# 3 Home range and habitat use

#### 3.1 Introduction

In this chapter we introduce the pivotal concept of the *home range* and consider how it relates to patterns of *habitat use*. The home range for an individual refers to the geographic area utilized for all normal activities, linked together through animal movement (Burt 1943). This is likely of course to depend on the time frame under consideration, so home ranges can be specified on a daily, seasonal, annual, or even lifetime basis. In order to meet an individual's full range of physiological and ecological requirements over an extended period, a suitable home range typically must have an adequate supply of food and water, shelter, breeding sites, and often locations that are secure against predators and parasites. The spatial locations associated with common sets of these attributes are often termed *habitats*, so we can refer to "nesting habitat," "shelter habitat," or "refuge habitat from predation."

Obviously, such a complex set of requirements is unlikely to be met routinely at every place in the environment, so home range locations often yield important insight into the requirements for life, particularly those resources (see Chapter 2) that have the greatest influence on survival and reproductive potential. As such, home range analysis provides wildlife biologists with one of the most important tools by which to assess ecosystem quality. Habitat attributes that reliably indicate home range use can offer insight into key ecological features of importance from the individual's point of view.

Comparison of home range size across different species or among populations of the same species can help us to understand better what ecological factors most strongly limit population abundance. These factors can be used to identify the *ecological niche*, central in any discussion about community structure (see Chapter 6) but also vitally important in defining suitable candidates for habitat restoration, improvement projects, and conservation. In species whose home ranges of individuals rarely overlap, the reciprocal of home range size essentially defines a social carrying capacity that naturally regulates population density (see Chapter 5). Even in species with extensive individual home range overlap, the locations of suitable habitats across the landscape can offer useful insights into potential population size, a characteristic that can be of enormous practical use with respect to species reintroduction or recovery programs (see Chapter 4). In other words, patterns of habitat use within the home range link to many different aspects of wildlife ecology and play a useful role in many conservation and management initiatives.

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## 3.2 Estimating home range size and utilization frequency

There are a wide variety of ways in which home ranges can be estimated, but all start with a requirement for spatial field data. In rare circumstances, such data might be estimated from direct observation of individually recognizable individuals over continuous time, such as in many primate studies. More commonly, wildlife biologists rely on remote sensing apparatuses, such as radio collars, to provide the spatial coordinates of animal locations sampled at regular time intervals. Until recently, such data were laborious and enormously time-consuming to gather for field biologists, with substantial effort required to get close enough to radio-collared animals to allow reliable positioning of directional antennae. Multiple fixes of this sort were then used to estimate coordinates using triangulation methods derived from basic trigonometry. An inevitable consequence of the uncertainty in determining the direction of the telemetry signal relative to the receiver was that even the most careful field research yielded positional data ("fixes") of dubious reliability.

In more recent years, however, there has been an explosion of new technologies for the gathering of animal location data using *global positioning systems* (GPS) identical to those used in modern cell phones. GPS radio collars determine their own spatial positions at pre-assigned intervals through linkage with a set of satellites circling the globe. Such data are typically much more precise than hand-gathered radio-telemetry data, often yielding fixes within 10 m of the true location and sometimes within 1 m. This remarkable precision, coupled with major improvements in the number of fixes possible even for multiple organisms, has opened exciting new avenues of research and allowed for much more reliable information on which to base home range assessment.

As an example, consider the fix data shown in Fig. 3.1 for a gray wolf in northern Ontario, Canada (Kittle 2014). Sequential positions of the study animal at 24-hour



Fig. 3.1 Sequential radio-telemetry fixes from GPS radio-telemetry fixes for a gray wolf from Canada taken every 5 h over the course of a year. intervals are connected by lines. This example demonstrates several common features of positional data: first, the researcher knows only that at some point over the course of a single day the study animal transferred between sequential locations, not typically how long it remained or if it remained at all at any single site; second, while on occasion the individual moved a large distance between sequential fixes, short "moves" outnumber long "moves"; third, much of this individual's time was spent in a small fraction of the available area – that is, it seemed to prefer some locations to others. The typical goal of home range analysis is to characterize the overall pattern suggested by the collection of fixes, measure the areal coverage, and identify correlations between habitat elements in areas of heavy versus light use to assess selectivity.

Once one has gathered spatial fixes for a given individual, there are a variety of ways to estimate home range size, differing largely in the underlying assumptions about the individual's position during the intervals between fixes. The oldest method is simply to connect the outermost fixes, forming what is termed a *convex polygon* (Fig. 3.2a). This has several virtues, simplicity being paramount. It does not come heavily loaded with preconceptions about the normal patterns of home range use. Moreover, it is inclusive, in that all fixes are part of the home range. On the negative side, convex home range polygons are often thought to be too inclusive, with the border including some regions that might not be used at all. Most importantly, the convex polygon method offers little insight into identification of areas of intense use.

The most common alternative to convex polygons is what is known as a *kernel estimator* for the putative home range (Kie *et al.* 2010). This can take essentially two forms: a bivariate kernel tries to fit as many fixes as possible within an ellipse centered over the observed fixes, whereas an adaptive kernel is a complex surface draped over the observed fixes (Fig. 3.2b). Contoured isopleths drawn on the surface demarcate areas of similar frequency of visitation. One can immediately see the advantages of the kernel method. The complex pattern of folding allows the researcher to discriminate between



Fig. 3.2 Alternate home ranges estimated from daily GPS radio-telemetry fixes for a gray wolf in Canada based on (a) convex polygon, (b) adaptive kernel, (c) Brownian bridge kernel, and (d) local weighted polygon methods (Kittle 2014). For subplots (b) and (c), areas of intense use are lighter in tone, whereas areas of minor use are shaded darkly.

those areas that were used versus those not used at all. More importantly, locations of intense use are nicely captured by peaks in the fitted surface. The height of the kernel home range at any spatial location is proportionate to the utilization probability, so the kernel itself represents a *utilization distribution* in space. This is an improvement on simply assuming that all parts of the home range are equally important, because we know that animals almost always spend disproportionate amounts of time in different parts of the home range (Fig. 3.1). Improved understanding of the most heavily utilized parts of the home range can often lead to insights about the most important factors, in a sense giving us an animal's-eye-view of the things that matter ecologically.

One slightly disturbing feature of kernel home ranges is that they have no absolute limit, because, for mathematical reasons associated with fitting a complex surface to point data, the fitted surface extends without limit in all directions, albeit with low levels of use. To circumvent this logical impossibility, scientists routinely truncate the kernel home range at the point where the surface includes 95 or 99% of the observed fixes (a so-called isopleth), eliminating the infinity conundrum. The advanced software required to fit such complex home ranges to data are included with some commonly used GIS packages (e.g. Spatial Analyst, available as a toolbox in ARCmap) or in R statistical packages freely available on the Internet (e.g. adehabitat, available at http://cran.r-project.org). The quality of kernel-estimated home ranges obviously depends on the accuracy and the number of fixes, as well as on the degree to which fixes are clumped across the landscape.

A recent modification of the kernel approach is termed *Brownian bridge kernel* estimation (Horne *et al.* 2007). Like other kernel methods, it fits a complex surface to the collection of fixes, accommodating local variation in home range use. Unlike other kernel estimators, however, the Brownian bridge approach estimates the probability of space use by an animal with typical movement characteristics during the intervals between fixes, assuming so-called Brownian movement during each interval (Fig. 3.2c) (Brownian movement refers to a random pattern of movement, such as that of small pollen grains suspended in a water droplet). This helps to identify corridors of likely importance linking sites used repeatedly by the study animal. On the negative side, presumption of purely Brownian movement adds to an already ponderous set of assumptions.

A fourth approach that has recently come into its own is termed *local convex hulls* (Getz and Wilmers 2004). This is a methodological approach that conceptually lies somewhere between the simplicity of convex polygons and the extreme complexity of kernel home range estimators. Simple geometric shapes (convex hulls) are constructed around subsets of the fix data (Fig. 3.2d), thus permitting researchers to construct a sequence of home ranges for different seasons. This can be helpful in understanding more complex patterns of movement or for comparing patterns of home range use for multiple animals over short time intervals. R code for the calculation of local convex hulls is available over the Internet.

## 3.3 Estimating habitat availability and use

The pattern of animal fixes that generates a home range estimate and indicates the degree of utilization of parts of the home range can also be used to define habitat usage. It is rarely possible to know all the relevant attributes of every spatial position of an animal's home range. Nonetheless, it is often possible to make educated guesses about the most important features using *geographic information systems* (GIS). This is a means of linking complex geographical information on physical structure, topographic

relief, biological features, and human-made landscape elements into a computerized database. One important feature of GIS is rapid and simple construction of tailor-made "maps" that are readily accessible from a computer screen. This allows users to sift rapidly through complex spatial information in a visual context. Just as importantly, GIS allows the user to identify and measure spatial interrelationships among variables that would be exceedingly difficult to perform in the field. For example, one can rapidly calculate the sizes of forest stands of similar species composition, measure the distance of each of these stands from the nearest road, and calculate what fraction of the stands falls within the home range of a wildlife species of interest. From the point of view of assessing habitat selection, GIS also offers a convenient means of random sampling of geographic features across complex landscapes. GIS is clearly a technological break-through in the analysis of wildlife habitat needs and is transforming the way that we think about conservation and management issues.

The remarkable capacity afforded by GIS data does not come without cost. First, someone has to gather spatial data and map them in the first place. The quality of that initial data collection (sometimes termed "ground-truthing") and how recently it has occurred have a strong bearing on the utility of the GIS database. For example, it is quite common to rely on GIS databases to assess the degree of wildlife preference for specific vegetation communities, such as forest stand types. Such habitats are often defined in rather crude terms, representing a few predominant species that can be identified from aerial photos or limited samples taken at a limited number of accessible sites, rather than field data sampled extensively across the landscape. The aerial coverage of each habitat type is then based on extrapolation from a limited number of ground-truthed sites to a much larger landscape. Different forest stands have different spectral reflectance characteristics, allowing remote-sensing specialists working with a satellite image to fill in a GIS database, much as a child would fill in a line drawing in a coloring book. Statistical extrapolation of such derived variables is always tenuous and the reliability of GIS databases is affected accordingly.

Sometimes GIS data cannot provide information on the actual resources used by animals. For example, the rich mix of forbs used by browsing deer may be poorly predicted by forest stand type. One way around this is to use satellite-generated estimates of plant abundance, such as NDVI (Normalized Difference Vegetation Index), rather than plant community types. Alternatively, changes in NDVI from one satellite pass to the next can be used to ascertain areas of rapid vegetation growth, often indicative of the most nutritious forage (Pettorelli *et al.* 2005; Bischof *et al.* 2012). Such variables lump all vegetation classes together, so they inevitably yield a rather coarse view of the world. The information in GIS databases may also be out of date and therefore irrelevant to current conditions. Human population growth, industrial development, habitat disturbance due to natural or anthropomorphic causes, and ecological processes such as community succession are rapidly changing habitat availability in many if not all landscapes.

Finally, many relevant variables are dynamic in nature, which is difficult to accommodate in static GIS databases. Plant biomass grows over the summer or wet season and then declines over the winter or dry season in most ecosystems. Prey distribution can shift markedly from month to month and even in cases where prey are resident, local snow conditions influencing access to those prey may vary considerably over time and space across large landscapes. From the prey point of view, the spatial distribution of predation risk is itself highly dynamic, depending on the manner in which predators use their home range. All of these factors introduce uncertainty into wildlife habitat assessment. Statistical modeling can never eliminate the uncertainties introduced by inadequate habitat data.

3.4 **Selective** By now it should be apparent that there are good reasons for wildlife species to choose habitat use habitats carefully, in order to enhance the opportunities for feeding while reducing the risk of being eaten. Moreover, most species have a suite of other needs to meet, including obtaining shelter from inclement weather, gaining access to water, and locating suitable breeding sites, such as cavities in dead trees or burrows. Quantification of specific habitat needs is known as *habitat assessment* and is an important area of wildlife ecology. Much of this interest derives from practical benefits: knowing pre-

ing suitable breeding sites, such as cavities in dead trees or burrows. Quantification of specific habitat needs is known as *habitat assessment* and is an important area of wildlife ecology. Much of this interest derives from practical benefits: knowing precisely which wildlife habitats are essential allows appropriate management decisions regarding alternate forms of land use. Moreover, good understanding of habitat requirements can improve the odds of success when wildlife species are reintroduced to areas from which they were extirpated.

There are many ways to quantify wildlife habitat selectivity (Aarts *et al.* 2008). All such methods rest on a common assumption: that selectivity can be determined by comparing use to availability of alternative habitat types. This is often assessed by taking S = use/availability. If the proportion of occurrences in a particular habitat type exceeds the proportion of the landscape composed of that habitat then S > 1 and positive selectivity (preference) is implied. If use is less than proportionate availability, on the other hand, then S < 1 and negative selectivity (avoidance) is implied.

The simplest way to evaluate such logic is through contingency tables. The number of actual occurrences in a given habitat is compared with the number expected under the null hypothesis of nonpreference. If 30% of the environment is composed of grassland and 70% of woodland then the null hypothesis will be that of 500 radio-telemetry fixes of elk, we should expect to get 150 (=  $0.3 \times 500$ ) fixes in grassland and 350 in woodland. One can test statistically whether the actual observed values significantly deviate from this expectation using a  $\chi$ -squared test. A similar analysis can be used to determine whether animals preferentially choose diets or other resources.

A commonly used variant on this simple contingency test is known as *composition analysis* (Aebischer *et al.* 1993). Using this approach, one converts the proportions of use for each habitat *i* to a log-ratio using the formula  $y_i = \ln(u_i/u_1)$ , where  $u_1$  is the proportion of use of one arbitrarily chosen habitat type. Log-ratios of availability are similarly calculated as  $z_i = \ln(a_i/a_1)$ . Preference is then indexed by the difference between the log-ratios ( $p_i = y_i - z_i$ ) for all habitat types. If these log-ratios are available for a number of individuals then it is possible to rank the habitats in terms of mean preference and to use a MANOVA to test whether patterns of preference differ from what one might have expected at random. The strength of composition analysis is that the individual becomes the logical sampling unit, rather than fixes, which are rarely truly independent of one another and thus bias statistical tests. The primary weakness, however, is that selectivity can only be assessed for those habitats that are actually used to some degree, hence complete avoidance presents a serious problem.

While simple tests based on use versus availability can help us identify important habitat needs, they are not very useful for predicting patterns of occurrence across the landscape. For such purposes, wildlife biologists use a different approach, termed a *resource selection function* (Manly *et al.* 1993; Boyce and McDonald 1999). Resource selection functions offer a flexible means of quantifying the degree of habitat

preference. Complex combinations of categorical and continuous variables can be readily accommodated using this method. Moreover, the method can use a GIS to locate, manipulate, and analyze habitat data of interest.

Perhaps the easiest way to understand the most typical resource selection procedure is to walk through an example. The rufous bristlebird is a threatened passerine species living in coastal areas of Australia. Gibson *et al.* (2004) used GIS to evaluate critical habitat needs for bristlebirds in a site with competing land use interests (biodiversity values versus mining). Along a series of trails bisecting the study area, Gibson *et al.* recorded the presence (scored with a 1) or absence (0) of bristlebirds, noting the exact geographic coordinates of each positive identification made. They later transferred these sightings to a GIS, overlaying digitized topographic data on aspect, slope, and elevation, as well as spatially explicit data on hydrology and vegetation complexity derived from multispectral remote-sensing imagery. The probability that a habitat is used (*w*(*x*)) is given by the following logistic regression model:

$$w(x) = \frac{\exp(\beta_0 + \beta_1 X_1 + \dots + \beta_k X_k)}{1 + \exp(\beta_0 + \beta_1 X_1 + \dots + \beta_k X_k)}$$

where the logistic regression coefficients  $\beta_1 - \beta_k$  measure the strength of selection for the *k* different habitat variables (symbolized by  $X_i$ ) over the full set of sample units. The S-shaped logistic function w(x) is bounded between 0 and 1 and represents a probability of usage, given the set of habitat characteristics within a spatial unit. Given the descriptive nature of both the data on bristlebird presence or absence and habitat variables derived from the GIS, Gibson *et al.* elected to use model evaluation (Chapter 15; Burnham and Anderson 1998) rather than classical hypothesis testing (Chapter 14). They found that there was a positive association between bristlebird presence and "elevation," "distance to creek," "distance to the coast," and "sun incidence." This suggests that bristlebirds require densely vegetated stands in close proximity to coastal fringes and drainage lines. Such habitats composed approximately 16% of the study area, demonstrating how resource selection can help in the assessment of land use priorities for wildlife conservation in a planning context.

There are many variations on this basic statistical design, discussed in detail in the comprehensive treatise by Manly *et al.* (1993). If one can visit all spatial units and know for sure whether each has been used or not, the logistic function w(x) can be treated as a true probability of occurrence. An example of this might be the study of squirrel nests in a small wooded area at a time of year in which nests are readily observable from the forest floor. While it might require a good deal of work, one could probably say with reasonable certainty that spatial units without a nest were not used as nesting habitats.

In most cases in the contemporary literature, however, resource selection is based on sampled radio-telemetry data, used to identify used habitats and sample available habitat randomly from a larger set of sites. While this kind of study design unambiguously identifies sites that were actually used by the marked population, one cannot be sure that sites without fixes were not used at least some times by at least some individuals (Keating and Cherry 2004). This means that recorded "0"s would actually be "1"s if the biologist had completely accurate data. Under these circumstances, the proper procedure is to use logistic regression to estimate the coefficients of w(x), discard the denominator and intercept  $\beta_0$ , and use the resulting modified formula  $z(x) = \beta_1 X_1 + \ldots + \beta_k X_k$  to estimate the relative magnitude of use (z(x)) for each habitat. In other words, the model cannot be treated as a true probability function, but the resource selection function is still appropriately scaled to preferences (Keating and Cherry 2004) and therefore useful in assessing conservation or management objectives.

# 3.5 Using resource selection functions to predict population response

Resource selection can in principle be used to evaluate the potential success of reintroduction programs (Boyce and McDonald 1999). This approach has been used, for example, to predict the potential for successful reintroduction of gray wolves to different parts of the United States (Mladenoff *et al.* 1995; Mladenoff and Sickley 1998). Data for existing wolf populations were first used to determine the suite of critical habitat variables for wolves and to relate local wolf densities to habitat features. GIS data were then fed into the resource selection models to predict the potential of different areas to support gray wolves. The model has been validated against data for an expanding wolf population in Wisconsin, demonstrating that this approach can be a useful planning tool.

Resource selection functions are also a powerful means of linking habitat characteristics with spatially realistic models of population viability. For example, Akçakaya and Atwood (1997) used logistic regression to develop a habitat suitability model for the threatened California gnatcatcher (*Polioptila californica*) in the highly urbanized environment of Orange County, California. Gnatcatcher distribution data were mapped on to a GIS map. Numerous geographical habitat features were then evaluated and a resource selection probability function was developed on the basis of the strongest suite of variables. Suitable habitat fragments were mapped on to the Orange County landscape and this spatial configuration was modeled as a metapopulation in order to evaluate the long-term viability of gnatcatchers (see Chapters 16 and 22). This is a valuable way of evaluating the conservation needs of threatened populations. It is particularly appropriate for species utilizing fragmented landscapes, because it gives useful insights into the ecological implications of alternative land use policies and planning scenarios.

## 3.6 Sources of variation in habitat use

A number of factors can have a strong influence on habitat selectivity and use. First and foremost, estimates of habitat selectivity are strongly influenced by the spatial scale at which the assessment is made. A useful set of habitat use categories is in common use by wildlife biologists (Johnson 1980). Type 1 habitat selection is based on the entire range occupied by a given species relative to the unoccupied area. Type 2 habitat selection is based on the full home range chosen by an individual relative to the area encompassed by the species range. Type 3 habitat selection is based on the use of specific habitats within the home range of a single individual. Finally, Type 4 habitat selection is based on the selective use of particular food types by a single individual within a single resource "patch."

Although not commonly done, analyses conducted at multiple spatial scales often find quite different patterns of selection at each scale (DeCesare *et al.* 2012). It is not entirely clear what this means, but it has been suggested that the most limiting demographic factor will elicit selection at the most coarse scale (Rettie and Messier 2000). So, giant pandas might be expected to coarsely select for bamboo forest, because that is a crucial, nonreplaceable food resource, but to select for ancillary features such as slope, aspect, or stem density at finer spatial scales. At the very least, repetition of resource selection studies at multiple scales is more likely to identify robust habitat predictors that happen to have their greatest effect at different spatial scales.

Even if one maintains a similar spatial scale, patterns of selectivity will often be intrinsically sensitive to variation in habitat availability in the local environment, potentially clouding the ability of use-availability sampling designs to identify preference (Beyer *et al.* 2010). This is an inevitable outcome of the mathematics used to estimate preference coefficients combined with spatial heterogeneity in habitat distribution that occurs routinely in nature. It is also a likely consequence of animals valuing choices differently when resources are common as opposed to rare (Mysterud and Ims 1998). One remedy is to repeat resource selection studies at a variety of spatial scales or to repeat studies at sites with different levels of habitat availability, if only to appreciate the robustness of statistical inferences. It is also advisable to use some form of cross-validation, a statistical method of resampling one's dataset to evaluate the robustness of conclusions. Caution in accepting resource selection functions at face value is often well warranted.

Given that there are differences in the intrinsic suitability of habitats, due to variation in resources, cover, and risk from predators, one might expect animals to concentrate in the most favorable habitats. It has been long appreciated, however, that habitat selectivity tends to vary with densities of both consumers and their resources (Rosenzweig 1991). Birth rates tend to fall and mortality rates to climb as forager density increases (see Chapter 5). As a consequence, habitat suitability is often negatively associated with density. Density-dependent decline in habitat suitability can arise from a variety of causes, including resource depletion, direct interference among individuals, disease transmission, and elevated risk of predation.

At low consumer densities, individuals tend to be highly selective of habitats, but the range of used habitats expands as consumer density increases (Rosenzweig 1991). This is often interpreted as evidence of adaptive changes in foraging decisions that should have positive fitness consequences (Rosenzweig 1981, 1991; Brown 1988; Brown *et al.* 1994). Animals that do not expand their range of acceptable options when preferred items (habitats) are scarce face an opportunity cost that can be deadly (Brown 1988).

Density-dependent decline in habitat suitability can be extended to multiple habitats. Individuals should concentrate in the best habitat until the density there reduces in suitability to that of the next best alternative (Fig. 3.3). Thereafter, both habitats should receive equal use. The resulting pattern of distribution among alternative habitats is known as the *ideal free distribution* (Fretwell and Lucas 1970). It is free in the sense that every individual is presumed equal and capable of choosing the best option available. It is ideal in the sense that all individuals are presumed to have perfect knowledge about the relative suitability of each habitat on offer. Hence, it would not pay for any individual to deviate from the ideal pattern of distribution, because their fitness would be compromised. This is a prime example of an *evolutionarily stable strategy* (ESS; Maynard Smith 1982). Once adopted by all individuals in a population, no mutant or deviant strategy could do better. Hence, the ESS will be favored by natural selection.

The ideal free hypothesis predicts that most individuals should be found in preferred habitats when forager population density is low, spilling over into less preferred habitats when forager density is high. This pattern has been demonstrated several times in Fig. 3.3 Schematic diagram of the ideal free distribution. As density in the preferred habitat 1 increases, suitability declines to a point indicated by the light broken line where it equals that in the poorer habitat 2 (60 units). At this point it pays some individuals to use habitat 2.





different bird species (Fig. 3.4). One of the earliest examples was Brown's (1969) pioneering studies of great tits (*Parus major*) in the woodlands near Oxford, UK. Brown showed that adult birds nested predominantly in woodland habitats in years with low bird abundance, expanding outwards into less attractive hedgerows only when densities were high. Krebs (1971) tested the assumption that this distribution stemmed from differences in fitness by experimentally removing birds from woodland habitats, resulting in vacancies that were filled rapidly by former hedgerow "tenants."

A powerful way to test the ideal free hypothesis is to compare the feeding rates of individuals in different patches with different rates of food delivery. Milinski (1979) delivered food at differing rates to the two ends of an aquarium and measured the consequent pattern of distribution of sticklebacks. The ideal free hypothesis predicts that once they have determined the rate of food delivery at each end of the tank, the density of fish at each end should be proportional to the same. In other words, delivering twice as much food to one end of the tank should lead to two-thirds of the fish congregating in the food-rich patch. The sticklebacks redistributed themselves in precisely this manner (Milinski 1979). Similar results have been recorded in continuous-food-input experiments with numerous other species, including mallard ducks (Harper 1982), cichlid fish (Godin and Keenleyside 1984), and starlings (Inman 1990). Measurements in the field have been less supportive. However, animals in preferred habitats generally obtain higher rates of food intake than those relegated to poorer habitats (Sutherland 1996). Researchers frequently find that individuals vary in the quantity of food that they acquire, with more dominant or larger individuals securing more of the food delivered than lower-ranking individuals. This hierarchy suggests that although animals are

capable of adjusting their behavior in predictable ways to accommodate the presence of other competitors for scarce resources, differences in dominance status tend to maintain differences in fitness (Sutherland 1996).

One way to accommodate these effects is through a modified model known as the *ideal despotic distribution* (Fretwell 1972). This model assumes that individuals choose the best habitat possible on the basis of their dominance status. In extreme cases, this process can lead to *territoriality*, in which an individual, pair, or social group defends an area of exclusive use against all intruders. The most dominant individuals choose first, followed by others in rank order of their dominance status. Under these conditions, individuals of lower status might well choose to split their time between two habitats offering similar levels of suitability, whereas high-ranking individuals invariably choose the best habitat. More importantly, the ideal despotic distribution predicts that there will be disparities in food intake, mortality risk, and reproductive success among individuals. These differences dissolve when we focus on individuals of similar rank.

3.7 Movement within the home range

One nagging flaw in simple studies of habitat selectivity is that not all parts of an animal's home range are physically accessible from every other part of the home range at every moment. For example, imagine one has a dataset composed of daily telemetry fixes for a caribou occupying a circular home range with a radius of 24 km. If an animal never travels more than an 8 km straight-line distance in a day, only a small fraction of the home range can be exploited from any particular position in any given day. As a result, not all habitat types will be equally accessible, even if we lump data over the entire annual cycle.

Wildlife biologists have recently taken enormous strides in overcoming this intrinsic bias. The key is in thinking about the movement process itself. One simple way to characterize movement is simply to measure the distance between subsequent fixes over constant time intervals (termed steps) and the degree to which an animal deviates in direction from one step to the next (termed the turn angle). Such a distribution of steps and turn angles for elk in southern Ontario, Canada is shown in Fig. 3.5. Like most organisms, elk tend to make many short "steps" punctuated by a small number of long ones. While searching for food patches, elk tend to move in fairly straight trajectories, whereas they tend to turn tightly and take shorter steps once they have located a patch with abundant food (Hazell 2006; Fryxell *et al.* 2008).

By randomly sampling from such distributions of step length and turn angle, one can hazard a reasonable guess about the locations that an animal could have plausibly visited as it moved from one point in time to the next. This procedure is very similar to that described for resource selection functions, except that the set of available habitat types is defined by the points that are plausible in light of the observed movement process, hence the method is called a *step selection function*. By taking a random sample of 200 points realistically arrayed around every elk fix, Fortin *et al.* (2005) were able to estimate which local habitat variables were most highly preferred by elk in Yellowstone National Park. Using this procedure, they demonstrated that elk tend not to move away from roads and preferentially move towards stands of aspen trees or open grasslands when wolves are rare in the vicinity, but move preferentially towards coniferous forest when wolves are locally common. This suggests that elk are able to make a subtle assessment of the relative value of food versus predation risk. When risk is high, elk tend to choose sites with heavy forest cover, presumably for concealment, whereas

when risk is low they choose sites that offer better opportunities to feed on grasses or young aspen saplings, which are their preferred food resources.

This general approach using distributions of movement steps and turn angles has come into wide use in a variety of other contexts, allowing behavioral ecologists to predict better patterns of dispersal from newly-established versus long-standing populations (Ovaskainen *et al.* 2008), alternation in movement behavior between exploratory and encamped "phases" (Morales *et al.* 2004), and identification of seasonal and daily cycles of movement behavior for animals of different social rank (Wittemyer *et al.* 2008). A useful new framework for developing such integrated models of animal and plant movement is nicely outlined in Nathan *et al.* (2008).

Mechanistic movement models can also be used to develop a deeper understanding of the critical factors shaping animal home ranges. For example, behavioral studies



Fig. 3.5 Distribution of step lengths and turn angles for Ontario elk while foraging (top) and while searching for new foraging sites (bottom) and Yellowstone elk (next page). (Source: Hazell, 2006. Reproduced with permission of Megan Hazell, AMEC E & I, Toronto, Ontario, Canada.)





of coyote home range behavior suggest that individuals use scent-marking both to establish their own presence and as a means of assessing the identities of intruders on to their home range. The typical response to the presence of a foreign scent-mark is to mark on top of the intruder's scent, but then move away towards the center of the home range. By the same token, the size of movement "steps" tends to be small when prey abundance is high but large when prey abundance is low. As a result, coyotes tend to linger for long periods of time in parts of the home range with lots of prey (rodents and hares) but quickly move on to better opportunities when prey are scarce, a process termed *area-restricted search* (Smith 1974; Benhamou 1992).

Combining the process of habitat selection with that of movement, Moorcroft and coworkers (Moorcroft and Lewis 2006; Moorcroft *et al.* 2006) developed a predictive model of the home range that would eventually be formed by a population of coyotes that obeyed these mechanistic movement rules. Their model did a good job of explaining observed patterns of coyote home ranges in Yellowstone National Park.

Fig. 3.6 Home range use by Yellowstone coyotes in relation to prey (shading) and neighboring individuals. (Source: Moorcroft *et al.*, 2006. Reproduced with permission of The Royal Society.)



The coyote home ranges are clustered in the valley bottoms, because that is where prey are most abundant in this montane landscape (Fig. 3.6). No single coyote can monopolize the valley, however, because of the movement response to neighboring individuals. As a result, coyote home ranges become evenly strung out, like beads on a necklace, due to the coyotes' aversion to home range overlap but common interest in exploiting spatially clumped prey.

While mechanistic in nature, Moorcroft and Lewis's (2006) movement model does not necessarily maximize fitness of the individual. Other researchers have however taken this tack in trying to develop predictive home range models from first principles. For example, Mitchell and Powell (2004) developed an explicit model of trade-offs in time versus energy gained for a single individual black bear gathering a variety of resources across a complex landscape. Their model predicts that there are diminishing returns for an animal that tries to utilize too large a home range, as a result of both time wasted in travel from the home range center and resource depletion by neighboring animals. Hence, low home range overlap could be a natural consequence of animals striving to maximize their net energy gain, rather than avoidance of competitors.

In a follow-up to the underlying logic of these spatial movement models, Moorcroft and Barnett (2008) showed that the equilibrium spatial distribution of any animal following mechanistic movement rules should be scaled to the resource selection function. This suggests that animal home ranges, movement patterns, and habitat preferences are all intertwined as a bundle – opening exciting new opportunities for synthetic work in the future.

# 3.8 Movement among home ranges

The traditional view of home ranges is predicated on the notion that animals have well-defined homes in the first place. This is true, of course, for many species. On the other hand, some wildlife species have no fixed address at all, but rather wander over a large area each year. With this kind of movement variation, it is often convenient to consider whether patterns of movement are repetitive (i.e. is there a tendency to return to places visited before or not?) and whether movements of multiple individuals are coordinated. A cyclical pattern of movement by individuals among two or

more non-overlapping home ranges at different seasons of the year is termed *migration*, whereas *nomadism* refers to unpredictable patterns of movement among multiple non-overlapping home ranges (Mueller and Fagan 2008). Animals whose movements fall within a single boundary all year long are termed *residents*. Within each of these categories there are examples of species that move as a group and share the same home ranges at different points in time, as well as of those whose movements are independent of each other (Fig. 3.7).

A well-known example of a migratory species that moves en masse from one location to another in a periodic manner (Fig. 3.7b,c) is the Serengeti wildebeest, whose annual migration takes it from the arid Serengeti Plains to the moist woodlands of the Tanzania–Kenya border and back again. Offspring production takes place in a 3–4 week period while the wildebeest are on the plains; the precocious young then travel with their mothers, even during lactation. Recent models suggest that movements of Serengeti wildebeest track the wave of new grass growth triggered by monsoonal rainfall patterns, which sweep across the Serengeti landscape in an annual cycle



Fig. 3.7 Conceptual examples of (a) resident behavior, (b,c) migration, and (d,e) nomadism. (Source: Mueller and Fagan, 2008. Reproduced with permission of John Wiley & Sons Ltd.)

(Holdo *et al.* 2009). By relocating periodically to areas with new grass growth, wildebeest obtain more energy over the annual cycle than would be possible for an animal remaining in any single part of the migratory pathway. A secondary benefit is that wildebeest also make themselves less available to predators, such as lions and hyenas, which are far less mobile and are unable to track herds across the entire annual pathway (Fryxell *et al.* 1988).

There are lots of other species that migrate en masse, including red crabs on Christmas Island, hawks and vultures migrating from North to South America each winter, and jellyfish in the Pacific Ocean. Other migrations are conducted by individual animals moving independently of each other, such as Monarch butterflies; although the majority of the population has an overwintering site high in the forested mountains outside Mexico City, multiple generations of offspring fan across North America during the spring and summer, before a single generation of butterflies returns home to Mexico in the autumn (Flockhart *et al.* 2013). This pattern of movement allows different generations of Monarch butterfly to find appropriately aged stands of their single food source: milkweed plants. Return to Mexico allows individuals to overwinter as part of a truly spectacular aggregation.

A similar pattern of migration is often seen in many ungulates in montane environments. For example, elk, red deer, mule deer, and pronghorn antelope move from low elevations occupied during the winter to high-elevation pastures in the summer (Bischof et al. 2012; Monteith 2011; Middleton et al. 2013). By taking advantage of variation in the timing of snow melt and subsequent green-up at different elevations, it is possible for migrants to improve access to the most nutritious forage available across the montane landscape (Hebblewhite et al. 2008; Bischof et al. 2013). Although different individuals fan out to independent summer home ranges, migrants must often pass through narrow valley corridors as they move upwards in elevation. Such narrow corridors can become critical habitat if competing human concerns, such as oil rigs or other industrial developments, block the passageway. Such blockages are increasingly common on a crowded planet, where migrants must share limited real estate with humans. This is a pressing concern in montane environments, where suitable terrain for human and wildlife use is in particularly short supply (Berger et al. 2006; Sawyer et al. 2009). There is also growing evidence that while elevational migration improves access to food resources, it can also expose migrants to heightened risk of mortality en route, perhaps due to increased exposure to multiple predator territories or to a lack of familiarity with refugia along the way (Nicholson et al. 1999; Hebblewhite et al. 2008, 2012; Middleton et al. 2013).

Many of the most impressive movements are conducted by nomadic species, whose movements take them unpredictably across a vast landscape (Fig. 3.7d,e). A spectacular example is the Mongolian gazelle, which roams unpredictably across the steppes of eastern Mongolia. This grazing species has a well-defined preference for pastures that are at an intermediate level of abundance, rather than the tallest grass swards (Mueller *et al.* 2007), probably because of trade-offs between cropping rate and nutritional quality. In semi-arid environments, the location of suitable pastures is uncertain, because rainfall is highly unpredictable in both space and time. Monitoring of radio-marked animals (Mueller *et al.* 2011), supported by herd distributions conducted from lengthy ground transects (Mueller *et al.* 2008), suggests that gazelles continually shift nomadically across this unpredictable landscape, lingering at sites with suitable pasture much more reliably than at poorer sites (Fig. 3.8), so that a dynamic landscape feature





(grass biomass) represents a continuous habitat variable that is well correlated with home range use, at least at short timescales. Human pastoralists in the same region adopt a similar land use strategy, moving nomadically with their herds of yaks, sheep, and goats in search of short-lived patches of suitable pasture.

Fitting home range models to migratory or nomadic species obviously presents challenges. For a seasonal migrant, one might demarcate seasonal ranges, restricting habitat assessment to particular periods of the year. For truly nomadic species, home range analysis has to be conducted at multiple times per year in order to provide a useful picture of the area meaningfully occupied and for habitat assessment at any point in time. It is still possible to assess patterns of space use and habitat utilization, however, provided that the spatial frame of reference is well specified and fits the animal's lifestyle (Mueller *et al.* 2007).

#### 3.9 Summary

Animals tend to move within a restricted home range that defines those areas used in their effort to acquire resources, seek suitable mating sites, and avoid predators. There are various ways in which home ranges can be identified from sequential location data obtained from marked animals, including simple convex polygons, adaptive or fixed kernel distributions, and local convex hulls. Comparisons across animal taxa suggest that home range size has an allometric relationship with body size, with different relationships in herbivores and carnivores, as well as in animals living in aquatic versus terrestrial environments.

The nonrandom positioning of home ranges in the larger landscape and the preferential use of parts of the home range suggest preferential use of specific habitats. We discuss various ways that habitat data are typically gathered for use in preference studies, as well as the telemetry data that are now routinely applied. Habitat selection can be measured in a variety of ways, including comparisons of use versus availability and more complex nonlinear resource selection functions. The methodology, strengths, and limitations of each of these statistical approaches are briefly examined.

Habitat selection is shaped by a variety of behavioral and ecological variables, including availability, consumer density, social processes, movement mechanics, optimal foraging, and anti-predatory behavior. Fitness-based movement rules, heterogeneous resource distribution (as well as risk), and social interactions can be linked to predict patterns of habitat use and home range shape.