Why is connectivity important for wildlife conservation?

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Summary

Connectivity is often very important for maintaining wildlife populations. Without connectivity, small, isolated populations are driven toward local extinction by many factors; for example reproduction may be lower and mortality higher due to the negative effects of inbreeding. Furthermore, the entire population is much more prone to chance events such as fires or droughts. In isolation, small populations will not persist. Connectivity between populations allows several small populations to function as a group. Together they behave more like a single large population, and many of the deleterious small population effects are mitigated. Dispersers from one population can settle in other populations augmenting the numbers, bringing new genes, and potentially colonizing habitat islands where the species has been extirpated. Thus, both the total numbers and the range of an organism are increased through connectivity. In fragmented landscapes some level of connectivity is often essential for the persistence of many species.

Increasing connectivity, however, is not a conservation panacea. The same passageways that allow a target species to recolonize a habitat island may also allow exotic pests to invade, or may act as a conduit for parasites and diseases. Increased connectivity must therefore be carefully planned, both to make sure that the needs of the target organisms are met, and to minimize potential negative consequences.

The importance of connectivity

Connectivity has been touted by many as critical to the conservation of wildlife populations. Here we present some of the arguments behind the promotion of connectivity between sub-populations, while also noting circumstances when it may hinder conservation efforts. The importance of connectivity is directly related to the size of sub-populations on isolated habitat islands. When the sub-populations are very small everything is working against their abilities to persist without help from other islands. This help comes in the form of organisms that travel from one island to the next. In population biology, these travelers are called ***dispersers***. The interaction between habitat islands has the effect of reversing many of the negative effects associated with a small, isolated population.

Reversing loss through dispersal

In many species, the young disperse widely. On a small habitat island, most of the dispersing young are forced to leave the island. Whether they die or simply wander off and find habitat elsewhere, these young are lost, as far as the island is concerned. For the population on the island to be stable, other young need to arrive from other islands to make up for those that are locally lost. As long as this occurs, a group of islands can form a stable ***metapopulation***, but any single island population in isolation will diminish in size and the organisms will become locally extinct. So one role of connectivity is, through population augmentation, to allow a population to persist in an area where lacking connectivity, it would not.

Reversing chance extinctions

Even with good connectivity, there are many factors that can cause the local extinction of a sub-population. One is simple chance. For instance, consider a small mammal that lives 1 year and each female produces 2 young each year. If there are a lot of these organisms, the population will be stable. If there are, say, 3 breeders, there is a 3% chance that the young of the year will be all male or all female (assuming equal likelihood of a male or female). If this happens, the population will go extinct. However, the effects of chance don't need to cause extinction in a single year. If only 1 female were born, then only 2 young would be born the next year, and the probability of 2 males or 2 females (and therefore extinction) is 50% for the following year. This process is called ***demographic stochasticity*** and mostly affects very small populations.

There are, however, other problems that affect the whole population, and these are probably more likely to lead to extinction. One, termed ***environmental stochasticity***, refers to the fact that some years are "good", in that survival and/or reproduction is high, and some are "bad". Populations should go up in numbers during good years, but on small islands, most of the organisms produced in good years will be excess, and will be lost to dispersal. However, there is nothing to prevent the population from declining during bad years. Both good years and bad years tend to come in clumps. Clumps are produced by pure random chance (if you flip a coin it won't come up HTHTHT, but rather will come up with runs of heads and tails), or are the consequences of weather. We are currently (2002) in a drought cycle. If drought causes a "bad" year, then next year is likely to be bad. A series of bad years in a row can either drive a small population extinct, or can reduce it to very low numbers where demographic stochasticity finishes the job of driving the population to extinction.

Lastly, there is ***catastrophe***, a sudden extreme event causes local extinction. Large fires can be catastrophic for many species. Clearly, the smaller the habitat island, the more likely it is that a catastrophe will envelop the entire island, and cause local population extinction.

Because of all of these factors, the expectation is that small populations will naturally become locally extinct from time to time. If this happens, and there is no colonization from other islands, the number of occupied islands will gradually decrease, and eventually the entire metapopulation will go extinct. Levins (1969, 1970) found that the critical factors in the maintenance of a metapopulation were rates of local extinction and colonization.[1] Importantly, he found that for most of the islands to be occupied, rates of colonization needed to vastly exceed rates extinction. For the most of the habitat islands in a metapopulation to occupied, there needs to be a lot of colonization, and therefore metapopulations only work if there is a lot of connectivity.

Reversing the effects of inbreeding

There are genetic consequences associated with small, isolated populations as well. These negative effects arise from the inability of individuals in a population to avoid breeding with relatives. Whereas in a large population individuals can readily avoid inbreeding, in a small population this is inevitable. The offspring of inbred individuals often have lower levels of genetic variability than offspring of non-inbred pairs. This difference in genetic variation has been correlated with fitness in a variety of animals and plants. For example, it has been shown that lower levels of genetic diversity leads to declines in larvae survival, egg hatching rate, and adult longevity of a fritillary butterflies in Finland (Saccheri et al. 1998). Another example is the positive association between genetic variation and germination and survival rates in *Clarkia pulchella*, a Rocky Mountain plant (Newman and Pilson 1997).

As if it were not bad enough, small, isolated populations also have a second genetic problem called genetic drift. ***Genetic drift*** is similar to demographic stochasticity defined above. By definition drift is the random changes in the frequencies of gene types within a population. For example, imagine a wolf population where a single gene determined coat color and there is no benefit to having one coat color over another. If the gene is in one "state" the animal is black, and if the gene is in another state the animal is gray. If there are 1000 wolves in the population and half are black and half are gray, we would predict that next generation we would see nearly 500 black and 500 gray wolves. We would not be surprised to see 530 black and 470 gray, nor would we be surprised to see 490 black and 510 gray. However, it would be a near impossibility to randomly have 1000 black and 0 gray wolves in the next generation, or vice-versa. This same principal holds for a population of 10 wolves; only this time despite expecting 5 black and 5 gray wolves we may also expect by chance that all 10 individuals could be black or gray. Drift, however, does not have to occur in one generation. It can ratchet forward such that one year there are 5 gray, 5 black; the next there are 7 gray, 3 black; the next there are 9 gray, 1 black, the next there are 8 gray, 2 black, and the next there are 10 gray and 0 black. At this point where there are zero wolves with black fur, the black fur gene is now

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[1] These understandings were quantified in 1969 by Richard Levins in the first ***metapopulation model***. Levins found that the proportion of occupied islands, on average, was related to rates of extinction and colonization through the following equation:

$$P = 1 - e/c$$

where P is the proportion of islands occupied, e is the extinction rate, and c is the colonization rate. The interesting thing about this relationship is that when extinction = colonization ($e = c$), $P = 0$; that is, the entire metapopulation goes extinct. If you want most of the islands to be occupied, colonization rates must swamp extinction rates ($e \ll c$).

extinct in the population, and the population has lost genetic variability. Losses in genetic variability reduce the ability of a species to adapt to changing environments, and therefore increase the risk of extinction.

Both inbreeding and genetic drift are countered by movement between populations, and therefore by the presence of connectivity. In fact, it has been suggested that once connectivity is restored it takes relatively little exchange between populations to maintain genetic diversity. One rule of thumb has been the "one migrant per generation" rule, which states that one genetic migrant moving and breeding in another population each generation will prevent the loss of rare genetic material. This rule-of-thumb has recently been empirically validated through inbreeding experiments with Rocky Mountain mustard plants (*Brassica campestris*). Plant populations that received a migrant had higher fitness than those that didn't receive a migrant, but also importantly plant populations that received more migrants didn't have higher fitness than those that received only one migrant (Newman and Tallmon 2001).

The role of habitat quality in metapopulation stability

Connectivity and habitat quality are both important to produce stable metapopulations. In a metapopulation increasing the habitat quality in the habitat islands, will generally lead to larger and more robust populations, and more immigrants and colonizers to help stablize the system. Increasing connectivity will allow these colonizers to reach other islands more reliably and thereby keep most of the islands occupied. Similarly, a metapopulation can be destabilized by either declines in habitat quality or connectivity. Activities that simultaneously decrease habitat quality and connectivity are particularly destructive.

Potential negative consequences of increased connectivity

Are there any circumstances where connectivity is undesirable? In fact there are. First, connectivity can allow disease or parasite transmission into a population that may have been disease-free. Second, connectivity, while facilitating movement of a target organism, may also allow exotic or other competitors to enter a habitat as well. Third, some species may have adapted to isolation, and could suffer negative effects from the introduction of distantly related genetic material (a phenomenon called ***outbreeding depression***). For these reasons, attempts to increase landscape connectivity should be carefully considered and well planned. However, for most species, connectivity is desirable and has aided in the maintenance of healthy wildlife populations.

Conclusions

So, for what species does landscape level connectivity really matter? It matters most for organisms with extremely large home ranges relative to the habitat patch sizes, and relatively low birth rates. Wolverine are a good example. They appear to be present in most of the mountain islands in western Montana and northern Idaho, however, with non-overlapping female home ranges of about 300 km^2, only about 30 wolverine can fit into every 1,000,000 ha of habitat. This means that, in most cases individual management areas have few animals, and are therefore critically dependent on dispersal, which in turn is critically dependent on connectivity. However, scientifically understanding how much connectivity is necessary, and what imposes a barrier to connectivity are difficult questions, especially for rare, elusive animals. Our current research unit focuses on employing new methods such as DNA and satellite technology to answer these connectivity questions.

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