What is a home range?

ROGER A. POWELL* AND MICHAEL S. MITCHELL

Department of Biology, North Carolina State University, Raleigh, NC 27695-7617, USA (RAP)
United States Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT, USA (MSM)

* Correspondent: newf@ncsu.edu

"Home range" is a standard concept in animal ecology and behavior but few people try to understand what home ranges mean to the animals that have them and often assume that a home-range estimate, quantified using some method, *is* the home range. This leads to 2 problems. First, researchers put much energy into discerning and using the "best" methods for estimating home ranges while no one understands, really, what a home range is. Second, maps delineating home-range estimates may have little connection with what home ranges are and what they mean to the animals that have them. To gain insight into these problems, Roger Powell (hereafter, Roger) documented his own use of space for 65 days, obtaining complete data on where he went, what he did, and how much energy and money he expended and gained in each place. Roger's use of space is consistent with how other mammals use space and, therefore, examination of his data provides insight into what a home range is and how ecologists should approach quantifying other animals' home ranges. We present estimates of Roger's home range in 5 different metrics, or currencies, that provide important and different insights. Home-range estimators that combine different types of information to estimate the spatial distribution and qualities of resources that structure animal behavior (i.e., fitness surfaces) will probably provide the most insight into animals' home ranges. To make reasonable estimates of home ranges, researchers must collect data on habitat, resources, and other attributes of the landscape, so that they can understand basic behaviors of animals and understand how animals may view their environment. We propose that the best concept of a home range is that part of an animal's cognitive map of its environment that it chooses to keep updated.

Key words: cognitive map, currency, fitness surface, global positioning system, hippocampus, home range, telemetry

The advent of radiotelemetry expedited the study of secretive mammals, allowing researchers to observe where these animals travel (Craighead and Craighead 1966). Aggregated telemetry locations provided insights into what animals call home and allowed researchers to estimate the total use of space by an animal, commonly considered to represent an animal's home range. Rapid increase in use of telemetry and home-range estimators that use telemetry data has produced an enormous literature on "home ranges" of animals.

Problematically, the technology of radiotelemetry, our understanding of how that technology and the environment affect distributions of telemetry locations, and estimating home ranges have far outpaced theoretical exploration of the biological processes that also affect the distributions of telemetry locations collected by researchers. The paucity of conceptual underpinnings for home-range behavior means researchers generally estimate home ranges with little understanding of what, precisely, they are estimating, leading to

myriad potential problems (Houle et al. 2011). Having the technological cart before the conceptual horse has resulted in a confusion among researchers, who try to understand the statistical descriptions of location or movement data but not the biological behaviors and processes that generated the data. (Similarly, those researchers who study behavior and processes by direct observation [e.g., Altmann1998; Bekoff and Wells 1981; Byers 1998, 2003] seldom explore how behaviors build home ranges.) Thus, we believe that much research devoted to collecting more location data and analyzing them with ever-better statistical procedures is misguided until we understand better what, exactly, we are estimating. Continuing to measure home ranges, however better we do it, without understanding them is simply to give more sophisticated tools to the blind

men describing the elephant, an approach unlikely to advance our understanding of pachyderms. In this paper, we present insights from measuring home ranges, suggest new views of home ranges, suggest ways to measure home ranges that should provide new insights, and hope to stimulate thought about home ranges.

Presuming that home-range behavior is the product of decision-making processes shaped by natural selection to increase the contributions of spatially distributed resources to fitness (Mitchell and Powell 2004, 2012), then a home range represents an interplay between the environment and an animal's understanding of that environment, that is, its cognitive map (Börger et al. 2008; Peters 1978; Powell 2000; Spencer 2012). To understand the mechanistic, biological foundations of home-range behavior, therefore, the estimated home range of an animal must be linked explicitly to its cognitive map. This explicitly biological approach is far more likely to be productive for interpreting and predicting home ranges of animals than is inventing new ways to describe them quantitatively.

The biological roots of the home-range concept run far deeper than methodologies for estimation. Darwin (1861) noted that animals restrict their movements to home ranges, as did Seton (1909). Burt (1943:352) outlined the basic concept of an animal's home range as we now understand it: "That area traversed by an individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range."

Burt (1943) defined "home range" with mammals in mind but he grounded his definition biologically and broadly by basing "home range" on an animal's requirements. Consequently, his definition applies beyond mammals. Mammals, birds, reptiles, amphibians, and fish all exhibit site fidelity and live in restricted areas for long periods (e.g., black bears [*Ursus americanus*—Powell et al. 1997], Ipswich sparrows [*Passerculus sandwichensis princeps*—Reid and Weatherhead 1988], anoles [*Anolis aeneus*—Stamps 1987], reef fish [*Eupomacentrus leucostictus*—Ebersole 1980]). These animals demonstrate familiarity with the areas where they live and they know the locations of resources, escape routes, and potential mates. Some biologists believe that Burt's (1943) definition is obsolete because he did not explain how to measure or estimate an animal's home range (White and Garrott 1990). Ecology is replete, however, with fundamental concepts that are difficult to define empirically (e.g., carrying capacity, density dependence, fundamental niche, etc.) but that, nonetheless, structure our interpretations of empirical observations. Similarly, Burt's (1943) definition has underlain generations of home-range estimators (Anderson 1982; Bullard 1999; Dixon and Chapman 1980; Hayne 1949; Jennrich and Turner 1969; Powell 1987; Seaman and Powell 1996; Worton 1989), each making a modest step toward bringing our estimates closer to Burt's (1943) definition.

Today, researchers quantify estimates of animals' home ranges most commonly as densities of use calculated from estimates of the animals' locations across a landscape (Laver and Kelly 2008; Powell 2000). Because animals do not distribute their use of space in statistically well-behaved patterns, nonparametric approaches (e.g., kernel density and convex-hull estimators [Getz and Wilmers 2004; Seaman and Powell 1996; Worton 1989]) have become popular for analyzing location data (Laver and Kelly 2008; Powell 2012). Use of space is often presented as a probability distribution, the utilization distribution, for the use of space *with respect to time*. That is, the utilization distribution usually calculated shows the probabilities of where an animal might have been found at any randomly chosen *time*.

Utilization distributions allow one to estimate such important attributes as apparent preferences for different types of land cover, the effects of topography on home-range locations and shapes, and the probability that 2 animals might be in their area of home-range overlap at the same time (Fieberg and Kochanny 2005; Horner and Powell 1990; Mitchell et al. 2002; Powell 1987, 2012; Powell and Mitchell 1998; Ryan et al. 2006). Nonetheless, our present home-range estimators are not always (perhaps even are seldom) the best tools for quantifying an animal's home range. When the scale at which an animal uses space (e.g., a bear following a commonly used trail) differs from critical scales of the home-range estimator (e.g., the bandwidth, h, of a kernel estimator or k for the convex-hull estimator chosen using standard methods), the resulting utilization distribution may assign relatively high probabilities of use to places unlikely to be used (e.g., areas near the bear trail that can be used for escape but seldom are), even if animals are located frequently. Similarly, home ranges are dynamic and change, often on timescales that differ from the timescale needed to collect enough data to estimate a home range. In addition, an implicit assumption in most analyses of home-range estimates is that the probability of spending time in a place is a measure of the importance of that place to the owner of the home range. For an animal that does not have an important requirement met only in a restricted location, time may indeed be a reasonable currency (metric) for indexing importance. For moose (*Alces alces*), however, which can meet sodium requirements only in restricted places (Belovsky 1978; Belovsky and Jordan 1978), and for beach mice (*Peromyscus polionotus*), which seldom use escape routes from predators but know the routes, nonetheless (Dawson et al. 1988; Sumner and Karol 1929), importance will simply not be indexed by time spent in those restricted places.

Consequently, time spent in an area may not be the best currency to use in quantifying home ranges, and utilization distributions calculated using current home-range estimators may not provide the best estimates of home ranges, much less explain how and why animals use space. Other currencies may provide insight into what places are of great or small importance to an animal. For example, a currency that indexes limiting nutrients for moose would produce a different home-range utilization distribution than does time and would provide more insight into the importance of different places. Likewise, using fear as a currency (Laundré et al. 2001; van der Merwe

and Brown 2008) would produce a different home-range utilization distribution for chipmunks (*Tamias* spp.) than does time.

Home ranges differ among animals of different species, among individuals within a species, and even within individuals over time. Nonetheless, all animals use their home ranges to provide food and other resources, including avoiding predators. In this respect, humans are no different from other mammals: we go places to gain resources (e.g., earn money and buy groceries) and we avoid dangerous places (e.g., the interstate at rush hour and dark alleys). We even appear to make many of the same irrational choices that many other animals do (Real 1996). Consequently, home ranges of people have the potential to provide insight into aspects of home ranges of animals. In addition, we can gain near complete information about people (i.e., better data). To understand how different currencies provide insights into animal home ranges, we quantified the home range for one of us, Roger Powell (hereafter, Roger), using 5 different currencies.

Our exercise highlights several conceptual challenges, not only to understanding how to estimate a home range but to understanding what, exactly, a home range is. We shall present Roger's home range in its different forms, use this example to highlight problems with present methods of estimating home ranges and with present concepts of home ranges, offer a new way to conceptualize animals' home ranges, and conclude with suggestions for estimating home ranges that will provide more insight into why and how animals maintain home ranges. The illustration of Roger's home range is a conceptual beginning for reevaluating what the home ranges of animals really are and how they might best be understood.

METHODS

During the academic year 1990–1991, while on sabbatical at the University of Wyoming, in Laramie, Roger recorded his location at all times during 65 random days. Following each period of travel or period remaining in 1 place, Roger noted the beginning and ending times and, for travel, the exact route (always within 10 m, often within 3 m), mode of travel, and irregularities in travel speed, if any. He also noted other details of his activities, such as what he ate and how much money he spent and for what. For example, on a typical weekday, he noted when he awoke, when and what he ate for breakfast, when he left home for the university, how he travelled (walk, bike, or drive) and the exact route to the university (including walking on sidewalk versus center of a street), arrival time at the university, cups of coffee drunk, lunchtime, and so forth. If he went out for lunch, he noted times, routes and transport, what was eaten and drunk, and the cost. If he went into the field (Medicine Bow Mountains approximately 50 km west of town), he noted times and travel routes to the field, times and exact routes walked when in the field, return times, and so forth. He did not record his exact locations within buildings.

Roger's data are continuous and event driven (as are most direct, observational data), whereas most data used to estimate home ranges are discrete and time driven. No conventional home-range estimators can deal with event-driven data despite their completeness and desirability. Therefore, to illustrate Roger's home range, we forced the data into 2 nonparametric approaches, thereby losing (possibly important) detail. First, we superimposed a 10×10-m grid over a map of the Laramie area and calculated the duration of time that Roger spent sequentially in each cell (a grid cell approach). We totaled money spent in each cell. Even though Roger did little of the grocery shopping for his family, we assigned a proportion of his family's grocery budget to the grid cells for the grocery store (Roger has a wife and daughter and his wife did all of the grocery shopping during the 65-day sample). From Roger's budget records, we assigned proportions of money earned from university work and from freelancing to the grid cells for his university office, for his field research areas (and travel), and his home. From food eaten, we calculated energy gained in each cell (Davis 1970). From activity and duration (in hours to 3 decimal places), we indexed energy expended (*Ex*) in each grid cell as follows (Kleiber 1975; Powell 1979; Taylor et al. 1970):

$$\text{sleep: } Ex = 3W0.75t,$$

where W is weight (64 kg) and t is time duration; and

$$\text{active: } Ex = 5.1W0.75t + 3.3W0.6st,$$

where s is average walking speed.

For driving, we set $s = 0$. For biking, we used Roger's walking speed but biking time to calculate energy expenditure. For snowshoeing, we doubled Roger's walking speed to represent the increased energy expenditure. We did not include Roger's nonmetabolic use of energy. When Roger drove, for example, we did not include the energy of burning fuel. To do so would open a can of worms: would we have to include energy used to build his pickup, to drill wells, to refine and ship the fuel, and so forth? Calculating complete energy use is impossible, so we chose to limit energy to Roger's use of metabolic energy only. The calculations we used do not capture every nuance of Roger's metabolic energetic expenditure but they allow relative comparisons to other currencies. In addition, we converted total use of space in each currency to a utilization distribution that summed to 1.0.

Finally, we calculated 95% fixed kernel home ranges for each currency (Seaman and Powell 1996) setting $h = 250$ m to smooth over the minute details of Roger's use of space and to make his home range appear typical of those calculated for wild mammals.

RESULTS, INCONGRUITIES, AND RUMINATIONS

We distinguish throughout this paper between the biological reality of a home range and statistical estimates representing that reality. Actual home ranges are perceived by and used by animals themselves. People estimate those home ranges using home-range estimators and data.

Roger's home range, estimated and real.—Figure 1 shows a typical 95% fixed kernel estimate of Roger's home range. The prominent features of Roger's home range are his house, the biology building at the university, his walking routes to the university, the grocery store and businesses downtown, and the house of Steve Buskirk, a friend. Fig. 2 shows the grid cell estimate of Roger's home range. Fig. 2A shows Roger's movements while confined to the Laramie environs, whereas Fig. 2B shows all of Roger's travels, including those extending far from Laramie.

Comparing Figs. 1 and 2 highlights several points. First, because Roger's data are complete for all 65 days, we do not need to estimate travels between locations because we know them. For those 65 days, Roger's use of space is precisely shown by Fig. 2. Second, conventional home-range estimates (the kind most biologists appear to want [Kie et al. 2010]) misestimate his use of space (Fig. 3). The 95% fixed kernel estimate includes areas where Roger never went and that he did not consider part of his home range, and does not include areas where Roger did go and that he did consider part of his home range.

Third, Roger's 65 days are only a sample of his movements during his entire sabbatical, affecting the ways one can use the data. His 65 days were representative of his behaviors and movements and, thus, provide solid insight into his general movements and other behavior patterns. Thus, 65-day samples may be adequate for population-level questions about use of space (by people living in Laramie, by faculty at the university,

Fig. 2.—The grid cell estimate of Roger's home range showing his travels A) in Laramie proper and B) in Laramie and the surrounding area. Extreme travels that are labelled in roman in Fig. 2B, Roger considered part of his home range. Extreme travels labelled in bold italics, Roger did not. Those areas that he considered part of his home range were areas with which he was familiar and where he travelled with confidence. Darkness of line represents the amount of time Roger spent in each place; darkness has the same scale in both A and B. Locations of Fort Collins and the Sierra Madre are not drawn to scale.

etc.). One must have, of course, samples for many other people in the population.

In contrast, Roger's 65 days did not detail his total use of space during his entire sabbatical. Places not visited by Roger in those 65 days fell into 2 categories: places that he visited on other days because those places had resources that he needed on those other days, and places that he avoided. During days not sampled, Roger visited places he considered part of his home range. In contrast, he actively avoided houses of unknown people and businesses of no use and he did not consider them part of his home range. Neither Fig. 1 nor Fig. 2 is of any value for differentiating between these 2 categories of nonuse. Obviously, no home-range estimator can make up for a small sample size. To understand Roger's individual use of space completely, we need data for all days of his sabbatical. Using a home-range estimator can hide the nasty fact that a sample size sufficient to answer some questions may not be
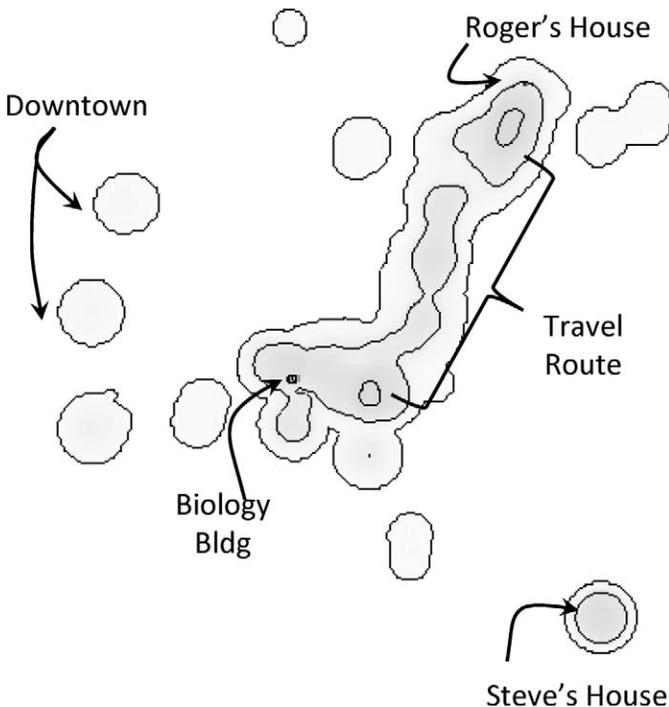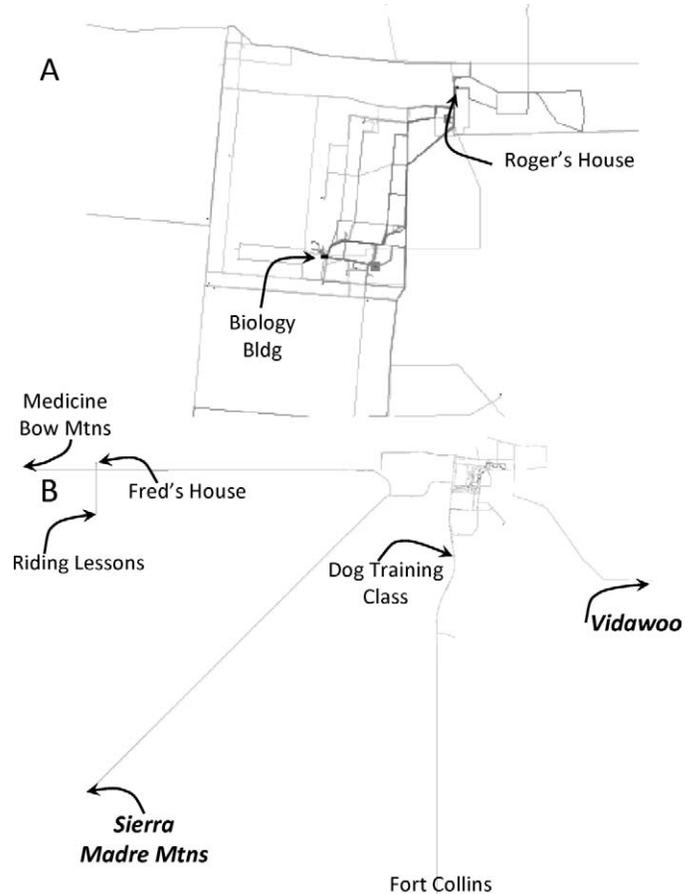

Fig. 1.—The 95% kernel estimate of Roger's home range in Laramie, Wyoming, where he spent sabbatical at the University of Wyoming in 1990–1991. Roger's house, the Biology Building on the university campus, Steve Buskirk's (a friend) house, and areas in downtown Laramie frequented by Roger are noted.
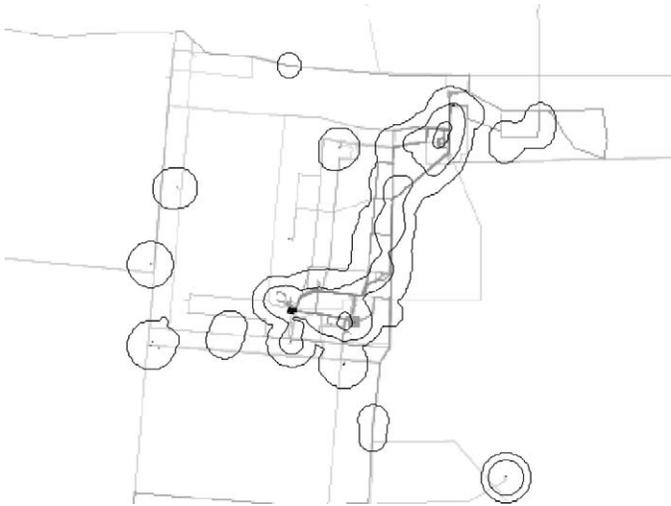
FIG. 3.—The grid cell estimate of Roger's home range within Laramie with 95% kernel estimate of his home range superimposed. Darkness of line represents the amount of time Roger spent in each place.

FIG. 4.—Grid cell estimates of Roger's in Laramie presented in different currencies. A) Time spent in different places. B) Energy expended. C) Energy gained. D) Money spent. E) Money earned. Darkness of line represents the proportion of each currency Roger "used" in each place; note that Roger gained energy and spent money in few places and that both were highly concentrated at the small gray rectangles and tiny dot in panels C and D.

adequate to answer other questions (also noted by Fieberg and Börger 2012).

Fourth, Roger noted distinct boundaries to his home range where private property restricted his movements but he did not consider his home range to have distinct boundaries where his familiarity with the landscape was limited by numbers of visits. In the Medicine Bow Mountains, for example, Roger's familiarity with different places varied in a continuous manner with numbers of visits and time spent in those places.

Figure 4 shows Roger's use of space using 5 different currencies, including the conventional currency of time spent in different places but also energy and money expended and gained in different places. No 2 panels in Fig. 4 are exactly the same and each provides a different picture of what was important to Roger during his sabbatical year. Energy could be gained and money spent only in restricted places (designated as small gray spots and a tiny black spot in each of Figs. 4C and 4D), whereas Roger expended energy and spent time everywhere he went. That energy gain and money spent were spatially restricted might suggest that sites for these activities were limiting. That was true only in part. Although Laramie had more than the 1 grocery store that Roger's family used, the other stores did not have the foods Roger's family wanted at competitive prices. Nonetheless, Roger did not frequent all places where he could have gained energy or spent money. He was selective.

The home-range concept.—Why do mammals maintain home ranges? A home range provides information on the locations of resources (Folse et al. 1989; Saarenmaa et al. 1988; South 1999; Spencer 2012; Stillman et al. 2000; Turner et al. 1994; With and Crist 1996) and such knowledge affects an animal's fitness. Dispersing mammals often have higher mortality or lower reproduction than conspecifics in familiar territory (Blanco and Cortés 2007; Gosselink et al. 2007; Soulsbury et al. 2008). Learning a home range requires time,

leading to site fidelity, and site fidelity has been used to define whether an animal has established a home range (e.g., Spencer et al. 1990).

Mammals create spatial maps using their hippocampus (Fyhn et al. 2004; Kjelstrup et al. 2008; O'Keefe and Dostrovsky 1971; Pastalkova et al. 2008; Peters 1978; Sargolini et al. 2006; Solstad et al. 2008) and hippocampus size varies with relative selection pressures on cognitive mapping abilities and spatial memory (Clayton et al. 1997; Galea et al. 1996; Jacobs and Spencer 1994; Krebs et al. 1989). Mammals plan movements and their cognitive maps are sensitive to where they find themselves within their environments (Kjelstrup et al. 2008; Solstad et al. 2008). In addition, an animal's movements depend on its nutritional state and motivation; resources with low travel costs or that balance the diet should have added value.

Mammals continuously update their cognitive maps. A researcher, in contrast, estimates a home range from locations of the animal over the time and deduces a changed cognitive map only by identifying changes in how the animal uses space over time (Doncaster and Macdonald 1991). Thus, for most research, a home-range estimate must be defined for a specific time interval, for example, a season, a year, or possibly a lifetime (also noted by Fieberg and Börger [2012]). The longer

the interval of time, the more data can be used to estimate the home range but, also, the more likely that the animal has changed its cognitive map since the 1st data were collected.

Many animals seldom use the peripheries of their home ranges; an animal may actually care little about precise boundaries of its home range because it spends the vast majority of its time elsewhere. Peripheries of home ranges can be diffuse (Gautestad and Mysterud 1993, 1995), making the area of a home range undefined. Nonetheless, a home range is critically important to its animal. Crudely estimated home ranges can provide insights into animal behavior and ecology when considered in the context of other data and when researchers remember the imprecision of home-range boundaries and areas to animals themselves. In the end, a mammal's cognitive map of its home range must allow it to make decisions that affect its fitness, such as where to hunt next for food, how to reach that hunting site while minimizing chances of becoming someone else's food, and what parts of its home-range overlap with that of a potential mate (Spencer 2012). An up-to-date cognitive map allows an animal to make quick, accurate decisions (Chittka et al. 2009)

We propose that a home range is that part of an animal's cognitive map that it chooses to keep up-to-date with the status of resources (including food, potential mates, safe sites, and so forth) and where it is willing to go to meet its requirements (even though it may not go to all such places). Mammals can sample and update many resources remotely using at least smell, hearing, or sight. We must use the actions of the animals to gain insight into their home ranges, which requires good research design.

Can we gain insights into the concepts that animals have of their own home ranges? We believe, yes. Fig. 2B shows everywhere that Roger actually went during his 65 days. Roger distinguished "occasional sallies" as trips to sites that were unfamiliar (in bold italics in Fig. 2). This distinction leads us to a way to conceptualize animals' home ranges. We suggest that readers should think of *their own* home ranges. Think about going to work or going to the grocery store or picking up the kids at day care. We all get mental images of those sorts of places. We can "visualize" the critical details that are important. We suggest that those routes and places and areas that a person can "visualize" are (usually) part of that person's home range. Those places that cannot be "visualized" are (usually) not. (Adult humans can often visualize, for example, childhood homes but do not keep those places up-to-date in the cognitive maps. In addition, we use the word "visualize" loosely to mean "have a mental concept" without limiting the concept to the sense of vision only.) We also suggest that this approach helps us understand how animals might conceive of their home ranges. Mammals do appear to "visualize" space that is familiar to them, to "visualize" familiar routes before deciding which specific route to travel, and to learn new places and forget ones not visited in a long time (Clayton et al. 1997; Fyhn et al. 2004; Galea et al. 1996; Jacobs and Spencer 1994; Johnson and Redish 2007; Kjelstrup et al. 2008; Krebs et al. 1989; Leutgeb et al. 2007; O'Keefe and Dostrovsky 1971;

Pastalkova et al. 2008; Peters 1978; Sargolini et el. 2006; Solstad et al. 2008). Thus, understanding an animal's home range as the places that it can "envision" makes biological sense. This concept of a home range adjusts home ranges over time, as areas of use change, and it includes in home ranges areas that animals know but do not visit. This concept also is consistent with Burt's (1943) definition.

Calculating an animal's use of space with different units provides insight into why the animal goes where it goes, what places are most important to it and why, and what aspects of the animal's life would be most affected by changes in its environment. Current home-range estimators can be used to calculate home ranges in different units (Fig. 4) provided we have information on resources, behavior, risk of predation, and so forth at different places. Conventional telemetry data alone, however, do not provide adequate information for using home-range estimators in this fashion and, therefore, are extremely limited and limiting. In fact, location data without associated data on resources and dangers provide few insights.

Understanding exactly how use of space affects survival, reproduction, and other aspects of fitness is elusive, if for no other reason than that survival and reproduction depend on the cumulative effects of movements. We suggest that comparing and combining home ranges calculated in different units (including weighting of units and including interspersion and juxtaposition) provides critical insight into how contributions to fitness vary across space. In Fig. 4, each unit represents different influences on Roger's fitness. We define Roger's fitness biologically and functionally as his ability to produce children and to raise them to become reproducing adults. Time and energy that Roger spent in different places document his attentions to tasks related to work and parenting. Amount of money earned represents his ability to do his job well. Money spent presents his ability to forage in the right places for food and other resources. Money earned and spent might represent, loosely, characteristics subject to sexual selection. For other animals, potential units include time, energy gained, energy spent, giving-up densities for resources, danger from predators, potential for competition, potential for mutualisms, and access to mates. State–space models and grid cell and kernel densities all can be used in units other than time (Fig. 4). Aldridge and Boyce (2007), Frair et al. (2007), Johnson et al. (2004), McLoughlin et al. (2007), and Moorcroft and Lewis (2006) linked fitness components of animals to characteristics of landscapes but did not map home ranges in other units. At the very least, units used should match the research questions being asked.

Estimating a home range in different units provides insight into an animal's cognitive map of its own home range. Can we measure cognitive maps? We believe so but it will be challenging, requires information not available from telemetry data, and will be less difficult in the future. Areas with high contributions to fitness (high values in several critical currencies) should be areas that an animal keeps updated. Present technology allows researchers to see action in a laboratory rat's hippocampus showing, for example, that the rat

"envisions" different potential routes through a maze before choosing one, and that it "envisions" the edges of its enclosure (Kjelstrup et al. 2008; Solstad et al. 2008). Techniques will be developed in the future, we believe, that will allow monitoring the hippocampus of free-living mammals, allowing researchers to gain better understanding of how wild animals perceive space around them and how they build cognitive maps. Does Roger's concept of his own home range match any of the home ranges shown in Figs. 1–4? No, not exactly. The contoured home ranges include many places that Roger did not know at all, especially the houses of strangers. Fig. 2B fails to include many streets and places around Laramie that Roger knew well. In addition, Roger's concept of his home range changed depending on his mental state. When he was hungry or tired, his route home from the university was more important than when he was sated or when he was working on an exciting analysis producing new insights. Thus, the layers of home range based on different currencies (Fig. 4) actually changed in importance for Roger depending on his physical and mental condition; the food-acquisition map became more important when Roger was hungry. Information on the mental states of wild animals can be deduced, for example, from data on the time since the last meal (hunger) or recent encounters with predators (fear). When prey are abundant, predators devalue what we map as layers related to food compared to times when prey are scarce; when predators are rare, prey devalue layers related to escape. Knowing the mental states of wild animals on fine timescales is more difficult. By observing animals in a way that does not affect behavior, researchers can document fine-scaled activity budgets and document apparent directional, goal-related travel (Altmann 1974; Altmann 1998; Byers 1998, 2003; Pulliainen 1984; Rogers and Wilker 1990). Finally, we assigned a proportion of the grocery budget to Roger even though Roger seldom went to the grocery store. This money spent affected Roger's fitness because its expenditure meant that he could not use the money in other ways and because he gained food from this expenditure. This situation is similar to that for cooperatively breeding species (e.g., red-cockaded woodpeckers [*Picoides borealis*], wolves [*Canis lupus*], and beavers [*Castor canadensis*]) where "helpers" affect the fitness of other individuals. Thus, obtaining the full picture about the importance of space for a particular individual may require data for other individuals.

Estimating home ranges.—A home-range estimator should provide a researcher with insight into how an animal values space, including places that are important but not necessarily frequented. Estimators must deal with location error and its variation across space and time, constraints on animal movements, and different currencies having different ultimate values to an animal. Finally, estimators should allow researchers to add their knowledge to home-range estimates. Current home-range estimators can and should be modified by individual researchers to reflect appropriately all the pertinent data that are available, not just location data. By making this statement, we do not mean to give carte blanc to researchers to throw all data into an analysis and go for a fishing expedition.

We highlight several examples of what we mean and why it is important.

Figure 3 shows Roger's actual movements through Laramie superimposed on the contours for his kernel home range using the unit of time. Which would be preferred if we were plotting the time–home range of a wild mammal? One might answer that the kernel, contour map is preferred; after all, the narrow travel lanes along streets do not represent a home range because people are weird and follow streets, something very different from what animals do. Except, of course, wild animals *do* follow "streets." Deer (*Odocoileus* spp.) follow game trails (Miller et al. 2003). Wolves (*C. lupus*) follow game trails and often travel along gravel roads (Paquet and Carbyn 2003). Bears follow bear trails, often *placing their feet in exactly the same places* every time (R. A. Powell and M. S. Mitchell pers. obs.). Voles (e.g., *Microtus* spp. and *Myodes* spp.) make tunnels in grass and underground (Pugh et al. 2003), which weasels (*Mustela erminea*, *M. frenata*, and *M. nivalis*) follow, in turn (King and Powell 2007).

A good home-range estimator must estimate use, or value, of the space between locations and estimate use, or value, of space for days poorly sampled. The kernel estimate in Figs. 1 and 3 *misrepresents* Roger's use of space in Laramie because the wide bandwidth forces the estimate to include many places Roger avoided. Home-range estimators must be constrained where animal movements are constrained by their environments (e.g., Benhamou 2011; Benhamou and Cornélis 2010; Horne et al. 2008; Matthiopoulos 2003). For Roger's data, Silverman's (1990) kernel k was more appropriate than a normal kernel, because a normal kernel has infinite tails. For walking on streets, a kernel with no tails would have been even more appropriate. Using a bandwidth of 10 m for travel, but 25 m when Roger was in the biology building at the University of Wyoming, and 15 m when Roger was in other buildings, leads to a kernel home-range estimate nearly indistinguishable from the grid cell estimate shown in Fig. 2. Even Brownian bridge estimators, which were developed specifically to estimate movements (Bullard 1999), can misestimate home ranges if not constrained (Powell 2012). Areas that are inhospitable (e.g., terrestrial areas for aquatic organisms) must be excluded from home-range estimates; areas that are avoided must be weighted by the degree of avoidance. Usually, a barrier will limit movement to distances that are shorter than error for location estimates, even by an order of magnitude or more. If constraints limit movements to areas narrower than kernel bandwidths, researchers can use different kernels and bandwidths in different places or for different behaviors; use kernels that are not circular; remove nonhabitat after estimating utilization distributions; incorporate other information as outlined by Fieberg and Börger (2012); Matthiopoulos (2003), and Moorcroft and Lewis (2006), or use a completely different approach, such as a convex-hull method (Getz and Wilmers 2004), a state–space model (Patterson et al. 2008), or a grid cell model. For data sets that are relatively complete with little error (observation data, snow tracking, some global

positioning system data sets), excellent utilization distributions can be derived from grid cell models.

Data on animal locations recorded from direct observations or tracks in the snow, or estimated using global positioning system technology approach the detail of Roger's data. Present global positioning system technology requires a trade-off between frequency of locations and numbers of days that an animal can be tracked (Fieberg and Börger 2012, Moorcroft 2012). Global positioning system data that approach the detail of Roger's data are appropriate for answering detailed, individual-level questions: did the individual tracked do specific things on the days tracked? By sampling many individuals for short periods, one can answer population-level questions related to detailed behaviors and short periods of time. Global positioning system data with sparse samples over long periods are similar to conventional (very-high-frequency) telemetry data and are appropriate for answering very general questions about individuals: did the individual change its area of intensive use over time? By sampling many individuals, one can answer population-level questions related to general use of space. Even when technology allows collection of data with the detail of Roger's data over long periods of time, answering population-level questions still requires data from many individuals in the population. Extensive data on a few individuals are not adequate to answer population-level questions (Fieberg and Börger 2012).

In Burt's (1943) discussion of home-range estimates, he included areas with which animals are familiar. Animals perceive the world around them and remember those perceptions. One might consider the kernel and bandwidth for a kernel estimator to represent, in some way, an animal's ability to perceive and to remember the environment around it. Many, and presumably most, mammals can smell, hear, and see up to hundreds of meters or more under reasonable conditions. Thus, an animal's home range can include areas sampled remotely and not visited regularly. Perception distance may not be constant. Researchers often learn where travel is constrained and where animals are most likely to respond to distant scents or sounds. They can, thereby, adjust kernels and bandwidths (for kernel estimators) or k (for convex-hull estimators) for different data subsets.

Adjusting estimator parameters cannot include in a home-range estimate all familiar areas not visited during a sampling period. To estimate areas not visited by Roger on his 65 days, we need more data than location data; for example, friends that Roger might visit at their homes and restaurants where Roger might dine. Simulations or mechanistic models of movements for days not sampled can be based on characteristics of movements on the 65 sampled days and on weighted probabilities of Roger going to specific places. For critters, travel to available resources not used during a sampling period, use of travel and escape routes, and other behaviors can be modeled as outlined by Horne et al. (2007, 2008), Matthiopoulos (2003), Moorcroft and Lewis (2006), and Patterson et al. (2008).

Detailed information about individual study animals sometimes provides insights into familiar places. For example, in fall 1985, a year of poor nut crop in the mountains of North Carolina, a 9-year-old female black bear that our research team had followed since 1981 travelled with her cubs more than 15 km directly to a ridge, presumably rich in acorns and far outside her documented home range. She and the cubs stayed on that ridge for more than a week and then returned directly to her documented home range (Powell et al. 1997). We deduce from her behavior that this female was familiar with that distant ridge and considered it part of her home range. No current home-range estimator or mechanistic model can assign to that ridge an appropriate probability or importance of use without data beyond telemetry data. A researcher's knowledge of those other data and insight are required to understand how that ridge could mean the survival of a female bear's cubs. Similarly, estimators cannot distinguish between the importance of having a particular travel route from the importance of having at least *a* travel route when any 1 of several will suffice.

Burt's (1943) definition of a home range directs us to exclude "occasional sallies"; but how are we to identify "occasional sallies?" Fig. 2B shows Roger's movements with occasional sallies highlighted (bold italics). Roger's 2-day trip to the Sierra Madre, for example, to join a research team studying martens (*Martes americana*) was an occasional sally because Roger was completely unfamiliar with the area upon arrival and did not stay long enough to become familiar with the site. Roger's trip to Fort Collins, however, included a meeting of a graduate student's advisory committee and took Roger to places with which he was familiar from many other visits outside the 65-day sample. Excluding the outermost 5% of Roger's travels or excluding locations that create large jumps in convex polygon area, 2 conventions used to exclude occasional sallies (Laver 2005), would exclude the Sierra Madre and Vidawoo correctly but exclude all of Fort Collins incorrectly. These conventions also would have excluded the female black bear's jaunt to the distant ridge. Another routine practice is to report 95% time-based home ranges (that area where an animal is expected to be found 95% of the time). This practice correctly excludes extreme areas whose probability of use is expected to be predicted poorly (due to sampling error), but includes occasional sallies that stay within the 95% contour, and may exclude areas important to an animal, such as the bear's ridge. To exclude occasional sallies, researchers must inspect extreme data points in the context of what is known about each individual animal and about the species.

In Burt's (1943) definition of a home range, "area" means a place on a landscape and not measured area (i.e., ha or km^2). That Roger did not envision distinct boundaries to his home range begs the question of whether other animals do. We expect that nonterritorial animals (and even some territorial animals) do not envision distinct boundaries to their home ranges, making home-range *area* undefined and a nonentity. If a nonterritorial animal perceives no boundaries, why should researchers value arbitrary boundaries that they assert? For such animals, using all the information in a utilization distribution is the only

quantification of a home range that makes sense. Many researchers today estimate home ranges using probabilistic estimators but use only outlines and areas in their analyses. Calculating an area for a home range that, in reality, has no biological boundary is irrelevant and misleading. For a field of enquiry that has focused so strongly on area estimation, this can be a hard fact to swallow. In contrast, however, knowing the resources where an animal spends 95% of its time, or knowing where it obtains 95% of its food, or knowing where its probability of survival exceeds some limit may be important when used in the context of data on the distribution of foods, data on cover, or data on use of space by predators.

Final thoughts.—We leave you with 4 final thoughts. First, *any* estimate of a home range is, at best, a limited model of reality. It is a statistical approximation of an animal's behavior that has the limitations of any statistic. Don't confuse your estimate with the biological process you are trying to quantify. When asking what a home range is, the means used to measure must not determine the definition to avoid circularity. Thinking that a 95% contour *is* an animal's home range lacks biological insight, placing the resulting biological inferences at risk. Thinking that an animal's home range has a definable boundary may be placing focus on the least biologically or statistically defensible aspect of an animal's home range; other measures of home-range characteristics (i.e., kernel density values) are far more likely to be defensible both biologically and statistically.

Second, no universal home-range estimator or model exists. No researcher should assume that the currently fashionable method of estimating home ranges is the best approach for answering any particular question. Choose the model that is the most parsimonious simplification of reality with the best potential to answer the question of interest; a mismatch between model and question (stated or not) will be uninformative at best, or misleading at worst.

Third, try to understand the biological, fitness-driven reasons behind animals' use of space before estimating home ranges or interpreting their meaning. Doing so will probably provide new, and more, insight into animals' use of space than simply plotting time spent in different places. Different fitness currencies tell us different things about home ranges of animals, none of which is necessarily incorrect, although on the surface they may seem contradictory. Apparent contradictions stem from the belief that a statistic is capable of fully representing reality and from failing to test multiple, competing hypotheses. Accurate, rigorous insights proceed from an appropriate match between the research question and the currency selected. In the absence of a fitness currency available a priori, test multiple currencies to the question at hand.

Fourth, understanding animals' home ranges from the animals' perspectives may provide the most insight of all. Doing so will likely not, however, produce neat-looking contour maps. Understanding animals' home ranges will be a messy, irregular, complex process and the results will be difficult to map. We must embrace this messiness; it simply represents the real behaviors of animals in complex and variable environments. We anticipate that understanding more about the fitness drivers of real home ranges, as animals conceive them, will provide us with far more insight than do the neat contour maps we draw now.

LITERATURE CITED

ALDRIDGE, C. L., AND M. S. BOYCE. 2007. Linking occurrence and fitness to persistence: habitat based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

ALTMANN, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:227–267.

ALTMANN, S. A. 1998. Foraging for survival: yearling baboons in Africa. University of Chicago Press, Chicago, Illinois.

ANDERSON, D. J. 1982. The home range: a new nonparametric estimation technique. Ecology 63:103–112.

BEKOFF, M., AND M. C. WELLS. 1981. Behavioral budgeting by wild coyotes—the influence of food resources and social-organization. Animal Behaviour 29:794–801.

BELOVSKY, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biology 14:105–134.

BELOVSKY, G. E., AND P. A. JORDAN. 1978. The time–energy budget of a moose. Theoretical Population Biology 14:76–104.

BENHAMOU, S. 2011. Dynamic approach to space and habitat use based on biased random bridges. PloS ONE 6:e14592.

BENHAMOU, S., AND D. CORNÉLIS. 2010. Incorporating movement behavior and barriers to improve kernel home range space use estimates. Journal of Wildlife Management 74:1353–1360.

BLANCO, J. C., AND Y. CORTÉS. 2007. Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. Journal of Zoology 273:114–124.

BÖRGER, L., B. D. DALZIEL, AND J. M. FRYXELL. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters 11:637–650.

BULLARD, F. 1999. Estimating the home range of an animal: a Brownian bridge approach. M.S. thesis, University of North Carolina, Chapel Hill.

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

BYERS, J. A. 1998. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago, Illinois.

BYERS, J. A. 2003. Built for speed: a year in the life of pronghorn. Harvard University Press, Cambridge, Massachusetts.

CHITTKA, L., P. SKORUPSKI, AND N. E. RAINE. 2009. Speed–accuracy tradeoffs in animal decision making. Trends in Ecology & Evolution 24:400–407.

CLAYTON, N. S., J. C. REBOREDA, AND A. KACELNIK. 1997. Seasonal changes of hippocampus volume in parasitic cowbirds. Behavioral Processes 41:237–243.

CRAIGHEAD, F., JR., AND J. CRAIGHEAD. 1966. Trailing Yellowstone's grizzlies by radio. National Geographic August 1966:252–267.

DARWIN, C. 1861. On the origin of species. 3rd ed. Murray, London, United Kingdom.

Davis, A. 1970. Let's eat right to keep fit. New American Library, New York.

Dawson, W. D., C. E. Lake, and S. S. Schumpert. 1988. Inheritance of burrow building in *Peromyscus*. Behavior Genetics 18:371–382.

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040–1044.

Doncaster, C. P., and D. W. Macdonald. 1991. Drifting territoriality in the red fox *Vulpes vulpes*. Journal of Animal Ecology 60:423–439.

Ebersole, S. P. 1980. Food density and territory size: an alternative model and test on the reef fish *Eupomacentrus leucostictus*. American Naturalist 115:492–509.

Fieberg, J., and L. Börger. 2012. Could you please phrase "home range" as a question? Journal of Mammalogy 93:890–902.

Fieberg, J., and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69:1346–1359.

Folse, L. J., J. M. Packard, and W. E. Grant. 1989. AI modelling of animal movements in a heterogeneous habitat. Ecological Modelling 46:57–72.

Frair, J. L., E. H. Merrill, J. R. Allen, and M. S. Boyce. 2007. Know thy enemy: experience affects elk translocation success in risky landscapes. Journal of Wildlife Management 71:541–554.

Fyhn, M., S. Molden, M. P. Witter, E. I. Moser, and M.-B. Moser. 2004. Spatial representation in the entorhinal cortex. Science 305:1258–1264.

Galea, L. A. M., M. Kavaliers, and K.-P. Ossenkopp. 1996. Sexually dimorphic spatial learning in meadow voles *Microtus pennsylvanicus* and deer mice *Peromyscus maniculatus*. Journal of Experimental Biology 199:195–200.

Gautestad, A. O., and I. Mysterud. 1993. Physical and biological mechanisms in animal movement processes. Journal of Applied Ecology 30:523–535.

Gautestad, A. O., and I. Mysterud. 1995. The home range ghost. Oikos 74:195–204.

Getz, W. M., and C. C. Wilmers. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography 27:489–505.

Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and P. C. Mankin. 2007. Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. Journal of Wildlife Management 71:1862–1873.

Hayne, D. W. 1949. Calculation of size of home range. Journal of Mammalogy 30:1–18.

Horne, J. S., E. O. Garton, and J. L. Rachlow. 2008. A synoptic model of animal space use: simultaneous estimation of home range, habitat selection, and inter/intra-specific relationships. Ecological Modelling 214:338–348.

Horne, J. S., E. O. Garton, and K. A. Sager-Fradkin. 2007. Correcting home-range models for observation bias. Journal of Wildlife Management 71:996–1001.

Horner, M. A., and R. A. Powell. 1990. Internal structure of home ranges of black bears and analyses of home-range overlap. Journal of Mammalogy 71:402–410.

Houle, D., C. Pélabon, G. P. Wagner, and T. F. Hansen. 2011. Measurement and meaning in biology. Quarterly Review of Biology 86:3–34.

Jacobs, L. F., and W. D. Spencer. 1994. Natural space-use patterns and hippocampal size in kangaroo rats. Brain, Behavior and Evolution 44:125.

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

Johnson, A., and A. D. Redish. 2007. Neural ensembles in CA3 transiently encode paths forward of the animal at a decision point. Journal of Neuroscience 27:12176–12189.

Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004. Modeling survival: application of the Andersen–Gill model to Yellowstone grizzly bears. Journal of Wildlife Management 68:966–978.

Kie, J. G., et al. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philosophical Transactions of the Royal Society, B. Biological Sciences 365:2221–2231.

King, C. M., and R. A. Powell. 2007. The natural history of weasels and stoats. Oxford University Press, New York.

Kjelstrup, K. B., et al. 2008. Finite scale of spatial representation in the hippocampus. Science 321:140–143.

Kleiber, M. 1975. The fire of life. 2nd ed. John Wiley & Sons, New York.

Krebs, J. R., D. F. Sherry, S. D. Healy, V. H. Perry, and A. L. Vaccarino. 1989. Hippocampal specializations of food-storing birds. Proceedings of the National Academy of Sciences 86:1388–1392.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology 79:1401–1409.

Laver, P. N. 2005. Cheetah of the Serengeti Plains: a home range analysis. M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg.

Laver, P. N., and M. J. Kelly. 2008. A critical review of home range studies. Journal of Wildlife Management 72:290–298.

Leutgeb, J. K., S. Leutgeb, M-B. Moser, and E. I. Moser. 2007. Pattern separation in the dentate gyrus and CA3 of the hippocampus. Science 315:961–966.

Matthiopoulos, J. 2003. Model-supervised kernel smoothing for the estimation of spatial usage. Oikos 102:367–377.

McLoughlin, et al. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88:3192–3201.

Miller, K. V., L. I. Muller, and S. Demarais. 2003. White-tailed deer (*Odocoileus virginianus*). Pp. 906–930 in Wild mammals of North America: biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.

Mitchell, M. S., and R. A. Powell. 2004. A mechanistic home range model for optimal use of spatially distributed resources. Ecological Modelling 177:209–232.

Mitchell, M. S., and R. A. Powell. 2012. Foraging optimally for home ranges. Journal of Mammalogy 93:917–928.

Mitchell, M. S., J. W. Zimmerman, and R. A. Powell. 2002. Test of a habitat suitability index for black bears. Wildlife Society Bulletin 30:794–808.

Moorcroft, P. R. 2012. Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. Journal of Mammalogy 93:903–916.

Moorcroft, P. R., and M. A. Lewis. 2006. Mechanistic home range analysis. Princeton University Press, Princeton, New Jersey.

O'Keefe, J., and J. Dostrovsky. 1971. The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. Brain Research 34:171–175.

PAQUET, P. C., AND L. N. CARBYN. 2003. Gray wolf (*Canis lupus* and allies). Pp. 482–510 in Wild mammals of North America: biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.

PASTALKOVA, E., V. ITSKOV, A. AMARASINGHAM, AND G. BUZSÁKI. 2008. Internally generated cell assembly sequences in the rat hippocampus. Science 321:1322–1327.

PATTERSON, T. A., L. THOMAS, C. WILCOX, O. OVASKAINEN, AND J. MATTHIOPOULOS. 2008. State–space models of individual animal movement. Trends in Ecology & Evolution 23:87–94.

PETERS, R. 1978. Communication, cognitive mapping, and strategy in wolves and hominids. Pp. 95–108 in Wolf and man: evolution in parallel (R. L. Hall and H. S. Sharp, eds.). Academic Press, New York.

POWELL, R. A. 1979. Ecological energetics and foraging strategies of the fisher (*Martes pennanti*). Journal of Animal Ecology 48:195–212.

POWELL, R. A. 1987. Black bear home range overlap in North Carolina and the concept of home range applied to black bears. International Conference on Bear Research and Management 7:235–242.

POWELL, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65–110 in Research techniques in animal ecology: controversies and consequences (L. Boitani and T. K. Fuller, eds.). Columbia University Press, New York.

POWELL, R. A. 2012. Movements, home ranges, activity, and dispersal. Pp. 188–217 in Carnivore ecology and conservation: a handbook of techniques (L. Boitani and R. A. Powell, eds.). Oxford University Press, London, United Kingdom.

POWELL, R. A., AND M. S. MITCHELL. 1998. Topographical constraints and home range quality. Ecography 21:337–341.

POWELL, R. A., J. W. ZIMMERMAN, AND D. E. SEAMAN. 1997. Ecology and behaviour of North American black bears: home ranges, habitat and social organization. Chapman & Hall, London, United Kingdom.

PUGH, S. R., S. JOHNSON, AND R. H. TAMARIN. 2003. Voles (*Microtus* species). Pp. 349–370 in Wild mammals of North America: biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.

PULLIAINEN, E. 1984. Use of the home range by pine martens (*Martes martes* L.). Acta Zoologica Fennica 171:271–274.

REAL, L. A. 1996. Paradox, performance, and the architecture of decision-making in animals. American Zoologist 36:518–529.

REID, M. L., AND P. J. WEATHERHEAD. 1988. Topographical constraints on competition for territories. Oikos 51:115–117.

ROGERS, L. L., AND G. W. WILKER. 1990. How to obtain behavioral and ecological information from free-ranging, researcher-habituated black bears. Bear Research and Management 8:321–328.

RYAN, S. J., C. U. KNECHTEL, AND W. M. GETZ. 2006. Range and habitat selection of African buffalo in South Africa. Journal of Wildlife Management 70:764–776.

SAARENMAA, H., ET AL. 1988. An artificial intelligence modelling approach to simulating animal/habitat interactions. Ecological Modelling 44:125–141.

SARGOLINI, F., ET AL. 2006. Conjunctive representation of position, direction, and velocity in entorhinal cortex. Science 312:758–762.

SEAMAN, D. E., AND R. A. POWELL. 1996. Accuracy of kernel estimators for animal home range analysis. Ecology 77:2075–2085.

SETON, E. T. 1909. Life-histories of northern animals. An account of the mammals of Manitoba. Charles Scribner's Sons, New York.

SILVERMAN, B. W. 1990. Density estimation for statistics and data analysis. Chapman & Hall, Ltd, London, United Kingdom.

SOLSTAD, T., C. N. BOCCARA, E. KROPFF, M.-B. MOSER, AND E. I. MOSER. 2008. Representation of geometric borders in the entorhinal cortex. Science 322:1865–1868.

SOULSBURY, C. D., P. J. BAKER, G. IOSSA, AND S. HARRIS. 2008. Fitness costs of dispersal in red foxes (*Vulpes vulpes*). Behavioral Ecology and Sociobiology 62:1289–1298.

SOUTH, A. 1999. Extrapolating from individual movement behaviour to population spacing patterns in a ranging mammal. Ecological Modelling 117:343–360.

SPENCER, A. R., G. N. CAMERON, AND R. K. SWIHART. 1990. Operationally defining home range: temporal independence exhibited by hispid cotton rats. Ecology 71:1817–1822.

SPENCER, W. D. 2012. Home ranges and the value of spatial information. Journal of Mammalogy 93:929–947.

STAMPS, J. A. 1987. Conspecifics as cues to territory quality: a preference of juvenile lizards (*Anolis aeneus*) for previously used territories. American Naturalist 129:629–642.

STILLMAN, T. A., J. D. GOSS-CUSTARD, AND J. ALEXANDER. 2000. Predator search pattern and the strength of interference through prey depression. Behavioral Ecology 11:597–605.

SUMNER, F. B., AND J. J. KAROL. 1929. Notes on the burrowing habits of *Peromyscus polionotus*. Journal of Mammalogy 10:213–215.

TAYLOR, C. R., K. SCHMIDT-NIELSEN, AND J. L. RABB. 1970. Scaling the energetic cost of running to body size in mammals. American Journal of Physiology 219:1104–1107.

TURNER, M. G., Y. WU, L. L. WALLACE, W. H. ROMME, AND A. BRENKERT. 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. Ecological Applications 4:472–496.

VAN DER MERWE, M., AND J. S. BROWN. 2008. Mapping the landscape of fear of the cape ground squirrel (*Xerus inauris*). Journal of Mammalogy 89:1162–1169.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.

WITH, K. A., AND T. O. CRIST. 1996. Translating across scales: simulating species distributions as the aggregate response of individuals to heterogeneity. Ecological Modelling 93:125–137.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.