t) = \frac{D_0\alpha}{\alpha + f(x,t)},$$

and

$$\frac{\partial f(x,t)}{\partial t} = u(x,t)[l + M(f(x,t))] - \mu f(x,t), \tag{2}$$

where the parameter α governs the sensitivity of the animal’s displacement per unit time to its familiarity with an area, the parameters l and μ , respectively, determine the rate at which the animal’s familiarity with an area increases as a function of its visitation rate and the rate at which its familiarity with an area decays over time, and the function $M(f(x,t))$ determines how familiarity is reinforced by previous visits. With regard to the latter issue, if we assume that rate of memory reinforcement increases in proportion to prior familiarity with the area, up to some maximum familiarity f_{\max} (i.e., $M(f(x,t)) = \max(Mf(x,t), f_{\max})$), then the above movement model gives rise to stable, well-defined home ranges for individuals (Fig. 5).

The model description above is formulated and motivated in terms of an animal’s response to its internal memory, modeled as a dynamic state variable that tracks the animal’s familiarity with different places on the landscape. Whereas the equations can be appropriately viewed in the above terms, equations 1 and 2 were actually advanced under a different biological premise: as a model for carnivore home ranges in which individuals scent mark as they move (equation 2), and how the presence of familiar scent marks affects the movements of

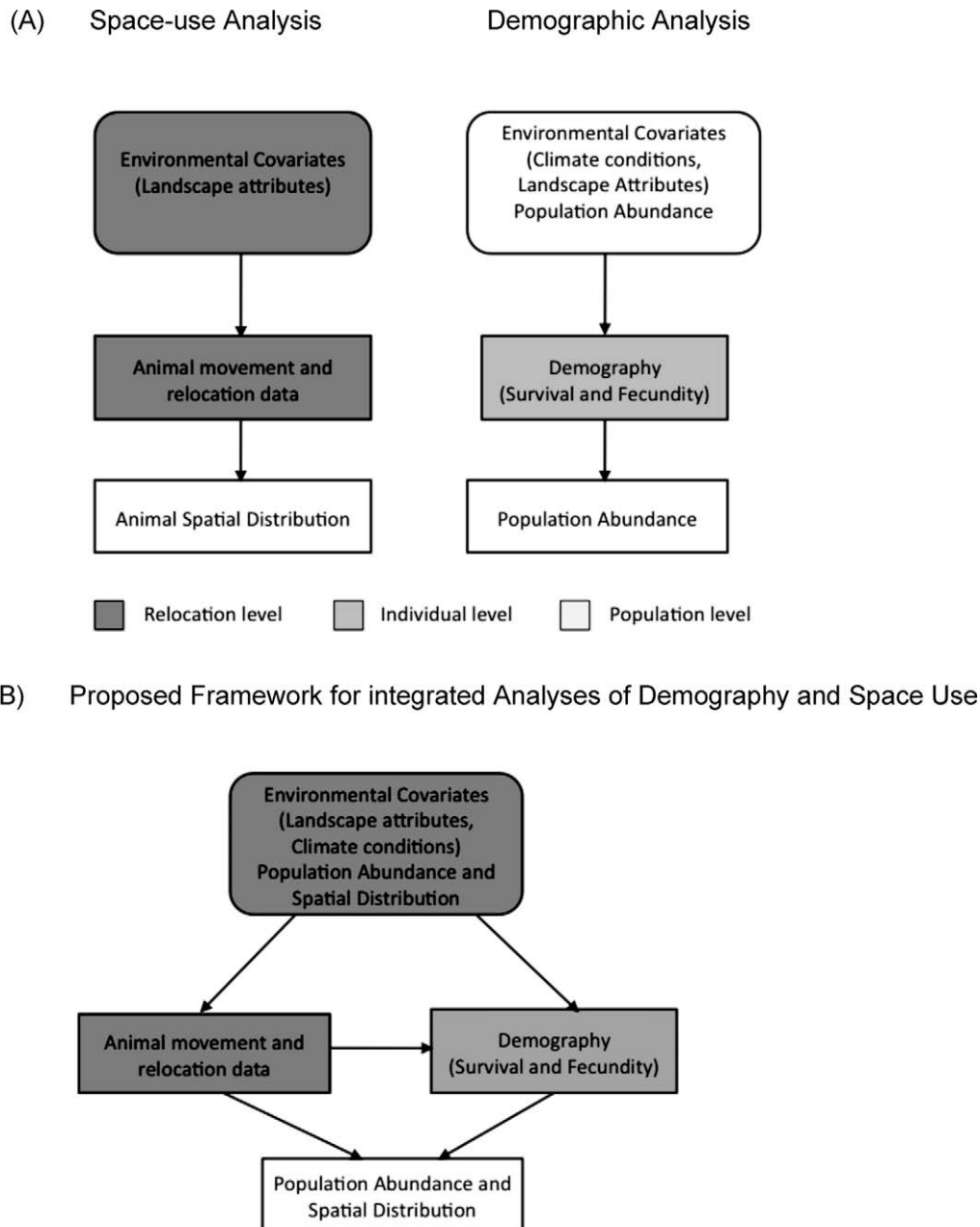


FIG. 6.—Schematic diagrams illustrating A) the conventional approach to analyzing animal distribution and abundance, and B) a proposed integrated method of analysis. The shade of each box indicates the relevant scale of the different forms of data: relocation-level (dark gray), individual-level (light gray), and population-level (white).

individuals (equation 1; see Briscoe et al. [2002] and Moorcroft and Lewis [2006] for further details).

That 2 distinct biological processes, 1 involving movement responses to internal memory, the other movement responses to external environmental stimuli, can give rise to identical patterns of space use emphasizes the challenges of distinguishing the effects of memory on animal movement behavior from other factors affecting animal movement. The latent, unobservable nature of memory places animal ecologists in the situation of trying to infer process from pattern, an inherently difficult exercise (Pielou 1977). The above example highlights the challenge of distinguishing the effects of memory from the

olfactory responses exhibited by many animals such as carnivores; however, similar challenges are likely to arise in separating out the effects of responses to habitat heterogeneity, especially aspects of habitat heterogeneity that are, at present, unmeasured. Thus, although considerable progress has been made over the past decade in developing mathematical models of animal movement that incorporate memory, the challenge of how to elucidate and to quantify the ways in which memories actually affect patterns of animal space use on real landscapes remains. What are the characteristic timescales over which animals utilize different forms of memory? And what are the signatures of these different forms of memory on patterns of

animal spatial distribution? Progress in answering these questions is likely to require a creative, multifaceted approach that draws upon not only telemetry measurements, but also behavioral observations, and insights gained from field manipulation experiments and laboratory studies where animal movement behavior and decision making can be examined under controlled conditions (Bailey et al. 1996).

Linking studies of animal movement and demography.—Although understanding how changes in the environment will affect home-range patterns and the resulting spatial distribution of animals is a central issue in animal ecology and wildlife studies, an often more pressing concern is understanding how changes in the environment will affect species' demography and population abundance. The conventional approach to analyzing environment–demography relationships within species has been to look for associations between demographic rates (such as fecundity, juvenile survival, and adult survival), and population-level estimates of environmental covariates (such as winter temperature or forage availability). For example, Catchpole et al. (2000) used logistic regression to show that March rainfall and winter storm severity both significantly influence survivorship of both male and female Soay sheep (*Ovis aries*) on a Scottish Island. Similar methods have been used to identify environmental correlates of demographic rates in a variety of mammalian species.

This approach for analyzing environment–demography relationships, shown in Fig. 6A, has 2 important limitations. First, this approach does not distinguish between the direct effects of environmental conditions on demography and the indirect effects of environmental conditions arising from environmentally induced changes in the movement behavior and resulting home ranges of animals. As noted in a number of recent articles (Both et al. 2006; Post and Forchhammer 2008; Post et al. 2008; van der Graaf et al. 2006), the effects of climate variability and change on population demography acting via changes in the movement behavior are particularly significant in migratory animals, such as caribou (*Rangifer tarandus*) and musk oxen (*Ovibos moschatus*), in which the timing of large-scale movements in relation to seasonal shifts in climate and food availability has strong impacts on ensuing rates of fecundity and survivorship.

Second, in relating the demographic fate of individuals to a population-level average environmental condition, the traditional approach to analyzing environment–demography relationships shown in Fig. 6A averages over the differing environmental conditions that individuals actually experienced. In cases such as the relatively small insular populations studied by Catchpole et al. (2000), this assumption may not be unreasonable. However, in situations where the environmental conditions experienced by animals differs significantly among individuals (e.g., the widely dispersed population of elk in Yellowstone National Park), using population-level average environmental conditions in an analysis of individual demographic performance will change, and in some cases hide, causal relationships that exist between the actual conditions

experienced by individual animals and their subsequent demography.

Until recently, there was no real way to address the above concerns regarding the analysis of environment–demography relationships. However, the increasing availability of measurements of animal locations and spatially and temporally resolved environmental data opens the way to linking demographic performance to environmental conditions and an animal's social environment at the scale of individual animals, rather than at the population level (Fig. 6B). Fig. 6B emphasizes that the availability of information on the movements of individuals is central to the ability to conduct such integrated analyses because it makes it possible to disaggregate population-level average landscape and climate information appropriately into corresponding individual-level environmental covariates, which can then be related to subsequent individual rates of fecundity and survival; and because the analysis framework shown in Fig. 6B explicitly distinguishes between the direct effects of climate on survival, and those that have been mediated by changes in movement behavior and resulting home-range patterns. Analyses of this form would, in effect, integrate analyses of a population's demography with analyses of its spatial distribution. A natural framework for such analyses would be a hierarchical generalized linear mixed model approach incorporating both relocation data and demography data as key observables (see Bolker et al. [2009] for a discussion of generalized linear mixed models). Although such analyses would be more complex in nature, their broader scope offers the promise of developing a more accurate and consistent picture of how changes in the environment affect the movement behavior of individuals and their subsequent demographic fates.

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