
3 Vertebrate Habitat Selection

Managing forests to produce a desirable mix of forest resources, including timber products and wildlife species, requires an understanding of how animals respond to habitat in forests. Habitat provided within and among *stands* (units of homogeneous forest vegetation used as the basis for management) over a *landscape* (a complex mosaic of interacting patches including forest stands) can have significant effects on the abundance and distribution of animal species. Management strategies aimed at long-term population change are most likely to succeed if they alter habitat quantity, quality, and/or distribution. Knowing how species select habitat can provide clues as to what habitat elements to provide. *Habitat elements* are those bits and pieces of a forest important to many species, such as vertical structure, dead wood, tree size, plant species, and forage. We will cover these in more detail in Chapter 4.

Habitat selection is a set of complex behaviors that a species has developed among individuals in a population to ensure fitness. These behaviors are often innate and have allowed populations to persist under the variable conditions that occur over time in forests (Wecker 1963). These behaviors have also allowed each species to select habitat in a manner that allows it to reduce competition for resources with other species. So the evolutionary selection pressures on each species, both abiotic and biotic, have led species to develop different strategies for survival that link habitat selection and population dynamics. Some species are *habitat generalists*, and can use a broad suite of food and cover resources. These species tend to be highly adaptable and occur in a wide variety of environmental conditions. The deer mouse is a species that exemplifies this strategy in that it can be found in all stages of forest development and in many *forest types* across the United States. Deer mice have high reproductive rates and can demographically take advantage of abrupt increases in food and cover resources (Figure 3.1). This species is also a primary food resource for many forest predators. Hence, providing habitat for deer mice in a forest is quite easy, although they do tend to be more abundant in early successional forests than in late successional forests.

Other species are *habitat specialists*. These species are adapted to survive in forests by capitalizing on the use of a narrow set of resources and the resources that they are better adapted to use than most other species. Consider where you might find spring salamanders in the eastern United States or torrent salamanders in the western United States. Both species occur in clear, cold headwater streams and they tend to be most abundant where fish are excluded from the streams because fish are their predators. Both species are of interest to wildlife biologists due to the concern that forest management activities that reduce canopy cover and raise stream temperatures could threaten populations of these species (Lowe and Bolger 2002, Vesely and McComb 2002). Clearly though, habitat generalists and specialists are simply two ends of a spectrum of species' strategies for survival in forests faced with variable climates, soils, disturbances, competitors, and predators.

HIERARCHICAL SELECTION

Many studies have been conducted to assess habitat selection by forest wildlife species. The assumption made by biologists is that if we can understand what characteristics of the environment are selected by a species, then we can infer what characteristics we may wish to provide during forest management to accommodate them in our stand or forest. There are some concerns surrounding this assumption that we shall explore later, but the vast majority of information that we have available to manage habitat for species comes from these habitat selection studies. Consequently, we need to understand which level of habitat selection we can influence for a species through our forest



FIGURE 3.1 Deer mice are habitat generalists that use a wide range of forest conditions. (Photo by Mike Jones. With permission.)

management activities. Johnson (1980) suggested that many species select habitat at four levels and called these levels first-, second-, third-, and fourth-order selection (Figure 3.2).

WHERE IN THE WORLD SHOULD I LIVE?

First-order selection is selection of the geographic range. The geographic range defines, quite literally, where in the world this species can be found. In our example from Figure 3.2, pileated woodpeckers are found in forests throughout the eastern and western North America. Now consider two extremes. In Figure 3.3, I have provided geographic range maps for two species: Weller's salamander, found in spruce forests above 1500 m (5000 feet) in the southern Appalachians, and black-capped chickadees, found throughout the northern U.S. and southern Canada. The geographic range for humans is global, with infrequent excursions to other planetary bodies! Of course, the geographic range for a few other species is also global: cockroaches, Norway rats, and other human *commensals* (species that are typically associated with humans). So why is it that some species occur around the world and others are restricted to a few mountains in the Appalachians? Climate and history have had some effect on the distribution of some species. There is a complex set of geographic distributions for slimy salamanders in the southeastern U.S. that likely result from past

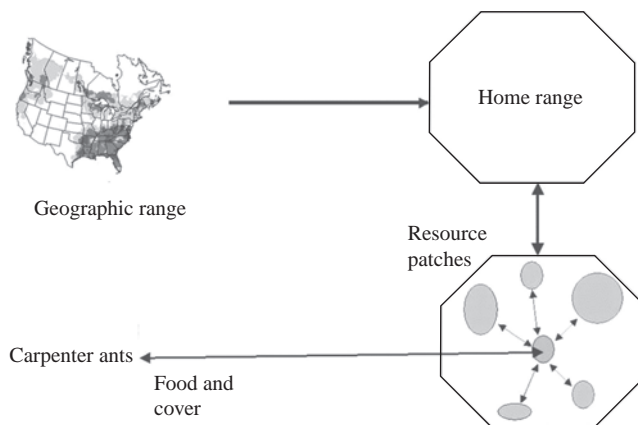


FIGURE 3.2 Hierarchical habitat selection as described by Johnson (1980). This generalized concept is illustrated using pileated woodpeckers as an example. (Range map from USGS Biological Resources Division.)

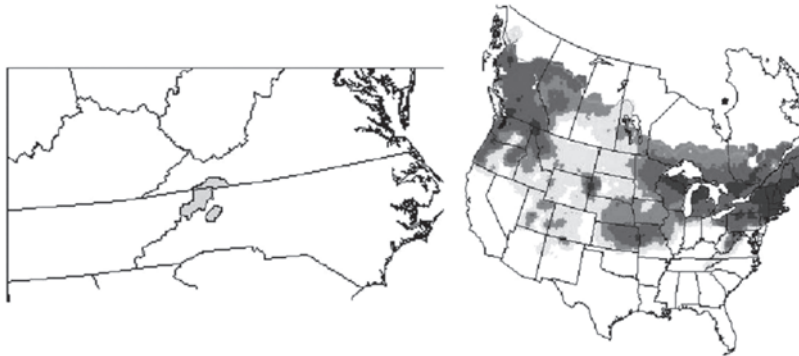


FIGURE 3.3 Range maps for a geographically restricted species, Weller’s salamander (left) and a cosmopolitan species, black-capped chickadee (right). (Maps from USGS Biological Resources Division.)

glaciation that has “packed” species into the southern Appalachians, in combination with species that have limited capabilities to disperse from one valley to another (Figure 3.4). Similarly, other species such as the Siskyou mountain salamander may have been more widely distributed during periods when the northwest was cooler and wetter. This species became more and more restricted as the climate has changed and now only occurs in a small region of southern Oregon and northern California.

In another example of the role of barriers as a mechanism for limiting the geographic distribution of organisms, consider that the Columbia River is the dividing line separating the geographic distribution of the western red-backed vole in Oregon and of Gapper’s red-backed vole in Washington. One can only guess how this might all change when one or more of them hitches a ride in an RV across the Dalles bridge! Humans, of course, have been important mechanisms for dispersing species into places that are climatically acceptable for a species but barriers had kept species separated until humans moved them. The list of examples is growing rapidly, but includes those well-known such as European starling, tree-of-Heaven, and gypsy moth. Humans are breaking down barriers and allowing opportunities for exotic species to become invasive. Implications for native flora and

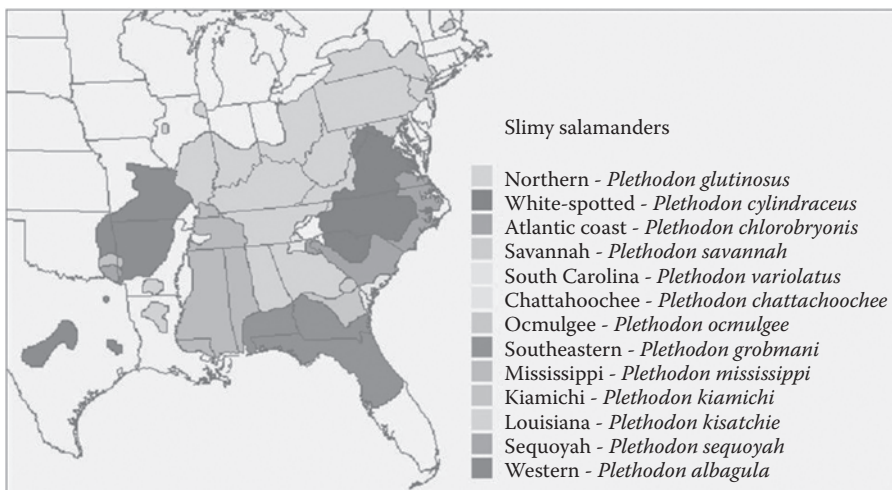


FIGURE 3.4 Distribution of a complex of slimy salamander species in the southern U.S. (Maps from USGS Biological Resources Division.)

fauna can be huge, and the geographic ranges of some native species can be significantly altered as these invasive species proliferate. The influence of hemlock woolly adelgid on eastern hemlock mortality has led forest managers to extensively salvage dead hemlocks (Howard et al. 2000). This mortality and forest management has led biologists to worry about declines in the distribution and abundance of black-throated green warblers and other hemlock-associated species (Yamasaki et al. 2000). Invasive species can also influence forest wildlife populations by predation. In Western Australia, a species of marsupial known as the woylie was once widespread over Western Australia, but by 1980 had been reduced to three small populations due to the expansion of introduced red foxes (Figure 3.5). With recent widespread control of foxes using warfarin poisons (woylies are not affected by this poison because it occurs naturally in shrubs in their environment), populations have once again begun to expand.

Species geographic ranges have also been influenced by invasive competitors. Recently, barred owls have been found within the geographic range of northern spotted owls in the Pacific northwest of the United States. There is increasing evidence that the northern spotted owls are declining in abundance in the presence of barred owls (Peterson and Robbins 2003, Livezey 2010), and there is clear evidence that the two species are hybridized (Hamer et al. 1994).

Just as humans have been the cause of changes in geographic ranges through species introductions, they have also been responsible for recovering species from areas where they were extirpated. Translocation efforts and re-establishment efforts have been successful in species recovery (Haight et al. 2000). For example, the red-cockaded woodpecker is a threatened species that occurs in forests of the southeastern United States. This species requires old, living pines with heart rot in which to nest. As trees grow and forests age, areas of suitable habitat can be recruited. Rudolph et al. (1992) demonstrated that re-establishment of this species in this newly recruited habitat is possible. There are numerous similar examples of successful reintroductions for game species such as wild turkeys.

Consider the importance of populations of a species at the center vs. the periphery of its geographic range. Populations at the periphery may be in lower quality habitat if either biotic or abiotic factors are limiting its distribution. But recall that environments are not static. They are constantly

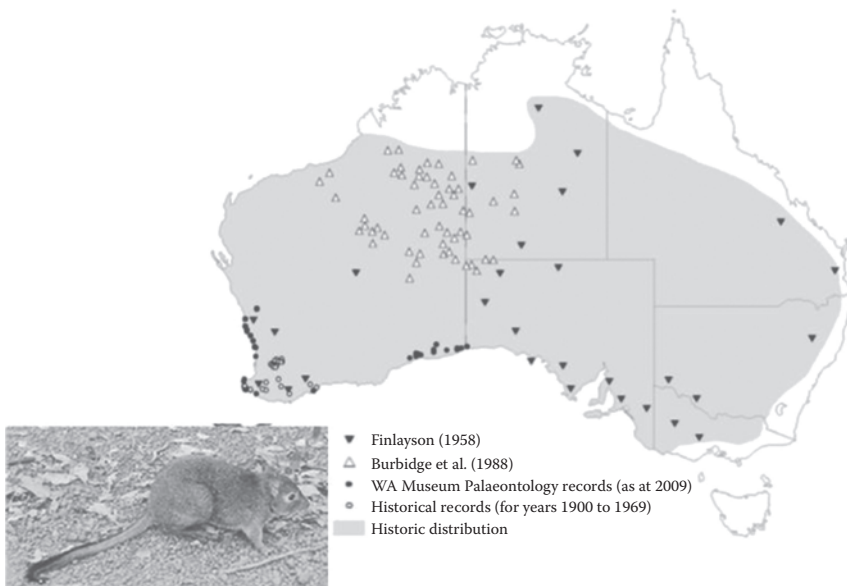


FIGURE 3.5 Past and current distribution of the woylie, a woodland marsupial. The introduction of red foxes reduced the geographic range of the mid-sized marsupial. (Map from the Department of Parks and Wildlife, Western Australia. With permission.)

changing. Climate changes, earthquakes change the topography, some species arrive while others leave. It is those populations at the periphery of their geographic range that are on the front line of these changes. Although it may be tempting to think of these peripheral populations as somewhat expendable, they may be critical to population maintenance as large-scale changes in habitat availability occur. Given the rate at which climate is changing, these peripheral populations may be even more important over the next few hundred years.

Although Johnson (1980) does not describe *metapopulation* distribution as a selection level, it is important to realize that within the geographic range, populations oftentimes are distributed among smaller, interacting populations that contribute to overall population persistence, or a metapopulation structure. Hence, these subpopulations may grow, go extinct, and be recolonized as habitat quality changes following forest disturbance and regrowth. The distribution of the subpopulations is important to consider during forest planning because if dispersal among subpopulations is restricted by forest management actions, then the subpopulations that might ordinarily be recolonized may be restricted from doing so.

LOOKING FOR A HOME IN A NICE COMMUNITY

Johnson (1980) described *second-order selection* as the establishment of a *home range*, an area that an individual or pair of individuals uses to acquire the resources that it needs to survive and reproduce. Not all species have established home ranges, but most do. Species that have nests, roosts, hibernacula, or other places central to its daily activities move in an area around that central place to acquire food, use cover, drink water, and raise young. Home ranges are not the same as territories. A *territory* is the space, usually around a nest, that an individual or pair defends from other individuals of the same species and occasionally other individuals of other species. Territories may be congruent with a home range, smaller (if just a nest site is defended), or may not be present at all. Many bird species, such as eastern bluebirds, defend a territory around a nest that includes the nest site and an area within which the pair finds food to feed their young. Other species such as fox squirrels defend a nest or den site when raising young, but have a home range that overlaps with other individuals. Species such as flying squirrels seem not to establish territories and coexist with other individuals within their home range.

Home ranges vary in size with the body mass of the species (Figure 3.6). Species with larger body mass need more energy to support that mass. Herbivores tend to have smaller home ranges than carnivores of the same size, because energy available to herbivores is more abundant but also

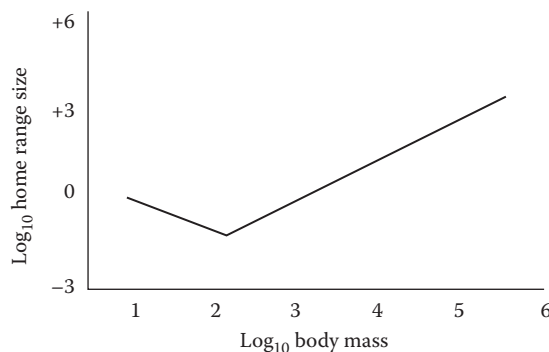


FIGURE 3.6 Relationship between body mass and home range size. Home range sizes are smallest for those species with body mass of ~100 g, and greater for sizes that depart from this size. (Based on data by Kelt, D.A., and D. VanBuren. 1999. *Ecology* 80:337–340; adapted from Harestad, A.S., and F.L. Bunnell. 1979. *Ecology* 60:389–402.)

because with each increase in trophic level there is a decrease in energy availability. A *trophic level* is the feeding position in a food web: Primary producers are typically plants, primary consumers are herbivores, secondary consumers are carnivores, and tertiary consumers are carnivores that eat carnivores. Hence, there is an energy or biomass pyramid, with more biomass in producers than in herbivores and more biomass in herbivores than in carnivores.

Home range sizes also vary among individuals within a species. As food resources are less abundant or more widely distributed home range sizes increase. But within a species, the home range size has an upper limit that is governed by balancing energy input from food with energy loss by movement among food patches. For instance, Thompson and Colgan (1987) reported larger home ranges for American marten during years of low prey availability than in years of high prey availability.

BUYING A HOUSE AND BUYING GROCERIES

Third-order selection is the use of patches within a home range where resources are available to meet an individual's needs. Biologists often can delineate a home range based upon observed daily or seasonal movements of individuals going about their business of feeding, resting, and raising young. But this area is not used in its entirety. Rather there are some places within the home range that are used intensively and other parts of the home range that are rarely used (Samuel et al. 1985). Selection of these patches is assumed to represent the ability of the individual to effectively find and use resources that will allow it to survive and reproduce. But as Garshelis (2000) makes clear, simply the amount of time or number of radio telemetry locations in a particular patch type does not necessarily reflect the importance or lack thereof to an individual. An individual may spend a small amount of time and be represented by relatively few locations in a particular patch type but receive important benefits from that patch type. For instance, you may spend 10% of your time in your kitchen and 30% of time in your bedroom, but the resources that you receive from your kitchen are as important, or more important, than the rest that you receive in the bedroom. It is exactly those resources located in the patch types that are most important to maintaining an animal's fitness.

WHAT WOULD YOU LIKE FOR DINNER?

Fourth-order selection is the selection of specific food and cover resources acquired from patches used by the individual within its home range. Given the choice among available foods, a species should most often select those foods that will confer the greatest energy or nutrients to the individual. Which food or nest site to select is often a trade-off among availability, digestibility, and risk of predation (Holmes and Schultz 1988). Factors that influence the selection of specific food and cover resources most often tend to be related to energetic gains and costs, but there are exceptions. The need for certain nutrients at certain times of the year can have little to do with energetics and much to do with survival and fitness. For instance, band-tailed pigeons seek a sodium source at mineral springs to supplement their diet during the nesting season (Sanders and Jarvis 2000).

Collectively, these levels of habitat selection influence the fitness of individuals, populations, and species. Habitat quality is dependent not only on the food and cover resources in the stand or forest but also the number of individuals in that stand. Many individuals in one stand means that there are fewer resources per individual. Habitat quality and habitat selection is density dependent. Indeed, even if a patch has excellent, but a fixed quantity, of food and cover quality, too many individuals in the patch can cause some to leave to find other habitat patches of lower quality, but which have fewer individuals.

DENSITY-DEPENDENT HABITAT SELECTION

Fretwell and Lucas (1969) provided the conceptual basis for understanding density-dependent habitat selection. Consider a fixed level of resource availability in two patches, with resource

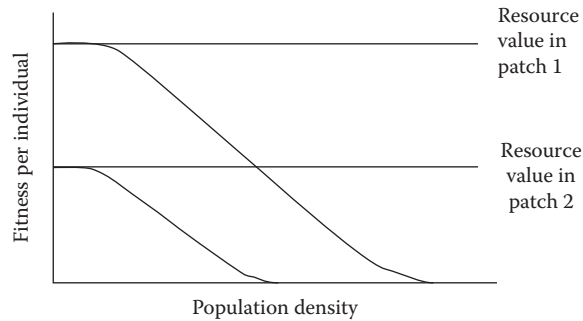


FIGURE 3.7 In the above diagram, the top horizontal line represents a fixed amount of resources in patch 1; the lower horizontal line represents the fixed amount of resources in patch 2. The resulting selection of habitat is dependent on the density of individuals in each patch. (Adapted from Fretwell, S.D., and H.L. Lucas Jr. 1969. *Acta Biotheoretica* 19:16–36.)

availability in one patch higher than that in another (Figure 3.7). As the population density in patch 1 increases, the resources available per individual and hence fitness per individual declines. Eventually at a high enough population density, the fitness per individual declines to a point where each individual is afforded a level of resources that would be less than what they received if they moved to patch 2, a patch with lower total resource availability than patch 1. Consequently, the selection of patch 1 and ultimately patch 2 by some individuals is influenced by the populations in each patch.

Under this approach, each individual is free to choose the patch that will provide the greatest energy or other required resources. This concept is called the *ideal free distribution*. But in many populations, especially those that have a dominance hierarchy or are territorial, some individuals are less likely to move to patch 2 and some are more likely to move. Consider the case where the species occupying patch 1 initially is territorial and as more individuals are added to the population each defends a specific territory. Territories help to ensure that individual fitness will not decline, and that each individual or pair in the patch remains fit. Eventually the patch will be saturated with territories and you cannot pack another territory into patch 1. If the territorial individuals are successful in patch 1, and they are successful at defending their territory from interlopers, then they help to ensure their fitness. Of course, the cost of territoriality is the energy expended defending it. Subordinate individuals in the population, those unable to displace an individual already on a territory, are relegated to patch 2. This situation represents an *ideal despotic distribution* where individual fitness is maintained in the highest quality patches at lower than expected densities through territoriality.

If the individuals in a patch are fit enough to support a stable or growing population, that is they are able to sustain that population through reproduction and survival, then they occupy a *source habitat*—one with high individual fitness. If the individuals in a patch have low reproduction and survival rates, often insufficient to maintain the population, then they occupy a *sink habitat*. It is important to keep in mind that in the Fretwell–Lucas example, both patch 1 and patch 2 could be source patches, or sink patches, depending on how the populations are maintained in each patch.

Since resources are already restricted in a sink habitat, increasing the density of territorial species may cause individuals to abandon territorial behaviors, not reproduce successfully, or face a higher risk of mortality. Indeed in some sink habitats, densities of individuals can be much higher than in source patches because in source patches individuals remain territorial, but in sinks they may not be territorial. Consequently, using density as an index to habitat quality may be inaccurate. Animal fitness is a better indication of habitat quality than animal numbers. Reproductive success, survival, and body mass are all indicators of animal fitness (Van Horne 1983).

RELATIONSHIP BETWEEN HABITAT QUALITY AND DEMOGRAPHICS

Foresters manipulate stand density to ensure that the trees that will eventually be harvested have sufficient resources to grow rapidly, produce seeds, and survive to maturity. Biologists do much the same thing when managing habitat for animals. Populations can be manipulated by modifying habitat and thereby influencing possibilities for survival and reproduction, the two primary indices to fitness. The linkages between animal demography and habitat are complex, but some understanding of these relations is necessary for successful habitat management. Each species has its own potential for population increase, and this potential is described as the *intrinsic rate of natural increase*. There is a solar constant so energy available to plants and animals is limited. Given adequate food, cover, and water populations will grow. But consider what happens as the density of individuals increases. Food becomes scarcer or of poorer quality as the population grows. Cover is occupied by more individuals so the risk of disease and parasitism increases. Intraspecific (among individuals of the same species) competition for resources causes some subordinate individuals to use suboptimal patches. As food, cover, or other resources become limited, the population growth rate decreases, due to either mortality increases or reproduction decreases, or both. This process is termed *logistic growth* (Figure 3.8). If we assume that resources are constant, then the population reaches a point where births equal deaths and growth becomes 0. This point is termed the *carrying capacity* of the habitat for the population.

But resources are not constant; they change daily, seasonally, and annually. Birth rates, death rates, and movement rates are variable over both space and time as habitat changes through forest disturbances and succession. Carrying capacity, consequently, is always changing. The concept of a *dynamic carrying capacity* is useful to land managers because it provides the link between the dynamics of forests, habitat quality, and population growth. Manipulating habitat to change carrying capacity is a particularly effective approach to long-term manipulation of wildlife populations.

But populations do not always reach carrying capacity in relation to habitat quality. Some species, such as voles, snowshoe hares, and ruffed grouse, follow a “boom and bust” population pattern. Populations grow for about 3–6 years and then rapidly decline for another 3–6 years. High-quality habitat usually increases the highs and decreases the lows of a population cycle, but habitat probably

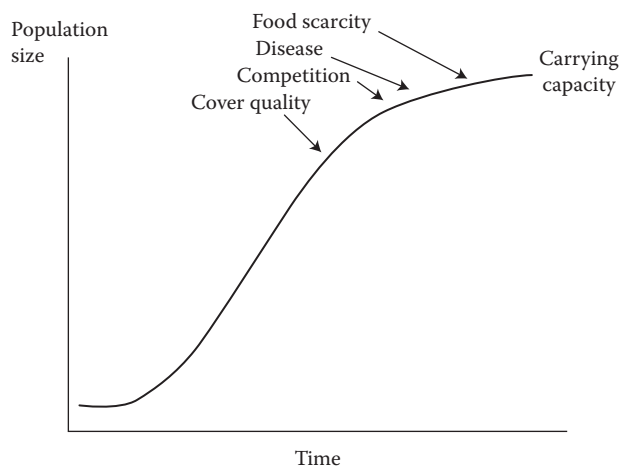


FIGURE 3.8 Population growth over time assuming fixed resource availability results in a carrying capacity where births balance with deaths and the population remains somewhat stable. In actuality carrying capacity is quite dynamic as resources change over time and space. (Adapted from McComb, W.C. 2001. *Wildlife Habitat Relationships in Oregon and Washington*. OSU Press, Corvallis, OR.)

does not directly mediate these cycles because they occur throughout much of the geographic range of the species (Keith and Windberg 1978).

POPULATION FITNESS

Individuals are fit when they have a high probability of surviving and reproducing successfully. Population fitness is high when the population is increasing or at least not declining. Individuals with high fitness can occur in populations with low fitness and vice versa. Since it is populations, and not individuals, that are sustainable over the long term, we need reliable indicators of habitat quality using population fitness. Habitat quality refers to the ability of a locality to provide for the long-term persistence of a population over time. Biologists tend to measure the habitat quality based on vital rates of the population. If a population is reproducing at an optimum rate and survival of young and adults is high, the habitat is considered as high quality. *Vital rates* are the demographic parameters that drive population change, primarily birth rates and death rates.

The rate at which animals reproduce is a basic component of population dynamics. Two measures of reproductive fitness are natality and fecundity. *Natality* refers to number of young individuals born or hatched per unit of time. *Fecundity* is the number of young produced per female over a given time period and relates population fitness to the average fitness per female. Usually, 1 year is the time period considered, but for smaller animals, especially those that may breed several times a year, a shorter time period may be selected. Thus, if a population of 1000 female bears produced 200 young in a year, the birth rate, or fecundity, would be $200/1000 = 0.2$.

A number of factors affect a population's birth rate. Animals that are young or in poor nutritional condition usually have fewer young and/or breed less often. Age at first reproduction is also an important factor in determining birth rate. Large, long-lived animals typically do not become sexually mature until they are several years of age. A vole might become sexually mature and breed for the first time at 18 days of age. An Asian elephant on the other hand will typically be 9–12 years old when it first breeds. The birth interval is also important in determining birth rates. A vole might produce a litter of young every 30 days during the breeding season, but a grizzly bear may only reproduce every 3 or 4 years. The average number of young produced is of obvious importance in a population's birth rate. Some animals, such as fish or amphibians, produce hundreds or thousands of eggs (not all of them hatch and few survive), while many species only have one or two young at a time (e.g., barred owls). Potential population growth rates are related to fecundity rates. A doubling in the fecundity rate will more than double the population growth rate.

Mortality rate is another indicator of population fitness. Mortality rate is measured as the number of animals that die per unit of time (usually 1 year) divided by the number of animals alive at the beginning of the time period. Thus, if 1000 fawns are born in June and 400 are alive the next June, then the mortality rate is 600 (the number that died)/ $1000 = 0.6$ or 60%. Survival and longevity are two other population parameters related to mortality. *Survival* is the number of animals that live through a time period and is the converse of mortality. Thus, if the mortality rate is 0.8 or 80% per year, then survival would be 0.2 or 20% per year. *Longevity* is the age at death of the average animal in a population.

Mortality rates are usually age—and often sex—specific, which means that animals of different ages or sexes die at different rates. In many species, the young and old animals die at faster rates than the mid-aged animals. Often, males have higher mortality rates than females because of activities associated with territorial or mating behavior.

Different species have different *survivorship functions* related to their life-history traits. A type I *survivorship curve* would be typical of animals that have relatively high survivorship until later in life when they become subject to age-related mortality (Figure 3.9). Typically, these are animals with a high degree of parental care. Many larger mammals, such as whales, bears, and elephants, might have type I survivorship curves. Some animals have fairly constant survivorship (type II). Some birds and most reptiles and amphibians probably fit this pattern, although our knowledge

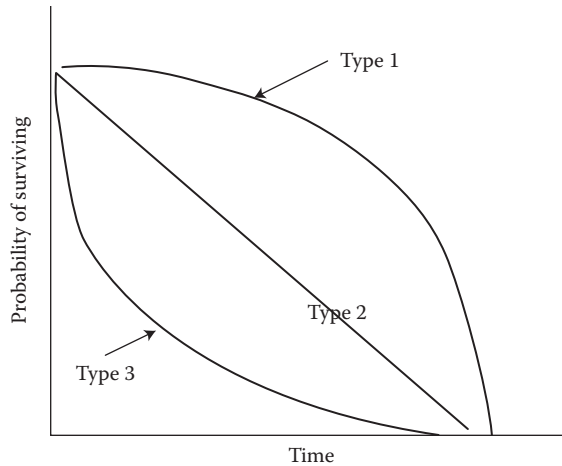


FIGURE 3.9 Survivorship curves for three example species. Type 1 species have high juvenile survival rates while type 3 species have low juvenile survival rates.

of survivorship in birds is not very complete because they are difficult to study. A type III survivorship curve would be typical of animals with little or no parental care and/or vulnerable young; mortality is high in the young age classes and low in older animals. Insects and fish often have type III survivorship curves.

MEASURING HABITAT SELECTION

Clearly, we should use estimators of fitness as a measure of habitat quality and selection. Rarely have biologists taken that approach largely because measures of fitness are expensive and difficult to assess for many species. Usually occurrence or abundance is used although some indirect indicator of fitness such as body mass and evidence of breeding may be used instead. Despite not measuring fitness attributes directly for many species, years of habitat selection research have produced repeatable patterns of use and selection for many species.

Assessing habitat selection is scale dependent. Most information available on habitat relationships of species in forests comes from one of two approaches: stand-based assessments or species-based assessments. In stand-based assessments, comparisons of abundance or occurrence are made between stands of different structure or following different treatments. This information can be very useful if the animal response is matched to the scale of the stands. For instance, we would not use number of northern goshawks detected in thinned and unthinned stands that are 10–15 ha in size (second-order selection) as a response variable because the home range of one goshawk could encompass many stands. Rather we might ask if stands were selected by goshawks for foraging (third-order selection) within their home range or if particular nest structures were used in these stands (fourth-order selection). Alternatively, we might place radio transmitters on goshawks and analyze the stand types used in comparison to their availability in each home range. Both approaches provide useful information, and both have potential weaknesses.

When considering how animals use habitat in forests, it is important to differentiate between use and selection. Animals can be found in various types of forest conditions. We occasionally find a species that is typically found in early successional stages occurring in old-growth forests and vice versa. We may find dispersing spotted owls in urban settings. It is important to know why they were found in these settings. Were they forced there by more dominant (and fit) individuals? Did random dispersal bring them there by chance? Are they surviving there? Reproducing? Observations of use can be important information, but they must be placed into the context of why the animal is found in these places.

Selection is the choice of one or more patch types among those that are available. For example, say you were able to make 100 unbiased observations of American marten—80 in old forest and 20 in young forest. Within your study area old forest comprises 40% of the area and young forest comprises 60%; therefore if marten were using the area randomly (no selection), you would expect 60 observations in young forest and 40 in old forest. In this simple example, marten were using old forest out of proportion to its availability and could be said to “select” old forest. Does that mean that young forest was avoided? Or is unimportant? Not necessarily. If marten were eating raspberries in the young forest during the summer then they may not spend much time there, but that food resource was sought (not avoided) and could contribute to marten fitness. Again, it is important to know why marten were found in these forest types. Further, selection can only be assessed among the choices available to an organism. The organism may actually prefer some other conditions that are not available. Given a choice of a beech–maple forest and a pine forest, a gray squirrel may demonstrate a selection for the beech–maple forest, but it would prefer an oak forest if it was available.

Use–availability studies are further complicated in that too often we classify forests by dominant tree species and/or age class and then see which classes are selected by a suite of species. The classes that were created often are done so based on human perceptions of differences (clearcuts, old-growth, hardwood, conifer) and may only be marginally related to providing the habitat elements needed by the species being assessed. Take, for example, Swainson’s thrush. Swainson’s thrushes are associated with shrub cover where they nest and are found in woodlands where shrub cover is dense. That there are hardwoods or conifers or pole-sized trees or old-growth trees in the overstory is somewhat irrelevant. But how often do we humans classify vegetation based on shrub cover beneath the overstory? And of course, habitat is more than just vegetation. Soils, slope, aspect, and so on could all be mapped and classified, but they would need to be mapped and classified differently for each species. And that too rarely happens. The results of selection studies based on *a priori* classifications of forest condition unrelated to habitat elements important to the species of interest should be viewed with caution.

Ideally, experiments that manipulate resources and measure population vital rate responses are most reliable. For example, if an experiment was designed to test the effects of thinning on ruffed grouse, we would randomly identify the located study sites and sample an aspect of fitness (e.g., survival rates and natality) for at least one full population cycle (~10 years) prior to thinning. Study sites would have to be large to ensure that we could sample multiple individuals in each stand. Since the home range for a ruffed grouse is approximately 4 ha (10 acres), then stands might need to be 120 ha (300 acres) in size, or more. Once the pretreatment data were available, then we would thin a randomly selected group of stands and monitor the same vital rates on the thinned stands as well as on untreated controls for another 10 years. Such an approach may be ideal but in most circumstances it is impractical due to expense and logistics. And for some species, such as those protected under the Endangered Species Act, it may be illegal.

Critical habitat is defined as specific areas that are essential to the conservation of a federally listed species under the U.S. Endangered Species Act, and which may require special management considerations or protection. If the best available information would suggest that thinning would be detrimental to the species, then the experiment above may simply not be allowed in the United States.

In addition, experiments as described earlier present difficulties when assessing species that show high affinity for an area, also called *site fidelity*. Pairs may return year after year to the same location despite drastic changes in the habitat around them. Effects of the treatment may only be apparent once these pairs are gone, because new breeders may not be recruited to this site because it no longer has the cues they look for in a breeding area.

PROXIMATE AND ULTIMATE CUES TO HABITAT QUALITY

Use–availability studies often result in evidence for selection of certain habitat types, tree species, or vegetation structures. These structures are often related to the availability of resources that an

animal needs for survival, but not always. The *ultimate* food and cover resources that each species needs are often found by the species using *proximate cues*. Migratory birds are a good example. As they move from breeding areas to wintering areas they must make choices about where to rest or settle such that food and cover will likely be available for them. In these situations, vegetation structure seems to be a key proximate cue to these choices (Cody 1985).

The *structure* of a forest provides a cue to an animal that certain insect or plant food resources might be available, or that nest sites might be available. These cues may cause animals to establish a territory before (e.g., early spring) the ultimate resources (e.g., foliage-dwelling insects) are even available. Animals use visual, aural, and/or olfactory cues when establishing a territory or home range. Managers can identify the habitat elements that may be proximate cues to habitat selection and ensure that these habitat elements are present for those species that are desired in a stand or forest. Managers manipulate aspects of the stand such as stocking levels, tree density, and tree size but need to consider other specific habitat elements that may or may not be related to traditional stand management for timber production. It may be important to grow a large tree, but if the ultimate resources associated with the large tree (proximate cue) are bark-dwelling insects in deeply dissected bark, then simply having large trees may not yield higher quality habitat. Consider a human example. Humans use proximate cues every day. When we are hungry and need food fast (quality may be a separate issue), we do not go into every building and hunt around for a hamburger but instead look for a proximate cue, for example, golden arches. If the place with the golden arches is out of burgers, then a typically reliable cue did not yield the desired resources, and you spent time and energy for nothing. Providing only proximate cues without considering ultimate resources is no different.

SOCIAL CUES IN HABITAT SELECTION

Say you drive by two restaurants on a Friday evening and the parking lot for one (the Greasy Spoon) is full and the other (The Pie Palace) only has a few cars. Which one would you likely try first? And then you ask your coworkers the next day if they had ever eaten at the Greasy Spoon and they indicate that the food is very good, then you may be even more likely to try eating there. You are using social cues, evidence from your conspecifics that one foraging patch is better than another. Some other animal species are no different. Danchin et al. (2004) described the importance of social cues influencing selection of habitat in a number of species. Subsequent work by Templeton et al. (2009) and Betts et al. (2008) supported the importance of bird song influencing habitat selection. Betts et al. (2008) conducted an experiment testing the effects of vegetation structure (proximate cues) and social information (bird song) in selection of patches by black-throated blue warblers and found that songs emanating from stands with structure completely different from where the bird fledged induced individuals to not only enter the poor quality site to feed but also return the next year and try to breed. It is very clear the social information is a key component of habitat selection for not only humans and warblers but for many other species as well.

CASE STUDY: AMERICAN MARTEN HABITAT SELECTION

American marten are mustelids, members of the weasel family. Their geographic range extends across North America in boreal forests. Females have a home range of approximately 2.3 km² and males, and being larger, have larger home ranges. There has been growing concern that this small carnivore may be adversely affected by intensive forest management in coniferous forests. This case study is based on a study by Potvin et al. (2000), who examined marten habitat selection at stand and landscape scales in intensively managed spruce forests in Quebec. About 10,000 km² of Canada's forests are clearcut each year. A consistent finding among many studies conducted throughout the geographic range of marten is that having more than 20%–30% of an area recently cut leads to declines in marten abundance. That does not necessarily mean that clearcuts are not used by marten. Indeed, some types of food, especially berries and other sugar-rich fruits, may be

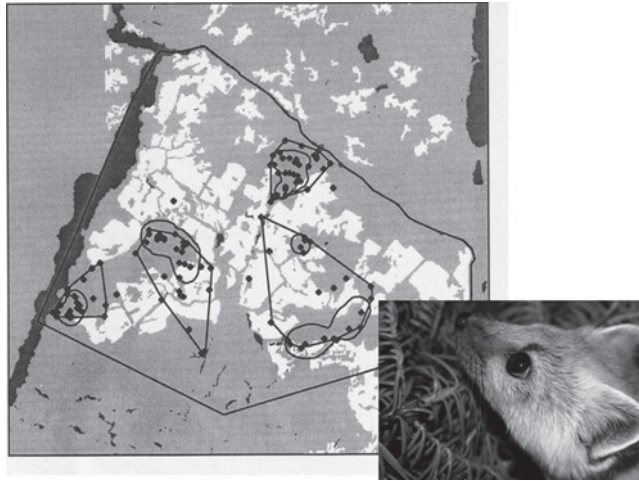


FIGURE 3.10 Radio locations, core areas and 95% polygon home ranges of American marten in Quebec boreal forests. White areas have been recently cut and shaded areas are older forest. (Map from Potvin, F., L. Belanger, and K. Lowell: Marten habitat selection in a clearcut boreal landscape. *Conservation Biology*. 2000. 14:844–857. Copyright Wiley-VCH Verlag GmbH & Co. KGaA. Reproduced with permission; Marten photo by Mike Jones. With permission.)

more available in openings, but if openings cover too large an area, then prey (primarily Gapper's red-backed voles) are not sufficiently abundant at other times of the year.

Potvin et al. (2000) attached radio transmitters to 33 marten and they estimated the winter home ranges for each marten. An example is shown in Figure 3.10. Several things are clear from this figure. First, marten did use regenerating stands but much less than would be expected by chance alone. Second, most locations were in the surrounding older forest. Stands of deciduous and mixed deciduous–conifer >30 years of age were selected out of proportion to availability. Conifer forests >30 years of age were used in proportion to availability. Recent cuts <20 years old where young trees had grown to a point where the crowns closed to form a continuous canopy were also used in proportion to availability, but recent cuts that still had an open canopy were used less than expected by chance.

The landscape level analyses showed similar patterns. Home ranges contained more area in forests >30 years of age and less area than expected of young, open forest. Indeed, marten with smaller home ranges had less area of young, open forest than marten with large home ranges suggesting that marten can find more of their required resources in a smaller area when there is less open, young forest. On the basis of these results and results of studies from Maine and Utah, it seems that marten cannot tolerate >30% of a home range in recent clearcuts, but that once young stands form a continuous canopy they will use the area. Consequently, forest planners developing a harvest schedule can use this information to guide where clearcutting could occur to minimize effects adverse on marten.

SUMMARY

Habitat is selected by many vertebrates at four levels: geographic range, home range, patches within the home range, and the ultimate resources needed for survival. Such selection is assumed to represent a complex set of behaviors that species have evolved to yield high population fitness despite environmental variability. Conspecifics influence selection of habitat in a myriad of ways, including the exchange of social knowledge. Selection of habitat also can be influenced by other species such as competitors and predators. Habitat selection is also density dependent, with the choice of habitat patches influenced by the effects of the population on individual fitness. In territorial species,

subordinate individuals may be forced into sink habitat where survival and reproduction rates may be lower than in source habitat occupied by dominant individuals. Although we often gather information on habitat selection employing use–availability studies, interpretation of these results must be done with caution unless we understand why species are using certain conditions. Lack of selection does not necessarily imply avoidance. Although experimental approaches that document effects of forest management on animal fitness are ideal, they often are impractical. Hence, forest wildlife biologists are usually faced with using information from associational studies to identify the proximate cues to habitat selection are provided during forest management.

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