16 Landscape Connections

Think for a moment about where you were over the past 24 h. Draw a map and on it place all the locations of those places where you spent more than 5 min in the past 24 h. Now draw a straight line from one place to the other in the order they were visited. Do these straight lines represent your path from one place to another? Probably not. Most likely you used roads, sidewalks, doors, and hallways to get to where you were going. These connections from place to place are similar in some respects to the connections used from patch to patch for some species of animals, but not all. Consider how you would use a compass or global positioning system (GPS) to find your way through an unfamiliar forest. You take a bearing, know a distance, and then walk through whatever is between you and your goal (within reason), more or less in a straight line. Some of the walking through closed canopy forests will be easy, and other places with dense shrubs will be very difficult. So rather than using a connection, you walk in a straight line with intervening patches representing various "risks" to your walking ability. These two types of movement are similar to the types of dispersal that other animal species experience. Some use corridors or connections across a landscape and others disperse across the *matrix* or the intervening conditions between patches of suitable habitat. And the matrix poses various risks to survival during dispersal depending on its habitat quality. This is analogous to a differentially permeable membrane in which some molecules can pass through the membrane easily and others cannot. For dispersing animals, matrix conditions represent differentially permeable conditions for moving organisms. Some intervening conditions allow the animal to move easily during dispersal, others present significant risks to survival (Martin and McComb 2003, Popescu and Hunter 2011).

DISPERSAL

Animal movements within a home range often follow paths that are used repeatedly. Deer, elk, and moose, for instance, develop well-worn paths through forests when moving to and from cover and food. Even birds repeatedly use somewhat predictable flight paths in their daily movements (Bélisle and Desrochers 2003). But when an animal is displaced from its home range by its parents (natal dispersal), by dominant individuals, or by a disturbance that alters the quality of habitat in the home range, then the animal disperses in search of a location to establish a new home range. Obviously an animal would not want to disperse any farther than needed, or it is expending energy unnecessarily and reducing its probability of survival. On the other hand, it should not settle into a sub-optimal home range if a better home range means spending only a bit more energy. How is it that animals find these potential home ranges and decide to settle in one?

Dispersal capabilities vary widely among species, likely being quite limited and more affected by boundaries for some species considered dispersal specialists (e.g., red tree voles; Hayes 1996) and quite extensive for others considered dispersal generalists (e.g., Pacific jumping mice) (Gannon 1988, Hansson 1991). Dispersal, especially natal dispersal, is a process that is critical to the growth and spread of populations, stability of metapopulations, recolonization of vacated habitat, and flow of genes and bodies among sub-populations. Body mass and trophic level seem to influence natal dispersal distances in mammals; large species disperse farther than small ones and carnivores disperse farther than herbivores and omnivores (Sutherland et al. 2000). Similar relationships have been documented for carnivorous bird species but not for herbivorous or omnivorous birds (Sutherland et al. 2000). Bowman et al. (2002) found that dispersal distances are often associated with the home range size of the animal more than with the body mass of the animal, but recent work by Whitmee

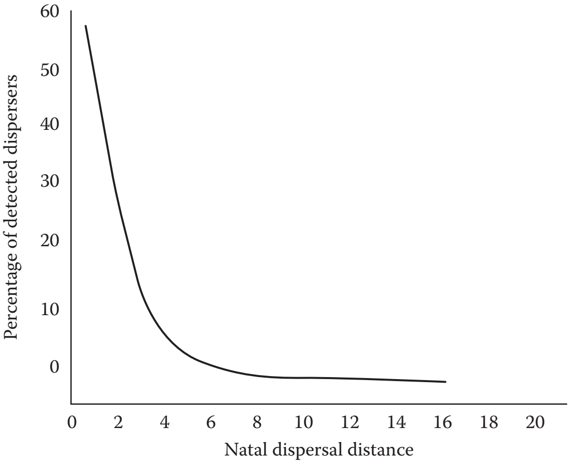

FIGURE 16.1 When dispersal distances are scaled to the median dispersal distance for the organism (in this case 29 species of mammals), a negative exponential pattern emerges. (Redrafted from Sutherland, G.D. et al. 2000. *Conservation Ecology* 4:16. With permission.)

and Orme (2013) found that home range size, geographic range size, and body mass best predicted natal dispersal distances in mammals. Birds and mammals tend to have a dispersal pattern that follows a negative exponential curve; that is, most animals disperse a small distance (relative to the median distance dispersed by the species) and few individuals disperse long distances (Figure 16.1). For many species dispersal distances decline as the number of home-range diameters increase (Bowman et al. 2002). This is an intuitively appealing way to consider dispersal because animals cruise around their home ranges regularly. To move another home range diameter would not seem to be too energetically costly, but as dispersal continues over multiple home-range diameters, the ability of the organism to expend that energy and still survive comes into question quickly. It may be more energy-efficient for an animal to settle into a suboptimal patch and survive there than to continue to disperse and risk the chance of dying by dispersing through low-quality patches.

So what conditions are necessary for successful dispersal across a landscape to allow recolonization of a patch or introduction of new alleles into a population? The probability of successful dispersal across a landscape can be considered a function of the probability of three interacting probabilities: encounter, survival and continuing. To examine the concepts behind successful dispersal, let's first consider a simple conceptual model, and then we will complicate it with reality.

UNDERSTANDING THE PROBABILITY OF SUCCESSFUL DISPERSAL

There are three dominant effects that determine if an individual dispersing from one patch is likely to reach another patch where it can find the resources to survive. Let's consider the patch from which it is leaving the *source patch* and the patch into which it could settle the *target patch*. First, an animal must travel in a direction that causes it to encounter a target patch. Many animals do not seem to disperse in a given direction, but rather travel in random directions (Figure 16.2). Although the actual path that an animal takes may appear to be like a pinball in a pinball machine, when it settles it will likely be in some random direction unless some totally inhospitable condition (i.e., the ocean for most terrestrial vertebrates) exists in one direction (Figure 16.3). Consequently, the probability that a dispersing animal will travel in a direction that would lead it to even encounter a target patch is a function of the angle formed from the center of the source patch to the outermost edges of the target patch (Probability of encounter = P_e, Figure 16.3). In our case, if the angle was 36° then the probability of an animal encountering the target from the source would be 0.10% or a 10%

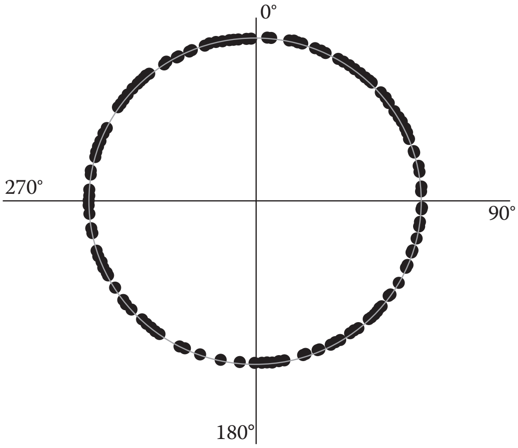

FIGURE 16.2 Dispersal directions of 151 juvenile male white-tailed deer in Pennsylvania. (From Long, E. S. et al. 2010. *Journal of Wildlife Management* 74:1242–1249.)

chance. Another way of looking at this is that for every 100 animals dispersing at random from the source, approximately 10 would be expected to encounter the target. Now consider what happens to that angle if the target patch were closer to the source—the angle increases and the probability of encountering the target increases. Increase the size of the target and the probability of encounter increases. Increase the number of targets in various directions and the probability of encounter increases. So, from this very simple example, we can see that if we want to maintain a metapopulation through dispersal, then more and larger target patches close to the source patch will increase the likelihood of maintaining the population. But dispersing animals not only have to encounter the target, they need to survive the trip.

The probability that an animal will survive a dispersal event is dependent on its fitness as it moves from one patch type to another. Recall that fitness is related to the probability of surviving and reproducing in a patch. When dispersing, reproduction is usually not a concern, but survival is a requirement. Consequently, if we can understand what the probability of survival might be for a species in each intervening patch as it moves across a landscape, we can predict the likelihood that it will survive its dispersal trip. One way of measuring this survival is using a time-specific probability of survival, such as its daily probability of survival. Do you know what your daily probability of survival is? I assure you that the life insurance companies have estimated this for you! It is not

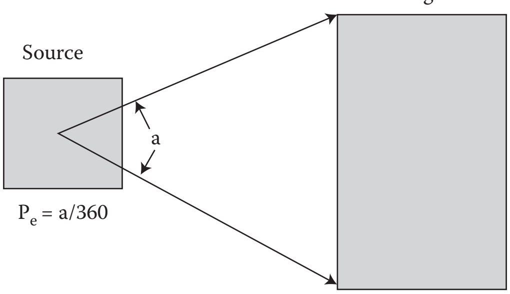

FIGURE 16.3 Conceptual diagram illustrating the probability of an animal encountering a target patch if dispersal is random. As the target increases in size or decreases in distance from the source, the probability of encounter increases.

100%, unfortunately; you just never know…; but it is high. Say your daily probability of survival is 99.9%, then you would have an annual probability of survival of $0.999^{365} = 0.694$ or a 69.4% probability of living a year. Not great odds! Now consider how that might change if you were living in Antarctica for that year, or Detroit, Michigan (the most dangerous city in the United States in 2012) vs. living in Plano, Texas (the safest city in the United States in 2012). Where you are matters, and for dispersing individuals with no prior knowledge of the resources available in intervening patches, the probability of survival can fluctuate considerably along its trip. But the overall probability that an animal would survive a dispersal event is not only related to the time-specific difference in survival probabilities among the patches along its route, it is also a function of the time it spends in each patch. Consequently, the movement rate through each intervening patch must be considered. So the probability of survival in a patch is $PS_x = PSD^d$, where PS_x = probability of survival in a patch x; PSD = daily probability of survival in patch x, and d = the number of days spent in patch x (Figure 16.4). For a dispersing individual, d will be dependent on the rate of movement (distance per day), and the distance traveled in the patch. If the species dispersing is a salamander and patch x is a closed canopy forest that would protect it from dessication, then it could probably spend quite a long time in patch x and survive (assuming it can find food). But if patch x is an interstate highway, then the salamander can run as fast as it can and spend as little time on the highway as possible and still face a very low probability of survival. But even in this case, that probability is not zero. Send enough salamanders across the highway and a few will make it (humans have also used this approach—this was the basis for a common military strategy for invasion during wars!). Nonetheless, these patches with an inherently very low probability of survival are considered *barriers*; those with high probabilities of survival can be considered *corridors*. But it is most useful to think of these intervening patches as having differential permeability or resistance to moving organisms. It is the product of the probabilities associated with all intervening patch types that yield an overall probability that the animal will survive the dispersal event (Figure 16.4). Species that are more mobile and have higher movement rates will realize higher survival rates in low-quality patches than less mobile species. Consequently, forest managers concerned about maintaining regional biodiversity tend to be concerned with providing habitat for low-mobility species such as salamanders, frogs, and small mammals (Spies et al. 2007).

There is still one other factor that must be considered when understanding how likely it is that an animal might travel to a target from the source. Most animals do not disperse more than one home-range diameter from their natal home range. Only a few go two home-range diameters, and fewer go three home-range diameters. The farther the distance between the source and a target patch, the

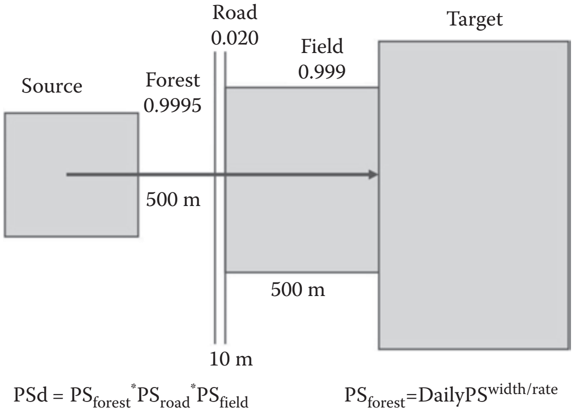

FIGURE 16.4 Conceptual framework for understanding the likelihood of an animal surviving a dispersal trip through various patch types, each with its associated own time-specific probability of survival. Barriers are those patch types with very low daily probabilities of survival.

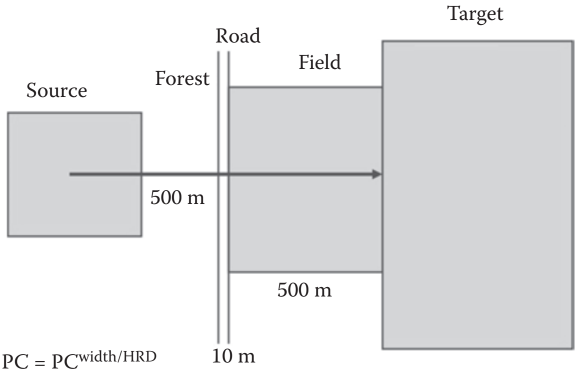

FIGURE 16.5 Conceptual framework for understanding the likelihood of an animal continuing a dispersal trip through various patch types, each with its associated own time-specific probability of survival. Settling into a patch with low fitness may be a reasonable survival strategy but may not allow a metapopulation structure to persist.

greater the likelihood that the animal will settle and perhaps settle in a low-quality habitat, perhaps even a sink. Consequently, the probability of continuing the dispersal (1-probability of settling) also influences the likelihood that an animal will make it to the target (Figure 16.5).

If you put these three factors together (the product of the probabilities) to understand the likelihood that a specific patch on the landscape might be colonized by individuals from another patch, the likelihood becomes overwhelmingly small as the distance between patches increases, as the size of the target patches decreases, and as the intervening habitat becomes more inhospitable (resistance increases) (Figure 16.6). Some of the problems associated with low survival probabilities can be overcome by the sheer numbers of dispersers. For example, consider that the number of successful dispersers among patches is a function of the cumulative probability of survival per individual among all patches crossed, animal density in the source patch, source patch size, and the percent of the population that are dispersers, then:

NSD = PS*AD*AREA*PROP where, NSD = number of successful dispersers, PS = cumulative probability of survival across the patch mosaic, AD = animal density per unit area, AREA = source habitat area, and PROP = the proportion of the population that are dispersers. For species with high

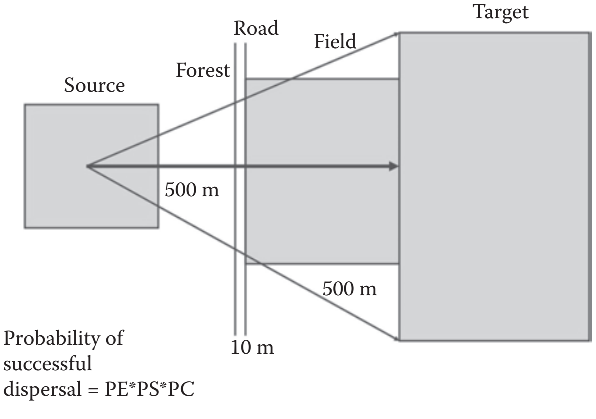

FIGURE 16.6 Conceptual framework that combines the probability of encounter, the probability of survival and the probability of continuing during a dispersal event from a source to a target. The overall probability associated with an individual dispersing to the target is the product of these probabilities.

reproductive rates, a low probability of successful dispersal may not be such a huge obstacle because of the sheer numbers of dispersers—it is just that most dispersers die. Plants use this strategy quite often. But for species that have low reproductive rates, are rather immobile, occur at low densities, and may have daily survival probabilities that vary considerably among patch types, isolation can be a significant problem. These are often the species of most concern to conservation biologists wishing to conserve regional biodiversity. So what can be done about this problem? We can manage our forests to influence the connectivity among the habitat patches on a landscape for a species.

CONNECTIVITY AND GAP-CROSSING ABILITY

Connectivity refers to the degree to which the landscape facilitates or impedes movement among habitat patches and, therefore, the permeability or resistance of the landscape to dispersing individuals, as measured by their survival and by passing genes on to the subsequent generations. Connectivity is largely a function of the size and arrangement of disjunct patches (i.e., area and isolation effects), the permeability of the intervening patches, and/or the physical connections among habitat patches using corridors.

Where a barrier occurs on a landscape impeding the movement of dispersing organisms in a particular direction, a corridor may facilitate movement across this barrier. Overpasses and underpasses built specifically for animals crossing highways have been quite successful in many areas (Jackson and Griffin 2000).

In theory, some of the negative effects of isolation can be mitigated by identifying and maintaining fixed or dynamic connections across the landscape. Connectivity can be managed as either *continuity*, the physical connectivity of habitat, or *connectedness*, the functional connectivity of habitat. Corridors represent one type of connection that can be designed for species with a poor ability to cross gaps. Maintaining a more hospitable matrix condition between patches is an alternative to corridors. In either case, it may be helpful to think of the demographic basis for developing connections. Using the life history characteristics of species can allow us to understand which species are relatively more at risk from isolation effects compared to others. Maintaining connectivity for species that show adverse effects from isolation (e.g., California red-backed voles) may be a much higher management priority (Mills 1995) than species that disperse across complex landscapes more freely (e.g., deer mice).

What ultimately influences the connectivity of the landscape, from the organism's perspective, is the scale and pattern of movement relative to the scale and pattern of intervening patches (With 1999). The size, number, and distribution of habitat patches influence the physical connectivity of habitat across the landscape and are the primary determinants of connectivity. So under what conditions does connectivity become an issue? Clearly, if most of a landscape is a high-quality habitat for a species, then there should be little concern about connectivity. But if only 1% of a landscape is high-quality habitat in many tiny patches, then connectivity may be a huge concern. Determining the point at which a reduction in habitat area leads to a disconnected habitat would seem to be an important piece of information when managing species in complex landscapes. Dr. Kimberly With developed a model to at least conceptually understand the relationship between habitat area and connectivity (With 1999).

With (1999) developed a simple landscape structure in which black squares were habitat and white squares were not habitat for a species and then used a simple percolation model (testing connectedness from one side of the landscape to another) to assess at what point(s) we would expect to see habitat connectivity disappear from a landscape. Habitat loss and fragmentation were simulated by removing habitat at random in one set of simulations and in clumps in another set of simulations (Figure 16.7a). As With (1999) decreased habitat area in the randomly fragmented landscapes, she observed a threshold at 50% habitat area, where connectivity declined abruptly and fell to zero connectivity when approximately 30% of the habitat area remained (Figure 16.7a) . The probability of

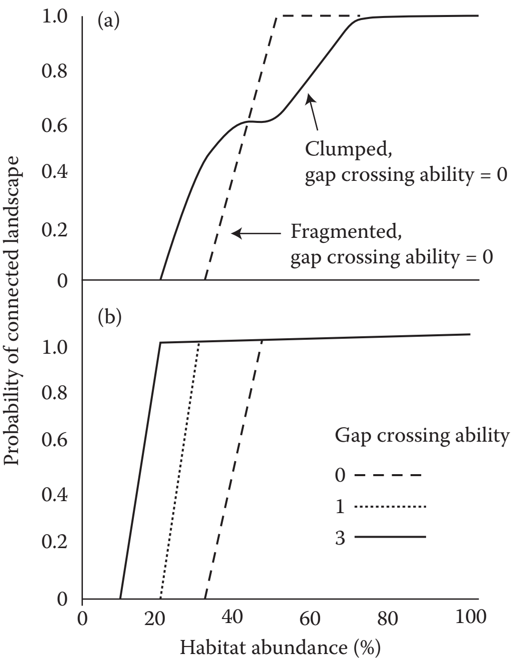

FIGURE 16.7 Simulated effects of landscape fragmentation in two patterns on the probability of maintaining a connection across a landscape (a) as affected by the species gap-crossing ability (b). (Redrafted and adapted from With, K.A. 1999. *Forest Fragmentation: Wildlife and Management Implications*, Pages 97–115. Brill Press, Netherlands.)

having a connected landscape in clumped fragmentation landscapes began to decline slowly when less than 65% of the habitat remained and fell to zero at about 20% of the habitat remaining. The latter finding was due to the random chances of losing a connection vs. maintaining a connection being highly influenced by the pattern of clumps of habitat on the landscape, with clumps more likely to be either connected or disconnected compared to random fragmentation. Consequently, for species that require a connection across a landscape, connectivity would seem to become an issue when about 30%–50% of the landscape remains as habitat; when habitat area drops below 30%, then maintaining or restoring connectivity is an important consideration for the species.

Some species do not need a complete connection to move across a landscape. Some species are quite well-adapted to crossing inhospitable areas that represent gaps in the connection across the landscape, while others are not (Bélisle and Desrochers. 2003). Some species can cross wider gaps (e.g., goshawks) than others (e.g., clouded salamanders). With (1999) also examined the potential effect of gap-crossing ability on these thresholds. As you would expect, the better able a species is at crossing a gap in habitat across a landscape, the greater the level of fragmentation of its habitat it can tolerate and still be able to move across the landscape (Figure 16.7b). For species with the ability to cross three blocks of non-habitat, the threshold for a disconnected landscape fell to 10%–15%. From this work, several management implications emerge. First, although habitat area is the landscape feature most associated with animal abundance across complex landscapes, connectivity emerges as an important feature when habitat area has declined to 30%–50%, or less, depending on the species gap-crossing ability. Second, when habitat area falls to or below this threshold, planning will be needed to either provide corridors or a matrix condition that is more permeable to the species.

What is missing from the previous example of the interrelationship of habitat area and connectivity is the concept of differential permeability of habitat patches across a landscape. The permeability of the matrix is not black or white, all or nothing; it is indeed shades of gray in its permeability to dispersing organisms. Permeability influences the degree to which the two patches are isolated or not.

Understanding Physical and Genetic Connectivity

The inverse of permeability to movement across landscapes is resistance to movement across a landscape. There have been recent advances to understanding movement of organisms across complex landscapes using a gradient rather than a patch-based approach. These approaches are based on the complex set of factors at any one point or pixel on a map having the characteristics that make it more or less resistant to movement by an organism. These resistant kernel approaches allow us to begin to understand how animals would be most likely to move across the landscape along pathways of least resistance. For instance, if a herd of caribou were making their way across a boreal forest on their way to summer calving grounds and they encountered the Alaskan oil pipeline (Figure 16.8), would they change their movement patterns or would they be oblivious to it? One can easily imagine that for species associated with shrubs, a regenerating clearcut would have low resistance to movement but a dense plantation may have high resistance, a river may have even higher resistance, and a highway could have even higher resistance, such that a map of resistance would illustrate the potential routes that animals would be most likely to follow (Figure 16.9, Cushman et al. 2006).

As far as we know, animals don't read maps. So, how can we begin to understand if our perception of resistance to movement as portrayed by a model is accurate or even reasonable? If dispersing animals not only find new patches but also find mates in those new patches, then they should leave a trail of their presence through their genes. Recent technologies allow us to examine patterns of species and individuals across landscapes and use genetic characteristics to infer relatedness and flow of genes from one population to the next. Two types of DNA are typically used to address different types of questions. DNA contained in the mitochondria of a cell is inherited from an individual's mother and does not change very much from one generation to another (Morin et al. 2010). The DNA in your mitochondria is very similar to the mitochondrial DNA found by your predecessors from many generations ago. DNA found in the nucleus of a cell however is inherited from both the mother and father. Nuclear DNA contains segments of the DNA strands that are highly variable from one individual to another, and these segments are called microsatellites (Morin et al. 2010). Hence, mitochondrial DNA (mtDNA) is useful for separating one species from another; nuclear DNA is useful for separating among individuals within a species.

FIGURE 16.8 The oil pipeline traversing Alaska provides a stark contrast to the surrounding forest. It may act as a corridor for some species, a barrier for others, or be differentially permeable to others.

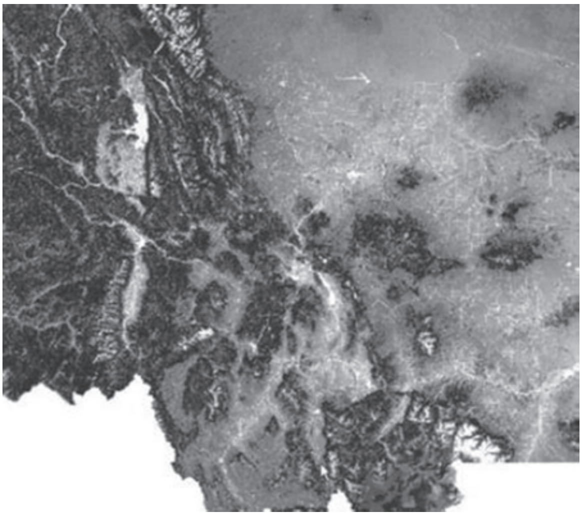

FIGURE 16.9 Example landscape resistance map for American black bear in an area of the U.S. northern Rocky Mountains encompassing Montana and northern Idaho. Dark areas are low resistance for movement, while light areas are high resistance for movement. (The map was developed by Cushman, S.A. et al. 2006. *The American Naturalist* 168:486–499.)

Say that you find some hair, and the hair has a piece of skin attached to it. If we examined the mtDNA and nuclear DNA found in the skin, we can learn two different things. We can compare the mitochondrial DNA to known samples to determine which species the hair is from. Once we know that, we can compare the nuclear DNA to other samples from that species to determine if the hair you found is related to individuals from other populations. But, a tiny bit of skin may not contain enough DNA to do both of these analyses effectively. Population geneticists amplify the DNA in that tiny sample using polymerase chain reaction (PCR) techniques that make multiple copies of the DNA or microsatellites of the DNA (Morin et al. 2010).

Tracing the trail of genes across a landscape is made possible by identifying segments of a genome that contain a series of base pairs (known as a microsatellite array) which vary from individual to individual, but the variation is less for those closely related to one another than for those that are unrelated (Cushman et al. 2006, Morin et al. 2010). Finding that microsatellite array in a genome can be a challenge unless the series of base pairs on either side of the array are stable and do not change from one individual to another over time. These stable series of base pairs (primers) allow identification of a marker that can help identify an individual and relatedness to other individuals (Morin et al. 2010). This approach is particularly valuable because even small traces of DNA that contain the array can be duplicated using PCR.

If we have two samples from either side of a mountain range (a potential barrier) and the nuclear DNA indicates that the two samples are related, then we can infer that perhaps the mountain is not a barrier; but, if we have 20 samples from each side of the mountain range and none are closely related, can we infer that there is no gene flow? We can only say that we were not able to detect a flow of genes between these populations and that the mountains may be representing a barrier to movement for this species. But we cannot be sure that it is a complete barrier (Cushman et al. 2006). Either we may simply not have detected relatedness, or animals are moving between populations but not interbreeding.

Consequently, genetic analyses can be useful in understanding connectivity if we detect relatedness or it can be used to assess the realism of a spatial model of resistance to movement across complex landscapes (Cushman et al. 2006). For instance, we can develop a model allowing us to infer resistance to movement to a set of landscape patches and then "allow" animals to disperse from one patch to another. Our model should be able to estimate the likelihood that an individual would survive, encounter, and continue to a target patch. If that likelihood were very low, but we then followed up by sampling individuals from the source and target patches and found that individuals in the two patches were related, then we would conclude that our estimates of resistance for one or more patches were incorrect. So, we can use genetic techniques to refine models of animal movement and allow us to infer the effects of changes in landscape pattern, or composition, on the likelihood that a species would be isolated or connected.

MANAGEMENT APPROACHES TO CONNECTIVITY

What is the best way to increase connectivity within a landscape? Unfortunately, little information is available on the gap-crossing abilities of most forest-associated species (Bélisle and Desrochers 2003). Further, gap-crossing abilities are species-specific. And dispersal is often seasonal. Cold wet winters and hot dry summers may represent periods of movement facilitation or reduction for various species.

When the area of habitat for a species falls below 30%–50% of the landscape (With 1999), then managers should begin to think about identifying connections across the landscape to reduce risks associated with isolation if the intervening matrix is indeed isolating the remaining patches of habitat. One approach is to purposefully manage a portion of the matrix to be very permeable for a species by developing a corridor between the patches. Corridors require an organism to follow a "path" through the otherwise inhospitable matrix if it is to have a high probability of moving from one patch to another. Connections may be in the form of static or dynamic corridors connecting specific patches on the landscape. *Static corridors* are those that are identified on a map and on the ground and purposefully managed over time to maintain connectivity in that location. *Dynamic corridors* "float" across the landscape over time, such that different portions of the intervening matrix are managed to provide connectivity at all times; it is just that the specific stands that provide the connection, change over time. This approach provides much more flexibility for the land manager to manage more stands for multiple values (Sessions et al. 1998).

Alternatively, the matrix condition as a whole could be managed to be made more permeable to dispersing organisms (*matrix management*). Such an approach does not require the animal to follow a path, but rather to move at random through the matrix. For species that are able to cross gaps, placing small patches of good-quality habitat close to one another between the two larger high-quality patches creates a *stepping stone* approach to connectivity. All of these techniques allow otherwise isolated patches to be connected through planning or patch management. In managed forests, this is usually achieved through harvest planning and silvicultural decisions (Bettinger et al. 2001).

CASE STUDY: MATRIX MANAGEMENT FOR A WIDE-RANGING SPECIES

The northern spotted owl is listed by the U.S. Fish and Wildlife Service as a threatened species under the Endangered Species Act. As such, in efforts to allow the species to recover, it has received more attention than probably any other species in the United States in the past few decades. Generally, northern spotted owls are considered a species associated with forests with certain structural features of old-growth forests (Carey et al. 1990) (although they also occur in younger forests when these features are present). The Northwest Forest Plan (NWFP) was developed to ensure habitat for this and many other species associated with old forests and to allow the northern spotted owl populations to recover (FEMAT 1993). The habitat conservation strategy developed for the northern spotted owl identified large blocks of forest on federal lands that established a metapopulation structure for the species (Thomas et al. 1990). These areas were termed late-successional reserves (LSRs) (Figure 16.10). The LSRs largely fall on U.S. Forest Service lands because of the size and distribution of remaining spotted owl habitat, as well as habitat for marbled murrelets and other late-successional associates. Under the Northwest Forest Plan, areas between the LSRs

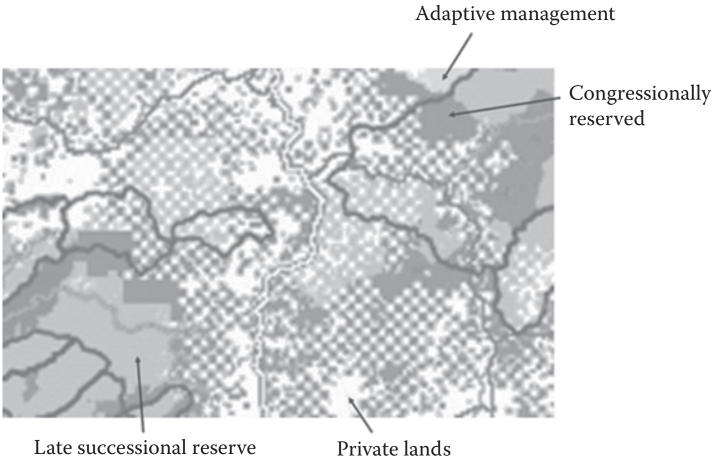

FIGURE 16.10 Land allocation pattern under the northwest forest plan. Notice the checkerboard pattern of Bureau of Land Management lands providing stepping stone connections among LSRs as well as the matrix lands. Not shown are extensive riparian reserves designed to enhance connectivity across the landscape. (Map from [FEMAT] Forest Ecosystem Management Assessment Team. 1993. *Forest Ecosystem Management: An Ecological, Economic, and Social Assessment*. USDA For. Serv., USDC National Oceanic and Atmos. Admin., National Marine Fish. Serv., USDI Bur. Land Manage., Fish and Wildl. Serv., National Park Serv., and US Environ. Protect. Agency. Portland, OR.)

are connected through a system of corridors falling largely along riparian management areas that extend 50–100 m from stream-sides (to provide habitat for salmonid fish as well as connecting LSRs for terrestrial late-successional associated species). The plan also used a matrix-management approach, proposing management of the intervening matrix in a way that allows stands to develop with the structural complexity needed to support dispersing spotted owls as the stands mature. In addition, forests on Bureau of Land Management (BLM) lands, which fall largely on alternating sections (one section = one square mile), provide a stepping stone connection among LSRs (Figure 16.10). Consequently, much of the basis for habitat management to recover this species is underpinned by providing landscape connections among LSRs. These connections utilize matrix management, stepping stones, and corridors to achieve landscape connectivity for northern spotted owls and other species across the northwest forested landscape.

This plan has been in place with little modification for over 20 years, so how is the northern spotted owl doing? Not so well in many parts of its range. Populations are declining in nine of 13 demographic study areas (Anthony 2004, 2006). Declines in three areas over the 23-year period have been 40%–60%. The reasons for a failure of many populations to recover is complicated and seem to be related to competition with barred owls that arrived in the northwest about 20 years ago; barred owl populations have expanded significantly, perhaps at the expense of the spotted owl populations. Weather patterns have changed, with winters in some areas being colder and wetter and some summers being hotter and drier. It is not clear if this is a result of climate change or if this is simply random fluctuation. Hotter and drier summers have resulted in large stand-replacing fires in some areas. West Nile Virus has affected bird species in many parts of North America, and it is not known if it is having an adverse effect on populations or it simply is the result of reserve areas that are too small or too poorly connected. Although past and current loss in habitat and competition with barred owls are considered the greatest threats to recovery, most likely it is a multitude of factors that come together to prevent populations from recovering. The newest strategy to encourage recovery for the species enhances the habitat area for spotted owls in the northwest beyond what was allocated in the NWFP (USFWS 2008) and is expected to take 30 years and cost US$489 million (USFWS 2008) (Figure 16.11).

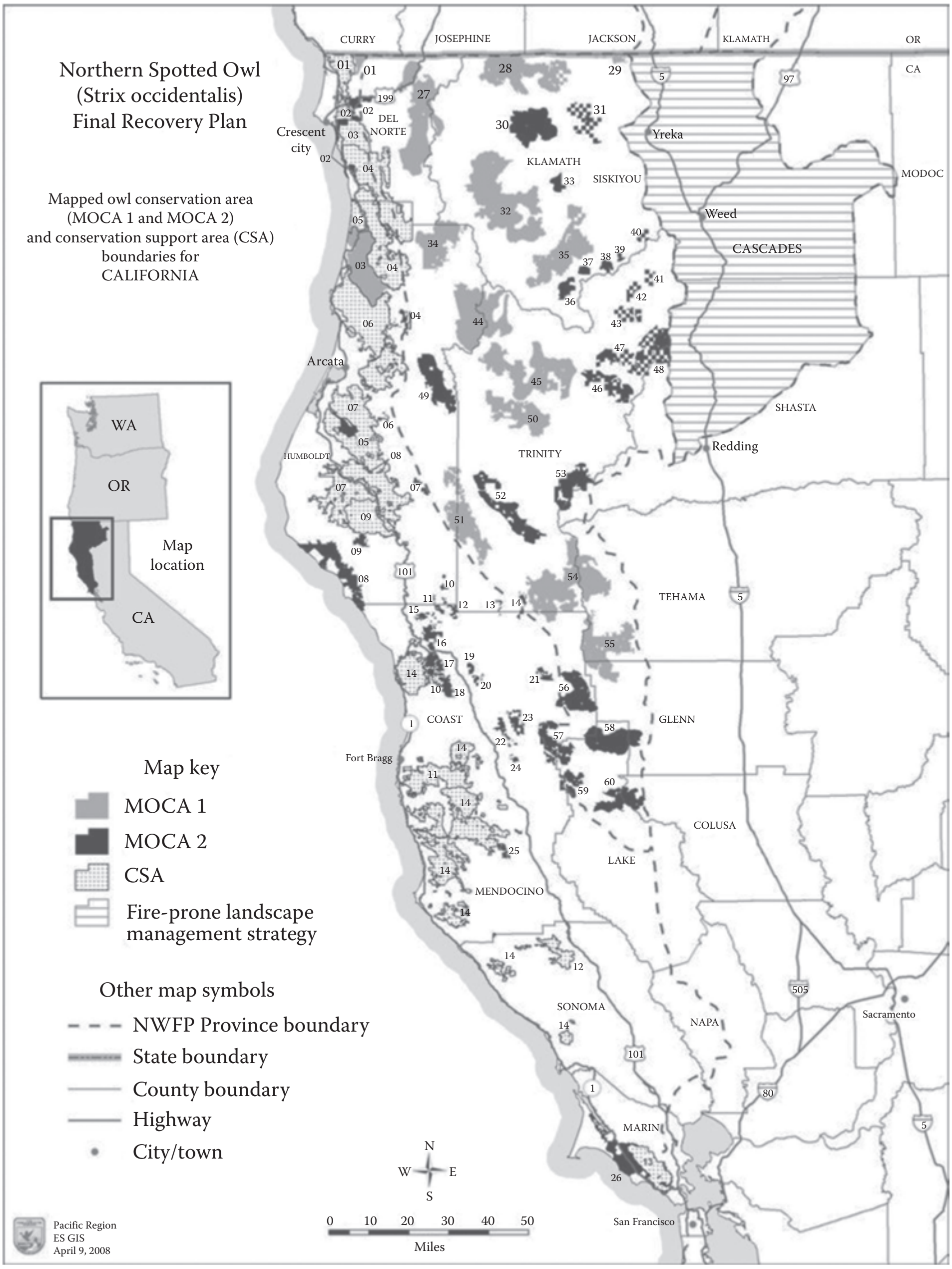

FIGURE 16.11 Land allocation under the 2008 Spotted Owl Recovery Plan. (Adapted from U.S. Fish and Wildlife Service. 2008. *Final Recovery Plan for the Northern Spotted Owl, Strix occidentalis caurina*. U.S. Fish and Wildlife Service, Portland, Oregon. 142 pp.)

SUMMARY

Although habitat area seems to be the most important feature affecting the occurrence and abundance of vertebrates on managed forest landscapes, at low levels of habitat availability, connectivity can become important. It is at these low levels of habitat availability that landscape pattern would be expected to impact the abundance and distribution of vertebrates. Connectivity mitigates some of the adverse effects of low levels of habitat area, providing individuals within a population the habitat they need to disperse among patches. Connectivity provides opportunities for exchange of genetic information and the ability to repopulate otherwise isolated areas as habitat improves. Connectivity is effective if dispersal is adequate to meet these population goals. Successful dispersal is influenced by the likelihood that an animal will encounter a patch, survive the dispersal event, and continue dispersal before settling into a patch regardless of its quality. Providing static or dynamic corridors, stepping stones, or undertaking matrix management can facilitate the likelihood of successful dispersal.

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