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Paul R. Moorcroft & Mark A. Lewis:
Mechanistic Home Range Analysis

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CHAPTER ONE

Introduction

The advent of radio telemetry in the late 1950s revolutionized the study of animal movement, enabling the systematic measurement of animal movement patterns (Cochran and Lord 1963). Following its introduction, telemetry rapidly became a mainstay in wildlife studies and now is routinely used to track the movements of a variety of animals, including ungulates, rodents, primates, and carnivores (Macdonald et al. 1980; Millspaugh and Marzluff 2001). Telemetry has also been successfully used to study the movements of birds, reptiles, amphibians, fish, and even insects (Priede and Swift 1993). The recent development of global positioning system (GPS)–based telemetry is further enhancing its scope, allowing ecologists and wildlife biologists to accurately track animal movements over any distance, under all weather conditions, and in any terrain (Rodgers et al. 1996; Girard et al. 2002).

As in other mammalian groups, telemetry studies have documented a diverse array of patterns of space use among carnivores (Macdonald et al. 1980). For example, figure 1.1 shows estimates of home range size for three northern hemisphere canids: red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), and gray wolves (*Canis lupus*). The home range sizes of these three species alone vary over three orders of magnitude, from a few square kilometers to over a thousand square kilometers, reflecting both intra- and interspecific differences in home range size: red fox home ranges vary between 2 and 16 km², overlapping the distribution of coyote range sizes, which span a 30-fold range between 2.5 and 70 km². Wolf territories are larger still, varying between 80 and 1800 km².

While the between-species differences in home range size seen in figure 1.1 can be accounted for by differences in body size (Gittleman and Harvey 1982; Gittleman 1985; Kelt and Vuren 2001), the substantial degree of intraspecific variation in home range size exhibited by all three of the species is testimony to the ability of carnivores to adjust their patterns of space use in response to the local environmental and social conditions they experience (Sheldon 1992). In addition to varying in size, carnivore home ranges also vary in degree of exclusivity, from loosely defended overlapping home ranges to non-overlapping territories that may be defended by individuals, pairs, or groups (Macdonald and Moehlman 1973; MacDonald 1983; Moehlman 1989). As in other groups

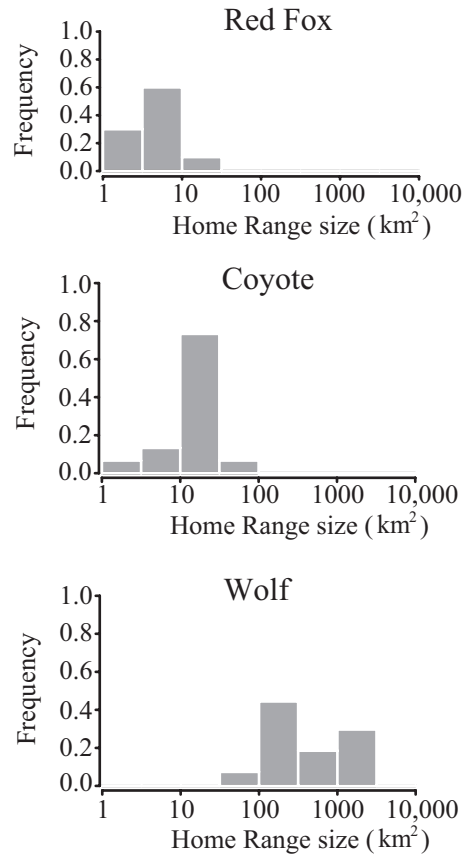


FIGURE 1.1. Frequency distribution home range sizes reported for red foxes, coyotes, and wolves.

of mammals, these differences in space use exert a powerful influence on carnivore population structure, affecting their social organization, mating systems, and demography (Bekoff and Daniels 1984; Rubenstein and Wrangham 1986; Clutton-Brock 1989).

1.1. STATISTICAL HOME RANGE ANALYSIS

Estimates of home range size such as those in figure 1.1 come from statistical home range models, which convert spatial distributions of telemetry relocations into an estimate of range size. A number of different models have been developed, including, most famously, the minimum convex polygon method (Odum and Kuenzler 1955), and subsequently, a variety of density estimation

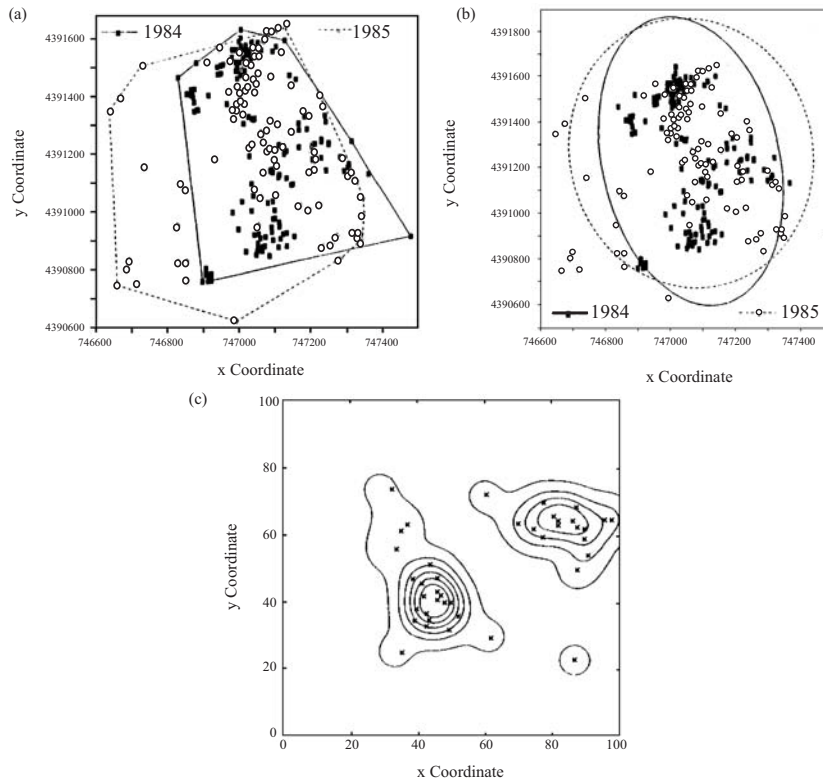


FIGURE 1.2. Examples of statistical home range models. (a) Minimum convex polygon method, (b) bivariate normal method, (c) kernel method. Redrawn from White and Garrott (1997) (panels a and b) and Worton (1989) (panel c).

models such as the bivariate normal (Jennrich and Turner 1969), harmonic mean (Dixon and Chapman 1980), and kernel home range models (Worton 1989)—see MacDonald (1980a), Worton (1987), and Kernohan et al. (2001) for reviews. Examples of these techniques are shown in figure 1.2.

While statistical home range models such as those depicted in this figure provide a useful way to summarize telemetry data, their descriptive nature means that the models have no theoretical or predictive value. Relocation datasets contain a wealth of fine-scale information on the precise spatial and temporal sequence of movements by individuals in relation to their environment and conspecifics. However, virtually all of this detailed biological information is lost when the observations are summarized into aggregate measures of home range size and home range overlap calculated using a statistical home range model (though see Marzluff et al. 2001). As a result, it has been impossible to quantify the underlying determinants of animal space use patterns in anything other than the most coarse-grained manner.

Moreover, statistical home range models are problematic even as descriptors, producing widely differing portraits of an animal's home range and varying estimates of home range size and overlap (Schoener 1981; Samuel et al. 1985). Issues include the treatment of outliers in minimum convex polygon methods, the long tails of the bivariate normal distribution, the problem of negative values in harmonic mean estimates, and appropriate levels of smoothing in kernel methods (Schoener 1981; Worton 1989; Kernohan et al. 2001). However, since the distributions used to characterize the data are purely statistical, there is no biological basis for preferring one statistical home range model over another.

In the 1980s an alternative to conventional statistical home range analysis emerged in the form of resource selection analysis (Johnson 1980). In contrast to the descriptive but spatially explicit approach of traditional home range models, resource selection analysis takes a phenomenological, spatially implicit approach to analyzing patterns of space use, identifying habitats and areas used disproportionately in relation to their availability. These analyses can be conducted at a variety of spatial scales including the scale of an individual's home range, sometimes referred to as "third-order" selection (Erickson et al. 2001). As results from a number of studies have shown, the phenomenological, "frequentist" approach of resource selection analysis provides a framework for identifying associations between relative space use by individuals and different forms of environmental spatial heterogeneity such as habitat type, topography, and resource availability (Manly et al. 1993; Cooper and Millspaugh 2001; Erickson et al. 2001). However, the phenomenological and spatially implicit nature of resource selection models limits their predictive capability and their ability to make full use of the biologically rich information contained within telemetry datasets.

1.2. MECHANISTIC HOME RANGE ANALYSIS

A promising alternative to both conventional statistical home range analysis and resource selection analysis is the development of mechanistic home range models. The origins of these models lie in the mathematical analysis of correlated random walks, in which the motion of individual animals is characterized as a sequence of movements at different speeds, orientations, and turning frequencies (Skellam 1951; Skellam 1973; Okubo 1980; Okubo and Levin 2001). The term "correlated random walk" indicates that the locations of an individual are correlated in time and that the individual's rules of movement are stochastic, specified in terms of probability distributions of movement directions, speeds, and rates of turning. This approach has been used to study the movements of cells and microorganisms (Berg and Brown 1974; Alt 1980; Berg 1993; Othmer and Stevens 1997; Hill and Hader 1997; Anderson and Chaplain 1998;

Palsson and Othmer 2000) and insects (Kareiva and Shigesada 1983; Marsh and Jones 1988; Turchin 1998); however, using correlated random walks to study the movements of vertebrates is still in its infancy (Couzin and Krause 2003, though see Gueron and Levin 1993).

The models are mechanistic in the sense that the pattern of space use by an animal is calculated by an explicit mathematical scaling of these underlying rules of movement. Thus unlike instatistical home range models, the patterns of space use obtained from mechanistic home range models are not arbitrary distributions but rather reflect the pattern of space use that results from the underlying set of rules governing the individual's movement, which may incorporate responses to both local and non-local orientation cues (Okubo 1980; Levin and Pacala 1996). This reductionist methodology captures the biological reality that the spatial distribution of relocations in each telemetry dataset shown in figure 1.2 is a macroscopic pattern, the net result of a vast number of movement decisions in response to a variety of environmental and social factors that have influenced the animal as it traversed the landscape.

As we illustrate in this book, mechanistic home range models offer a way to directly integrate theoretical and empirical investigations of animal home range studies. Using this framework, it is possible to formulate models that reflect different hypotheses for the ecological and social factors influencing movement behavior, examine how these alter patterns of space use, then test their predictions against both fine-scale, high-frequency relocation data and, at larger scales, against long-term relocation datasets. In recognizing the macroscopic, scaled nature of home range patterns, mechanistic home range models allow for a more comprehensive use of empirical home range data than statistical home range models. More fundamentally, they also provide the necessary theoretical framework for developing a predictive theory of animal space use.

Through the course of this book we develop and analyze a series of mechanistic home range models for carnivores. We begin in chapter 2 by describing the mathematical procedures for formulating mechanistic home range models from stochastic, individual-based models of animal movement behavior. We then use these methods in chapter 3 to derive a simple mechanistic home range model in which individuals preferentially move in the direction of a home range center, and analyze the properties and predictions of this model, comparing the model's predictions to datasets of red fox and coyote relocations. In chapter 4, we develop an alternative model formulation that incorporates a conspecific avoidance response to foreign scent marks, and compare the fit of this model to the coyote relocation dataset with the fit obtained with the simple model developed in the previous chapter. Chapter 5 examines the properties of the conspecific avoidance model in more detail, using numerical simulations to explore how patterns of space use and scent marks are affected by the movement and behavior of individuals, population density, and location of

neighboring home ranges. The qualitative properties of the conspecific avoidance model are then analyzed in chapter 6 by applying analytical methods to a simplified one-dimensional version of the model. In chapter 7, the conspecific avoidance model is extended to incorporate the effects of spatial heterogeneity, taking into consideration such features as terrain characteristics and resource density, and test these more detailed model formulations against observations of coyotes in Yellowstone National Park. The next three chapters are more speculative. In chapter 8, we explore a mechanistic home range model formulation for carnivores in which home ranges arise in the absence of a den site or core area. We then turn our attention to secondary ecological interactions in chapter 9, considering how home range patterns in carnivore populations can have community-level consequences, influencing the spatial distribution of both prey and competitors. In chapter 10, we revisit the localizing tendency model introduced in chapter 3 and establish some connections between the model's predictions and classical statistical measures of space use such as the minimum convex polygon and mean squared displacement. In chapter 11, we illustrate how mechanistic home range models can be combined with game theory to examine the functional significance of different movement strategies and determine evolutionary stable patterns of space use. Finally, in chapter 12, we outline some avenues for future research and discuss some of the broader implications of the mechanistic approach to home range analysis. Mathematical details of calculations are given in appendices A through H.