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# 1 Introduction

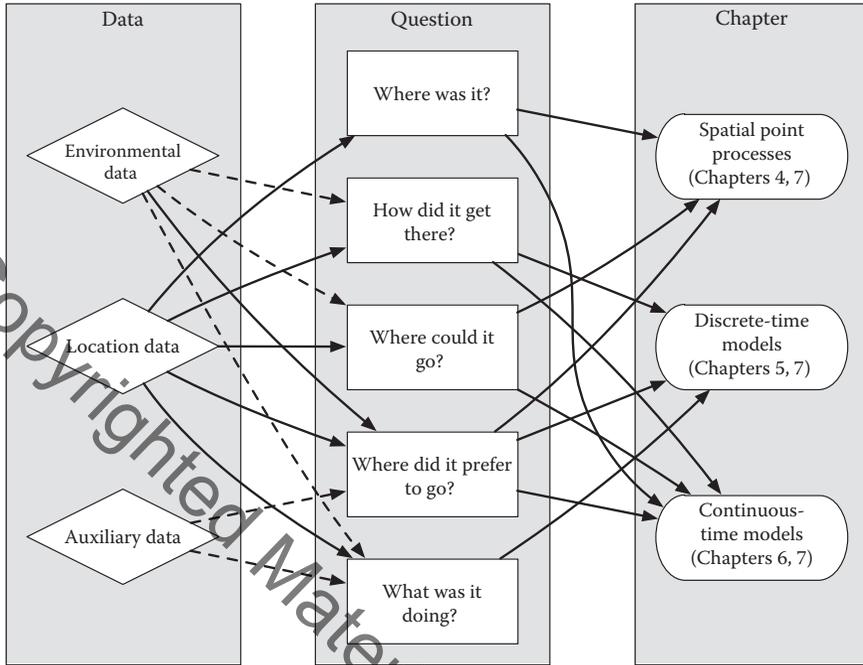
The movement of organisms is a fundamentally important ecological process. Voluntary movement is a key feature that distinguishes organisms from inorganic objects, and it is a critical aspect of animal biology and ecology. Humans have been keenly interested in the movement of individual animals and populations for millennia. Over 2000 years ago, Aristotle wrote about the motion of animals, and the associated philosophical and mathematical concepts, in his book, *De Motu Animalium* (Nussbaum 1978). Historically, it was critical to understand how and where wild food sources could be obtained. Thus, early humans were natural animal movement modelers. In modern times, we are interested in the movement of animals for scientific reasons and for making decisions regarding the management and conservation of natural resources (Cagnacci et al. 2010).

The study of wild animals can be challenging. Animals are often elusive and reside in remote or challenging terrain. Many animals have learned to minimize exposure to perceived threats, which, unfortunately for us, include the well-intentioned biologist approaching them with binoculars or a capture net. Therefore, it is no surprise that the development of animal-borne telemetry devices has revolutionized our ability to study animals in the wild (Cagnacci et al. 2010; Kays et al. 2015). Animal telemetry has helped us overcome many of the practical, logistical, and financial challenges of direct field observation. Telemetry data have opened windows that allow us to address some of the most fundamental ecological hypotheses about space use (“Where is the animal?”), movement (“How did the animal get there?” “Where could it go?”), resource selection (“Where does the animal like to be?”), and behavior (“What is the animal doing?”) (Figure 1.1).

## 1.1 BACKGROUND ON ANIMAL MOVEMENT

Animal movement plays important roles in the fitness and evolution of species (e.g., Nathan et al. 2008), the structuring of populations and communities (e.g., Turchin 1998), ecosystem function (Lundberg and Moberg 2003), and responses to environmental change (e.g., Thomas et al. 2004; Trakhtenbrot et al. 2005; Jönsson et al. 2016). The scientific study of animal movement has a deep history, and we are unable to explore all of the ecological implications and methodological developments in a single volume. Instead, we will focus on several specific inferential methods that can provide valuable ecological insights about animal movement and behavior from telemetry data.

The importance of animal movement in larger-scale ecosystem function probably inspired the Craighead brothers to develop and deploy the first radio collars on grizzly bears (*Ursus arctos*) from Yellowstone National Park in the 1960s (Craighead and Craighead 1972). Satellite tracking devices are now capable of pinpointing animal locations at any moment, remote sensing provides ever refined environmental



**FIGURE 1.1** Relationships among data types, analytical methods, and some fundamental questions of movement ecology. Location data are the cornerstone of all of the analysis methods described in this book. Environmental data, such as those acquired from remote sensing, are useful in drawing connections between animals and their surroundings. Auxiliary biotelemetry data, such as accelerometer or dive profile data, can help address questions about animal behavior. Dashed lines indicate where data can be helpful for addressing particular questions, but are not essential.

data, and biotelemetry tags allow for the simultaneous collection of important physiological and behavioral information from wild animals. These technological advances will lead to a better understanding of how individual decisions affect demographic parameters and ultimately translate into population dynamics. In this sense, animal movement can provide the long-sought bridge between behavior, landscape ecology, and population dynamics (Lima and Zollner 1996; Wiens 1997; Morales et al. 2010; Kays et al. 2015).

In what follows, we provide a brief summary of research findings, existing knowledge, and analytic approaches for important aspects of animal movement ecology. We organized these topics into 10 sections:

1. Population dynamics
2. Spatial redistribution
3. Home ranges, territories, and groups
4. Group movement and dynamics
5. Informed dispersal and prospecting

6. Memory
7. Individual condition
8. Energy balance
9. Food provision
10. Encounter rates and patterns

### 1.1.1 POPULATION DYNAMICS

In classical models of population dynamics, predators and prey encounter each other in proportion to their overall abundance over space and reproductive rates decrease as the global population density increases. This is because traditional models of population and community dynamics assume we are dealing with many individuals that are well mixed (Turchin 2003). Such “mean field” representations of population dynamics can provide good approximations when the physical environment is relatively homogeneous and organisms are highly mobile, or when organisms interact over large distances. However, when the external environment or the limited mobility of organisms results in lack of mixing, the conditions experienced by a particular member of a population or community can be quite different from the mean (Lloyd 1967; Ovaskainen et al. 2014; Matthiopoulos et al. 2015). That is, when *per capita* vital rates are affected by varying local conditions, the observed population and community dynamics can differ markedly from mean field predictions.

Population dynamics involve births, deaths, immigration, and emigration; modern tracking technology, together with new statistical models, can greatly improve our understanding of these processes. The individuals that comprise a population can vary in several traits and individual behavior can change in response to internal and external stimuli. Individual traits and behavior determine the way they interact with the environment and other organisms while the conditions that individuals experience ultimately translate to their performance (i.e., growth, survival, and reproduction).

Survival analysis can be used to model changes in hazard with time and in relation to covariates such as location, age, body condition, and habitat type. Detailed tracking through satellite telemetry enables spatial information and survival data to be combined at small temporal scales, leading to an increasingly sophisticated understanding of the determinants of survival (Murray 2006; Haydon et al. 2008; Schick et al. 2013). Likewise, changes in movement behavior can be used to infer reproductive events in some species (Long et al. 2009). However, to take full advantage of these data, new analytic techniques should take into account the sequential nature of individual survival and reproduction. For example, the chance of an animal dying of starvation depends on its history of encounters with food items and foraging decisions.

Coupling demographic data with movement models is an area of active research, but is still somewhat nascent. Spatial capture–recapture (SCR) models provide a way to formally connect animal encounter data with movement processes; we refer the interested reader to Royle et al. (2013) and references therein for additional details. The methods presented in this book will be critical for formally integrating location data and demographic data in future SCR modeling efforts.

### 1.1.2 SPATIAL REDISTRIBUTION

Classical reaction–diffusion models, such as those used by Fisher (1937) to describe the spread of an advantageous mutation within a population assume that mortality and recruitment rates depend linearly on local population density and that individuals move at random over a large and homogeneous area. Early implementations of these models were also used to describe the dynamics of population invasion and range expansion (e.g., Skellam 1951; Andow et al. 1990; Shigesada and Kawasaki 1997), and later, were embedded in a hierarchical statistical modeling framework (e.g., Wikle 2003; Hooten and Wikle 2008; Hooten et al. 2013a) to provide inference about spreading populations.

Diffusion equations have been justified as a good approximation to the displacement of individuals performing a “random walk.”\* Although we know that animals do not move at random, the diffusion approximation can still be sufficient at certain (usually large) scales and also serves as a null model to compare with more complex models (Turchin 1998).

More general forms of movement can be taken into account by formulating spatial population models as integral equations. These have commonly been formulated in discrete time, yielding integro-difference equations where local population growth is combined with a “redistribution kernel” that describes the probability that an individual moves from its current location to another one in a given time-step.† The temporal scale of these models is usually set to match reproductive events so that the redistribution kernel represents successful dispersal rather than regular movement. A great deal of theoretical and empirical work has explored the consequences of kernel shape, particularly in the tail of the distribution, on invasion speed (Kot et al. 1996; Powell and Zimmermann 2004).

There are many ways to make spatial population models more realistic and appropriate for particular species, places, and scales of interest. A good starting point is to consider the spatial structure of the population, which is generally accepted as an important prerequisite for more accurate ecological predictions (Durrett and Levin 1994; Hanski and Gaggiotti 2004).‡ The spatial structure of populations can range from classical closed populations to a set of subpopulations with different degrees of interaction (Thomas and Kunin 1999). As different degrees of connectivity among subpopulations can have important dynamical consequences, researchers are increasingly interested in understanding how connectivity arises from the interaction among individual phenotypes, behaviors, and the structure of landscapes.

One particular feature of the models described so far is that every individual is assumed to move according to the same kernel (whether Gaussian or otherwise). However, detailed tracking of individual movements consistently reveals differences among individuals. Theoretical and empirical studies have shown how the characteristics of redistribution kernels can depend on differences among individuals (Skalski

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\* We describe random walks in discrete and continuous time in Chapters 5 and 6.

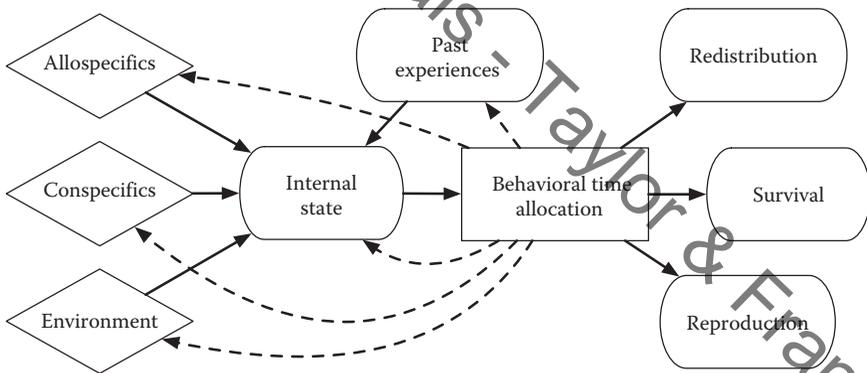
† We describe redistribution kernels and integral equation models for movement in Chapters 4 and 6.

‡ See Chapter 2 for a brief primer on spatial statistics.

and Gilliam 2000; Fraser et al. 2001; Morales and Ellner 2002; Delgado and Penneriani 2008), and on the interplay between individual behavior and features of the underlying landscape (Johnson et al. 1992; McIntyre and Wiens 1999; Fahrig 2001; Ricketts 2001; Morales et al. 2004; Mueller and Fagan 2008), including reactions to habitat boundaries (Schultz and Crone 2001; Morales 2002; Schtickzelle and Baguette 2003; Ovaskainen 2004; Haynes and Cronin 2006). In particular, population heterogeneity produces leptokurtic (i.e., heavy tailed) redistribution kernels when a subset of individuals consistently moves longer distances than others (Skalski and Gilliam 2000; Fraser et al. 2001).

Several factors can explain why two individuals belonging to the same population move differently. They may be experiencing different environments of heterogeneous landscapes; they can also have different phenotypes or condition, different past experiences (e.g., Frair et al. 2007), or even different “personalities” (Fraser et al. 2001; Dall et al. 2004). In a theoretical study, Skalski and Gilliam (2003) modeled animals switching between fast and slow random walk movement states and found that the resulting redistribution kernel depended on the total time spent in each of the states and not on the particular sequence of changes. This theoretical result highlights the importance of animals’ time budgets for scaling movement processes (Figure 1.2).

It is common to consider that individuals have a small set of movement strategies (Blackwell 1997; Nathan et al. 2008), and the time allocation to these different behaviors (or “activity budgets”) can depend on the interaction between their motivation



**FIGURE 1.2** Mechanistic links between animal movement and population dynamics adapted from Morales et al. (2010). We consider an unobserved individual internal state that integrates body condition (e.g., energy reserves, reproductive status). Several factors affect the dynamics of this internal state, including social interactions with conspecifics, trophic or other interaction with allospecifics (other species), and abiotic environmental effects and dynamics. Internal state dynamics determine the organism’s time allocation to different behaviors (e.g., food acquisition, predator avoidance, homing, and landscape exploration) but is also modulated by past experiences and phenotypic trails such as behavioral predispositions. As different behaviors imply different movement strategies, the time budget determines the properties of the spatial redistribution that describes space use. Time allocation to different behaviors also affect individual survival and reproduction, and hence, overall population dynamics.

and the structure of the landscape they occupy (Morales et al. 2004, 2005). The results of Skalski and Gilliam (2003) imply that knowing the fraction of time allocated to each behavior makes it possible to derive suitable redistribution kernels.

A common reaction in the visual inspection of movement data is to intuit that individuals are moving differently at different times. As a result, several techniques (including many *ad hoc* procedures) have been developed to identify and model changes in movement behavior from trajectory data (reviewed in Patterson et al. 2008; Schick et al. 2008; Gurarie et al. 2016). Clustering models, such as those we describe in Chapter 5, can be difficult to reliably implement, because biologically different movement behaviors can lead to very similar trajectories. For example, it can be difficult to distinguish relative inactivity (e.g., resting) from intense foraging, within a small patch, based on horizontal trajectory alone. However, as physiological and other information becomes available through biotelemetry devices, we may gain greater insight into how animals allocate time to different tasks and how this allocation changes in different environments (McClintock et al. 2013), thus providing a mechanistic way to model redistribution kernels conditional on individual state.

Another result from Skalski and Gilliam (2003) is that a mixture of movement states converges to simple diffusion if given enough time. The sum of  $n$  independent and identically distributed random variables with finite variance will be Gaussian distributed as  $n$  increases. Thus, if all individuals in a population move according to the same stochastic process, we would expect that, at some time after the initiation of movement, the distribution of distance moved becomes Gaussian because the distance traveled is the sum of movement vectors. However, this depends on the rate of convergence and independence assumption. Still, similar results may relate to the interaction between individual behavior and landscape structure (Morales 2002; Levey et al. 2005) and are the focus of ongoing research.

We return to redistribution kernels for animal movement in Chapters 4 through 6. In particular, we consider spatial redistribution from three different perspectives (i.e., point processes, discrete-time processes, and continuous-time processes) and highlight the relevant literature associated with each. We also show how to scale up from Lagrangian to Eulerian models for movement in Chapter 6.

### 1.1.3 HOME RANGES, TERRITORIES, AND GROUPS

Many animals have clearly defined home ranges or territories (Borger et al. 2008). If not, they usually exhibit some form of site fidelity and revisitation patterns that are not captured by simple random walks. Most likely, these animals will spend their reproductive life in a region that is small compared to their movement capabilities. Substantial progress has been made in developing mechanistic models of animal movement with territorial behavior (e.g., Moorcroft et al. 1999; Smouse et al. 2010; Moorcroft and Lewis 2013; Giuggioli and Kenkre 2014). However, territoriality models typically describe the space use by particular individuals (or members of a wolf pack, for example) rather than an entire population. As a result, they have not yet been linked to models of population demography.

For territorial animals, the carrying capacity of a particular region or landscape can be determined by competition for space. When the environment provides a limited

number of essential items, such as nest cavities, the maximum number of breeders is bounded and surplus individuals form a population of nonbreeders referred to as “floaters” (Brown 1969; Penteriani and Delgado 2009). When dispersal or mortality create vacancies in previously occupied territories, floaters may become a crucial population reserve for filling these empty territories. Floaters can also have a negative effect on population growth through interference, conflict, or disturbance. Furthermore, the aggressive behavior of breeders can also decrease the carrying capacity of the population.

We describe basic methods for estimating home ranges and core areas in Chapter 4, and discuss methods for modeling interactions among individuals at the end of Chapter 5. However, the formal statistical modeling of floaters, together with individual-level behavior and territoriality is still developing and an open area of research.

### 1.1.4 GROUP MOVEMENT AND DYNAMICS

Understanding the distribution of social animals over landscapes requires scaling up from individual movement patterns to groups of individuals and populations (Okubo et al. 2001). Most models of group dynamics focus on relatively short temporal scales (Couzin et al. 2005; Eftimié et al. 2007; Strandburg-Peshkin et al. 2015). However, the interaction between the group structure of a population and the movement of individuals is also relevant at longer time scales (e.g., Fryxell et al. 2007). Long time scales in group dynamics are particularly relevant for reintroduced species, where a balance of spread and coalescence processes will determine how individuals distribute themselves over the landscape. Often, individual survival and fecundity are higher in groups, so that the successful persistence of the introduced population may depend on coalescence dominating and limiting the spreading process, thereby enabling the establishment of a natural group structure within the release area. Haydon et al. (2008) developed movement models for North American elk (*Cervus canadensis*), reintroduced to Ontario, where as in Morales et al. (2004), animals can switch between exploratory (large daily displacements and small turning angles) and encamped behavior (small daily displacements and frequent reversals in direction). The rate of switching among these movement modes depended on whether individuals were part of a group or not. Haydon et al. (2008) combined their movement models with analysis of mortality and fecundity to build a spatially explicit, individual-based model for the dynamics of the reintroduced elk population. Their analysis showed that elk moved farther when they were solitary than when they were in a group, and that mortality risk increased for individuals that moved progressively away from the release location. The simulation model showed how the population rate of increase and the spatial distribution of individuals depended on the balance of fission and fusion processes governing group structure.

New approaches for studying the interaction among individuals in groups are appearing regularly in the literature. For example, Scharf et al. (2015) developed a discrete-time model that captures the alignment and attraction of killer whales (*Orcinus orca*) in Antarctica, and Russell et al. (2016) used point processes to model interactions among individual guppies (*Poecilia reticulata*). Using high temporal resolution telemetry data from a group of baboons (*Papio anubis*) in Kenya,

Strandburg-Peshkin et al. (2015) analyzed individual movement in relation to one another. They found that, rather than following dominant individuals, baboons are more likely to follow others when multiple initiators of movement agree, suggesting a democratic collective action emerging from simple rules. In a study of fission–fusion dynamics of spider monkeys (*Ateles geoffroyi*), Ramos-Fernández and Morales (2014) found that group composition and cohesion affected the chance that a particular individual will leave or join a group. As another example, Delgado et al. (2014) found that dispersing juveniles of eagle owl (*Bubo bubo*) were generally attracted to conspecifics, but the strength of attraction decreased with decreasing proximity to other individuals. However, statistical models for animals that decide to leave their territory or abandon a group, and how they explore and choose where to establish new territories or home ranges, have yet to appear in the literature.

### 1.1.5 INFORMED DISPERSAL AND PROSPECTING

Dispersal involves the attempt to move from a natal or breeding site to another breeding site (Clobert 2000), and is essential for species to persist in changing environments (Ronce 2007). The redistribution modeling ideas we introduced in the previous sections represent dispersal as a random process that may be sensitive to the spatial structure of the landscape or the presence of conspecifics. However, there is a great deal of evidence indicating that individuals are capable of sophisticated and informed decision-making when choosing a new place to live (Bowler and Benton 2005; Stamps et al. 2005, 2009). Clobert et al. (2009) proposed the concept of “informed dispersal” to convey the idea that individuals gather and exchange information at all three stages of dispersal (i.e., departure, transience, and settlement). Thus, movement involves not only the exchange of individuals among habitat patches but also information transfer across the landscape. Animals can acquire information about the environment by “looking” at others’ morphology, behavior, or reproductive success (Danchin et al. 2004; Dall et al. 2005). For example, in an experiment with the common lizard (*Lacerta vivipara*), Cote and Clobert (2007) quantified emigration rate from artificial enclosures that received immigrants. They found that when local populations received immigrants that were reared under low population density, the emigration rate of the local population increased, providing evidence that immigrants supplied information about the density of surrounding populations, probably via their phenotype.

We only have a rudimentary understanding of how individuals integrate different sources of information to make movement and dispersal decisions. Long-term tracking is needed to study how animals adjust to the changing characteristics of their home ranges or territories, and under what conditions they are likely to search for a new home. Detailed tracking of juveniles may shed light on the processes of exploration (i.e., transience) and settlement. In particular, movement data can be used to test ideas about search strategies, landscape exploration, and the importance of past experience in biasing where animals decide to attempt breeding.

### 1.1.6 MEMORY

The importance of previous experiences and memory is increasingly being recognized and explicitly considered in the analysis of telemetry data (e.g., Dalziel

et al. 2008; McClintock et al. 2012; Avgar et al. 2013; Fagan et al. 2013; Merkle et al. 2014). Smouse et al. (2010) provide a summary of the approaches used to include memory in movement models. Formulating memory models has largely been a theoretical exercise but the formal connection with data is possible. For example, the approach used to model the effect of scent marking in mechanistic home range models (Moorcroft and Lewis 2013) could be easily adapted to model memory processes. Avgar et al. (2015) fit a movement model that included perceived quality of visited areas and memory decays to telemetry data from migrating Caribou. It is less clear what role memory plays in population dynamics.

Forester et al. (2007) describe how certain discrete-time movement models can be reformulated to provide inference about memory. We explain these ideas in Chapter 5. In continuous-time models, Hooten and Johnson (2016) show how to utilize basis function specifications for smooth stochastic processes to represent different types of memory and perception processes. We discuss these functional movement modeling approaches in Chapter 6.

### 1.1.7 INDIVIDUAL CONDITION

Recognizing that the contribution of a particular individual to the population is a function of its fitness has historically promoted the development of physiological, age, and stage structured population models (Caswell 2001; Ellner and Rees 2006; Metz and Diekmann 2014). Body condition integrates nutritional intake and demands, affecting both survival and reproduction. For example, studies of ungulates living in seasonal environments have found that percent body fat in early winter is a very good predictor for whether animals die, live without reproducing, or live and reproduce (Coulson et al. 2001; Parker et al. 2009). Also, many populations show “carryover effects” where conditions experienced during a time period influence vital rates in future periods, which has the potential to generate many different population responses (Ratikainen et al. 2008; Harrison et al. 2011). Movement decisions and habitat use affect energy balance and body condition in animals. Linking individual condition to movement and space use is challenging because we usually need to recapture individuals to assess percent body fat, for example. However, some marine mammals perform “drift dives,” using their buoyancy to change depth without active propulsion and with their rate of drift determined largely by their lipid-to-lean-mass ratio Biuw et al. (2003). Working with Southern elephant seals *Mirounga leonina*, Schick et al. (2013) modeled changes in individual condition as a function of travel distance and foraging events. They also linked changes in behavior due to human disturbances to population-level effects.

The animal movement models we describe in Chapters 4 through 6 are mostly focused on modeling individuals. However, when scaling up inference to the population level (using random effects for parameters or other hierarchical modeling approaches), it may be important to account for variation in body condition among individuals to help describe differences in movement parameters. For example, see Sections 4.5 and 5.2 for examples of accounting for individual-level differences when obtaining inference at the population level.

### 1.1.8 ENERGY BALANCE

Many aspects of life history evolution, behavioral ecology, and population dynamics depend on how individuals consume resources and on how they allocate energy to growth and reproduction. Food acquisition is an important driver of animal movement to the point that relationships between scaling of space use and daily distance traveled in relation to body mass and trophic requirements has been hypothesized (Jetz et al. 2004; Carbone et al. 2005).

Technological developments in biotelemetry allows the possibility of observing a suite of relevant physiological data such as heart rate and core temperature, in addition to individual location (Cooke et al. 2004; Rutz and Hays 2009). Furthermore, accelerometers can be used for detailed movement path reconstruction and for recording energy expenditure, activity budgets (i.e., ethograms), and rare behavioral events such as prey captures (Wilson et al. 2007, 2008; Williams et al. 2014; Bidder et al. 2015). Combined with detailed environmental maps, these data could lead to empirically based models of animal performance in the wild, linking behavioral decisions with space use, survival, and reproduction (Figure 1.2).

The formal integration of energy balance information into dynamic statistical animal movement models is still in early development stages (Shepard et al. 2013). However, many approaches we describe in Chapters 4 through 6 allow for the use of auxiliary data pertaining to energy-intensive behavior. For example, Section 5.2.5 describes how to integrate dive data for marine mammals into discrete-time movement models.

### 1.1.9 FOOD PROVISION

Food acquisition in poor habitats (or in good habitats that have been depleted) demands more searching time and energy, which is reflected in their movement patterns (e.g., Powell 1994). These effects are best documented in central place foragers such as nesting birds or pinnipeds that forage at sea but breed on land. Many of these animals forage at particular oceanographic features (Boersma and Rebstock 2009) that change in location and quality from year to year. Magellanic penguins (*Spheniscus magellanicus*) breeding at Punta Tombo, Argentina showed a decrease in reproductive success with increasing average foraging trip duration (Boersma and Rebstock 2009). Also, penguins stayed longer at feeding sites in more distant foraging areas, presumably to feed themselves and recover from the increased cost of swimming (Boersma and Rebstock 2009). Thus, satellite telemetry technology has allowed a better understanding of the interplay between landscape or seascape variability and breeding success.

In Chapter 5, we show how to use discrete-time movement models to cluster animal paths into different behavioral types, which can help identify food acquisition modes based on telemetry data. We also demonstrate how to account for food-related aspects of movement in the continuous-time setting discussed in Chapter 6.

### 1.1.10 ENCOUNTER RATES AND PATTERNS

The “functional response” is a key component of population models that include trophic interactions; it describes the rate of prey consumption by individual predators

as a function of prey density (Holling 1959a,b). The dynamics and persistence of interacting populations usually depend on the shape and dimensionality of functional responses (Turchin 2003). Mechanistically, the functional response depends on encounter rates. Thus, a useful null model for encounter rates is one where individuals move randomly and independently of each other. More than 150 years ago, Maxwell (1860) calculated the expected rates of molecular collisions of an ideal gas as a function of density, particle size, and speed.\* The ideal gas model has been used and rediscovered in many ways, including Lotka's justification of predator-prey encounters being proportional to predator speed and size and to predator and prey densities. As a recent example, the scaling of home ranges with body size derived by Jetz et al. (2004) assumes that the proportion of resources lost to neighbors is related to encounter rates as calculated from the ideal gas model for known scaling relationships of speed, population density, and detection distance.

The thorough review by Hutchinson and Waser (2007) shows many more examples of the application of Maxwell's model plus several refinements, including different assumptions about detection, speed, and density. Recently, Gurarie and Ovaskainen (2013) presented analytical results and a taxonomy for a broad class of encounter processes in ecology. The movement of animals almost certainly deviates from the assumptions of Maxwell's model and we can use information about the characteristics of movement paths from real animals to derive better predictions of encounter rates, or in the case of carnivores, kill rates (e.g., Merrill et al. 2010).

Environmental heterogeneity can also be an important determinant in encounter rates and group dynamics. For example, Flierl et al. (1999) used individual-based models of fish groups to study the interplay among the forces acting on the individuals and the transport induced by water motion. They found that flows often enhanced grouping by increasing the encounter rate among groups and thereby promoting merger into larger groups.† In general, habitat structure will affect encounter rates among individuals of the same species but also among predators and prey.

Encounter rates and population dynamics are also altered when predators or prey form social groups. Fryxell et al. (2007) developed simple models of group-dependent functional responses and applied them to the Serengeti ecosystem. They found that grouping strongly stabilizes interactions between lions and wildebeest, suggesting that social groups, rather than individuals, were the basic building blocks for these predator-prey systems.

As satellite tracking devices become more affordable, and larger numbers of individuals can be tracked in the same study areas, we can expect to learn more about interactions among individuals. Furthermore, the use of additional telemetry technologies can make this more feasible. For example, Prange et al. (2006) used proximity detectors in collars fitted to free-living raccoons and were able to obtain accurate information in terms of detection range, and duration of contact. Animal-borne video systems also may help identify social interactions and foraging events for a focal individual (Hooker et al. 2008; Moll et al. 2009). Hence, the study of encounters offers great opportunities for marrying theory with data and to greatly improve our understanding of spatial dynamics.

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\* Assuming independent movements in any direction and with normally distributed velocities.

† Although the grouping effect breaks down for strong flows.

As animals face similar constraints and environmental heterogeneity, it is expected that they will exhibit similar movement rules and patterns. Early enthusiasm surrounding Levy flights and walks is now being taken with a bit more caution (e.g., Pyke 2015), but it is valuable to identify common movement rules based on individual animal's morphology, physiology, and cognitive capacity. There is also much theoretical and empirical work needed to better understand the costs and benefits of different movement strategies. Scharf et al. (2015) described a method for inferring time-varying social networks in animals based on telemetry data. Using data from killer whales, Scharf et al. (2015) developed a model that was motivated by encounter rate approaches that clustered similarities in movement patterns to learn about underlying binary networks that identified groups of individuals and how they change over time. We discuss these ideas more at the end of Chapter 5.

## 1.2 TELEMETRY DATA

Animal telemetry data are varied. This variation is an advantage because different field studies often have very different objectives and logistical (or financial) constraints. At a minimum, most animal-borne telemetry devices provide information about animal location. The earliest devices were very high frequency (VHF) radio tags designed for large carnivores and ungulates.\* VHF tags emit a regular radio wave signal (or pulse) at a specific frequency. A beeping sound (or ping) is heard whenever the signal is picked up by a nearby receiver that is tuned to this frequency, and the pings get louder as the receiver approaches the tag. As one hones in on the pings, the location of an animal with a VHF tag can be either closely approximated or confirmed by visual sighting. Accurate radio telemetry data acquisition requires practice and, often, triangulation. Radio tracking can sometimes be very challenging from the ground; thus, radio relocation surveys are often performed from small aircraft. Many VHF tags include a sensor that triggers a faster pulse rate after a pre-specified length of inactivity that is believed to be indicative of mortality or other events (e.g., hibernation). The analysis of radio telemetry data has historically been limited to descriptive statistical models of space use, home range delineation, survival, and abundance (e.g., White and Garrott 1990; Millsaugh and Marzluff 2001; Manly et al. 2007), but more sophisticated movement models have also been applied to radio telemetry data (e.g., Dunn and Gipson 1977; Moorcroft et al. 1999). Early VHF tags were too large for many smaller species, but improvements in battery technology now permit tags that are small enough for birds and even insects. The primary limitations of VHF tags are the limited range of radio signals and the cost and effort required to reliably locate animals via radio tracking. Radio tracking technology may seem archaic in the age of smart phones, but it still offers a relatively inexpensive and long battery-lived alternative to modern telemetry devices.

Since the mid-1990s, modern telemetry devices have been capable of storing and transmitting information about an individual animal's location as well as internal and

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\* We refer to "tags" generically here; for most terrestrial mammals, the telemetry devices are attached to neck collars and fitted to the individual animals. Telemetry devices have been fitted to animals in a variety of other ways.

external characteristics (e.g., heart rate, temperature, depth/altitude). Because modern telemetry devices can include additional sensors unrelated to location acquisition, the terms “biotelemetry” and “biologging” are increasingly used for describing modern animal telemetry techniques and devices (e.g., Cooke et al. 2004). There are two main types of modern (non-VHF) animal telemetry tags. These are often called storing (or “archival”) and sending (or “transmitting”) tags. Archival tags can be smaller than transmitting tags and store vast amounts of biotelemetry information, such as high-resolution accelerometer data, but they possess no mechanism for data transmission. Therefore, archival tags must be recovered from the animal before any data can be accessed. Transmitting tags send data in the form of electromagnetic waves to nearby receivers (similar to VHF tags) or to orbiting communications satellites. Satellite transmitting tags allow researchers to retrieve biotelemetry data without needing to recover or be close to the tag. Similar to archival tags, transmitting tags can store vast amounts of data. However, satellite tags require line of sight for transmission, and this limitation often necessitates careful consideration when designing and programming satellite tags. For example, marine animals do not surface long or frequently enough to transmit large quantities of biotelemetry data, so researchers must often make difficult trade-offs between data quality and quantity based on the specific objectives of their study (e.g., Breed et al. 2011).

Whether of the archival or transmitting type, most modern biotelemetry tags rely on satellites for determining an animal’s location. Tags that are equipped with an internal global positioning system (GPS) usually provide the most accurate locations currently available. GPS location errors (i.e., the distance between the observed and true location of the individual) tend to be less than 50 m, but GPS tags need to transmit larger data payloads and tend to be larger in size. Therefore, GPS tags are ideal for larger, terrestrial species in open habitat, but they are typically unsuitable for aquatic species such as marine mammals and fish.

Although not as accurate as GPS, Argos tags are a popular option for marine and small terrestrial species. Argos tags rely on a system of polar-orbiting satellites to decode the animal’s location from a relatively tiny packet of transmitted information. Argos tags can quickly transmit data to satellites within the brief intervals that marine mammals surface to breathe because the transmission packets are small. The main drawback of Argos tags is the limited size and duration of transmissions; this limits the quantity and quality of onboard biotelemetry data that can be recovered. Argos tags tend to perform best at higher latitudes (due to the polar orbits of the satellites), but location errors can typically range from hundreds to thousands of meters (e.g., Costa et al. 2010; Brost et al. 2015).\*

As a compromise between GPS and Argos, Fastloc-GPS (Wildtrack Telemetry System Limited, Leeds, UK) tags compress a snapshot of GPS data and quickly transmit via the Argos satellite system. With location errors typically between 50 and 1000 m, Fastloc-GPS is considerably more accurate than Argos overall.

Biotelemetry technology is rapidly improving,<sup>†</sup> and there are many tag designs and data collection capabilities that we have not covered in this brief introduction. These

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\* We describe specific aspects of Argos data and potential remedies in Chapters 4 and 5.

† See Kays et al. (2015) for a recent overview of tag technology.

include light-sensing “geologgers” for smaller species (e.g., Bridge et al. 2011), archival “pop-up” tags popular in fisheries (e.g., Patterson et al. 2008), proximity detectors (e.g., Ji et al. 2005), acoustic tags (e.g., McMichael et al. 2010), “life history” tags (Horning and Hill 2005), accelerometer tags (e.g., Lapanche et al. 2015), and automatic trajectory representation from video recordings (Pérez-Escudero et al. 2014). In what follows, we primarily focus on the analysis of location data such as those obtained from VHF, GPS, and Argos tags. However, many of the methods we present can utilize location information arising from other sources, as well as incorporate auxiliary information about the individual animal’s internal and external environment that is now regularly being collected from modern biotelemetry tags. Winship et al. (2012) provide a comparison of the fitted movement of several different marine animals when using GPS, Argos, and light-based geolocation tags.

### 1.3 NOTATION

In the literature on animal movement data and modeling, you will find that there is a wide variety of notation used. This variation in statistical notation used makes it quite challenging to maintain consistency in a comprehensive text on the subject. We have provided this section, along with Table 1.1, in an attempt to keep expressions as straightforward as possible. We recommend bookmarking this section on your first reading so that you may return to it quickly if the notation becomes confusing.

Conventional telemetry data consist of a finite set of spatially referenced geographic locations ( $\mathbf{S} \equiv \{s_1, \dots, s_i, \dots, s_n\}$ ) representing the individual’s observed location at a set of times spanning some temporal extent of interest (e.g., a season or year). We use the notation,  $\{\mu_1, \dots, \mu_n\}$  to represent the corresponding true positions of the animal. Sometimes, the observed telemetry data are assumed to be the true positions (i.e., no observation error); however, in most situations, they will be different. The times at which the location is observed can be thought of as fixed and a part of the “design,” or as observed random variables. In either case, a statistical notation with proper time indexing becomes somewhat tricky. To remain consistent with the broader literature on point processes (and with Chapter 2), we are assuming that there are  $n$  telemetry observations collected at times  $\mathbf{t} = (t_1, \dots, t_i, \dots, t_n)'$  such that  $t_i \in \mathcal{T}$  and  $\mathbf{t} \subset \mathcal{T}$ . The seemingly redundant time indexing accounts for the possibility of irregularly spaced data in time. If the differences ( $\Delta_i = t_i - t_{i-1}$ ) between two time points at which we have telemetry observations are all equal, we could just as easily use the direct time indexing where the data are  $s_t$  for  $t = 1, \dots, T$ . In that case, we have  $T = n$ . From a model-building perspective, it is sometimes less cumbersome to index telemetry observations in time (i.e.,  $s_t$ ) and deal with temporal irregularity during the implementation. However, there are some situations, for example, when the points are serially dependent, where we need the  $\Delta_i$  notation. A further perspective on notation arises when considering that the true animal location process is a continuous process in time. To formally recognize this, we often index the observed location vectors as  $\mathbf{s}(t_i)$  (or  $\mu(t_i)$ , in the case of the true positions). The parenthetical notation at least admits that we are often modeling animal locations as a continuous function. Thus, prepare yourself to see all types of indexing, both in this text and in the vast animal movement literature.

**TABLE 1.1**  
**Statistical Notation**

Notation	Definition
$i$	Observation index for $i = 1, \dots, n$ total observations.
$t$	Time point at which the data or process occurs (in the units of interest).
$\mathcal{T}$	The set of times at which the process exists; typically compact interval in continuous time such that $t \in \mathcal{T}$ .
$t_i$	Time associated with observation $i$ .
$T$	Either largest time in observations or process, or upper temporal endpoint in study, depending on context.
$s_i$	Observed telemetry observation for $i = 1, \dots, n$ . $s_i$ is a $2 \times 1$ vector unless otherwise stated. Also written as: $s(t_i)$ in continuous-time context.
$\mathcal{S}$	The spatial support for the observed telemetry observations (i.e., $s \in \mathcal{S}$ ).
$\mu_i$	True individual location (i.e., position) for $i = 1, \dots, n$ . $\mu_i$ is a $2 \times 1$ vector unless otherwise stated. Also written as: $\mu(t_i)$ in continuous-time context.
$\mathcal{M}$	The spatial support for the true individual locations (i.e., $\mu(t) \in \mathcal{M}$ ). Typically, the support for the true locations $\mathcal{M}$ is a subset of the support for the observed locations $\mathcal{S}$ (i.e., $\mathcal{M} \subset \mathcal{S}$ ).
$\mathbf{X}$	A “design” matrix of covariates, which will often be decomposed into rows $\mathbf{x}_i$ for row $i$ , depending on the context in which it is used.
$\beta$	Vector of regression coefficients (i.e., $\beta = (\beta_1, \beta_2, \dots, \beta_p)'$ ), where $p$ is the number of columns in $\mathbf{X}$ .
$\beta'$	The “prime” symbol ( $'$ ) denotes a vector or matrix transpose (e.g., converts a row vector to a column).
$\sigma^2$	Variance component associated with the observed telemetry data, true position process, or a model parameter.
$\Sigma$	Covariance matrix for either a parameter vector such as $\beta$ (if subscripted) or the data or process models.
$f(\cdot), [\cdot]$	Probability density or mass function. $p(\cdot), P(\cdot)$ , and $\pi(\cdot)$ are used in other literature. The $[\cdot]$ has become a Bayesian convention for probability distributions.
$E(y)$	Expectation of random variable $y$ ; an integral if $y$ is continuous and sum if $y$ is discrete.
$\propto$	Proportional symbol. Often used to say that one probability distribution is proportional to another (i.e., only differs by a scalar multiplier).

## 1.4 STATISTICAL CONCEPTS

We focus mostly on parametric statistical models\* in this book; thus, we rely on both Bayesian and non-Bayesian models using maximum likelihood. Occasionally, for example, in Chapters 2 through 4, we present statistical methods that are nonparametric or involve implementation methods that do not involve Bayesian or maximum likelihood approaches. A generic data model statement will appear as  $y_i \sim [y_i|\theta]$ ,

\* Parametric statistical models involve the specification of known probability distributions with parameters that are unknown but estimated in the model fitting procedure.

where  $y_i$  are the observations (we use  $s_i$  for telemetry observations instead of  $y_i$ ) for  $i = 1, \dots, n$ ,  $\theta$  are the data model parameters, and the bracket notation “[ $\cdot$ ]” represents a probability distribution. The data model is often referred to as the “likelihood” by Bayesians, but the likelihood used in maximum likelihood estimation (MLE) is proportional to the joint distribution of the data conditioned on the parameters. When the observations are conditionally independent, the likelihood is often written as  $[y|\theta] = \prod_{i=1}^n [y_i|\theta]$ , where individual data distributions can be multiplied to obtain the joint distribution because of independence. To fit the model using MLE, the likelihood is usually maximized numerically to find the optimal parameter values  $\hat{\theta}$ .

The Bayesian approach involves the specification of a probability model for the parameters,  $\theta \sim [\theta]$ , that depend on fixed hyperparameters assumed to be known. The prior probability distribution should contain information about the parameters that is known before the data are collected, except for cases where regularization-based model selection is desired (Hooten and Hobbs 2015), in which case, the prior can be tuned based on a cross-validation procedure. Rather than maximizing the likelihood, the Bayesian approach seeks to find the conditional distribution of the parameters given the data (i.e., the posterior distribution)

$$[\theta|y] = \frac{[y|\theta][\theta]}{\int [y|\theta][\theta] d\theta}, \quad (1.1)$$

where  $y$  is a vector notation for all the observations and the denominator in Equation 1.1 equates to a scalar constant after the data have been observed. For complicated models, the multidimensional integral in the denominator of Equation 1.1 cannot be obtained analytically (i.e., exactly by pencil and paper) and must be either numerically calculated or avoided using a stochastic simulation procedure. Markov chain Monte Carlo (MCMC; Gelfand and Smith 1990) allows us to obtain samples from the posterior distribution while avoiding the calculation of the normalizing constant in the denominator of Equation 1.1. MCMC algorithms have many advantages (e.g., easy to develop), but also limitations (e.g., can be time consuming to run).

Hierarchical models are composed of a sequence of nested probability distributions for the data, the process, and the parameters (Berliner 1996). For example, a basic Bayesian hierarchical model is

$$y_{i,j} \sim [y_{i,j}|z_i, \theta], \quad (1.2)$$

$$z_i \sim [z_i|\beta], \quad (1.3)$$

$$\theta \sim [\theta], \quad (1.4)$$

$$\beta \sim [\beta], \quad (1.5)$$

where  $z_i$  is an underlying process for individual  $i$  and  $y_{i,j}$  are repeated measurements for each individual ( $j = 1, \dots, J$ ). Notice that the process model parameters  $\beta$  also require a prior distribution if the model is Bayesian. The posterior for this model is a

generalized version of Equation 1.1 such that

$$[\mathbf{z}, \boldsymbol{\theta}, \boldsymbol{\beta} | \mathbf{y}] = \frac{[\mathbf{y} | \mathbf{z}, \boldsymbol{\theta}] [\mathbf{z} | \boldsymbol{\beta}] [\boldsymbol{\theta}] [\boldsymbol{\beta}]}{\iint [\mathbf{y} | \mathbf{z}, \boldsymbol{\theta}] [\mathbf{z} | \boldsymbol{\beta}] [\boldsymbol{\theta}] [\boldsymbol{\beta}] d\mathbf{z} d\boldsymbol{\theta} d\boldsymbol{\beta}}. \quad (1.6)$$

Throughout the remainder of this book, we use both Bayesian and non-Bayesian models for statistical inference in the settings where they are appropriate. Many complicated hierarchical models are easier to implement from a Bayesian perspective, but may not always be necessary. Hobbs and Hooten (2015) provide an accessible description of both Bayesian and non-Bayesian methods and model-building strategies as well as an overview of basic probability and fundamental approaches for fitting models. Hereafter, we remind the reader of changes in notation and modeling strategies as necessary without dwelling on the details of a full implementation because those can be found in the referenced literature.

## 1.5 ADDITIONAL READING

The timeless reference describing the mathematics of animal movement processes is Turchin (1998), and while newer references exist, Turchin (1998) is still the default for many scientists. For a newer synthesis, the special issue in the *Philosophical Transactions of the Royal Society of London B* provided a cross section of contemporary ideas for modeling animal movement and analyzing telemetry data (see Cagnacci et al. 2010 for an overview). Schick et al. (2008) proposed a general hierarchical modeling structure to modeling telemetry data that many contemporary efforts now follow.

Historical, but still very relevant, references describing approaches for collecting and analyzing telemetry data include White and Garrott (1990), Kenward (2000), Millsbaugh and Marzluff (2001), and Manly et al. (2007), although they focused more on vital rates (e.g., survival), resource selection, and home range estimation from radio telemetry data because that technology preceded current satellite telemetry devices.

Connecting telemetry data with population demographic data is still nascent. However, the field of SCR models is advancing rapidly and a few developments of SCR models have formally incorporated telemetry data to better characterize space use and resource selection. Also, individual-based movement models, in general, provide us with a better understanding about how animals are interacting with each other and their environment and the learning that is gained from fitting them can be used to develop smart demographic models that best account for features of population and community dynamics that depend on movement.

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