The Conservation Value of Peripheral Populations: the Supporting Science

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Abstract: Traditionally, populations at the periphery of the geographic range of a species have been regarded as having little value in conserving biodiversity. This view developed from the expectation that populations at the edge of their geographic range are more vulnerable to extinction than populations in the central portion of the range. Conservation biologists have also assumed that the genetic diversity of a species is greatest near the center of its geographic range. This low regard for peripheral populations has been incorporated into guidelines for conserving biodiversity. Conservation practitioners are told to direct limited conservation resources to conserving central populations because peripheral populations have little chance of survival and are genetically impoverished. These expectations and their related guidelines have caused officials at many governmental levels to question including species at the periphery of their distribution in lists of protected species.

Despite the often uncritical acceptance of the low conservation value of peripheral populations, recent research suggests that peripheral populations may play an important role in conserving declining species. Contrary to expectations, in species that have undergone large range contractions, peripheral populations persist significantly more often than do the central populations. In addition, examinations of the genetic diversity of populations across the geographic range of a species are beginning to call in to question the assumption of higher central diversity. Furthermore, studies on both persistence and genetics suggest that the distinction between central and peripheral populations may not be an important distinction for conserving biodiversity. Thus, conservation plans should include populations found both near the center and the periphery of a species' distribution.

Key Words: central populations, peripheral populations, conservation priorities, extinction, genetic viability

Introduction

Deciding which species merit special protection is a major challenge to implementing legislation that protects biodiversity. While science is vital to making this decision, the decision is also often influenced by the availability of resources and other political considerations. Scientists are encouraged to help develop conservation priorities that make the best use of these limited resources; however, scientists disagree on whether species that have only a restricted distribution in a political jurisdiction merit special protection and the use of limited resources within that jurisdiction if the species' distribution also includes other jurisdictions.

Abbitt et al. (2000) examined bird and butterfly distributions in the United States. They found that 46 of the 650 species of birds and 266 of the 575 species of butterflies that occur there have restricted distributions in the United States. Species with small or restricted distributions are of special conservation concern because they have higher extinction probabilities and may be easily overwhelmed by environmental changes (Terborgh 1974; Jablonksi 1987; Simberloff 1994; Channell and Lomolino 2000a). Of the species with restricted distributions, Abbitt et al. (2000) found that 45 species of birds and 249 species of butterflies also occurred in other countries. Many of these species have much larger distributions in those other countries, and the populations in the United States are peripheral to these larger distributions. A decision has to be made about whether peripheral populations of species such as these merit special protection. Many scientists have argued that populations at the edge of a species' distribution do not merit special protection.

Scientists cite five arguments against extending special protection to peripheral populations:

1. Conservation resources are limited, and those resources could be used more effectively elsewhere (Hunter and Hutchinson 1994; Lesica and Allendorf 1995).
2. Management for peripheral populations may be inappropriate for species that are more typical of the region in which conservation management is occurring (Hunter and Hutchinson 1994).
3. Extension of special protection to peripheral populations dilutes the effectiveness of the legislation enacted to protect declining species (Peterson 2001).
4. Peripheral populations are often inviable.
5. Peripheral populations have low conservation value because of their low genetic diversity.

The first three arguments are administration and implementation issues. Scientists making these arguments need to indicate that these arguments are not based on science but represent their opinions or value judgments. The last two arguments are scientific issues and deserve closer scrutiny.

The Viability and Genetic Diversity of Peripheral Populations

The expectation that peripheral populations have lower viability than central populations rests on two patterns: (1) populations are larger near the center of the species' distribution and smaller near the periphery (Brown 1984; Gaston 1990; Brown et al. 1995), (2) extinction probability of a population rises as population size falls (MacArthur and Wilson 1967; Goel and Richter-Dyn 1974; Pimm et al. 1988; Tracy and George 1992). This has led conservation biologists to predict that peripheral populations are more prone to extinction because of their smaller size (Brown 1995; Lawton 1995; Rodrigeuz 2002).

The expectation that peripheral populations have little genetic diversity is supported by three assumptions:

1. Small populations should maintain little genetic diversity because of genetic drift (Lewontin 1974). This assumption also draws on the idea that peripheral populations are smaller than populations near the center of the species' distribution; thus, peripheral populations should be less able to maintain genetic diversity than central populations.
2. Strong selective forces at the edge of the species' distribution could erode the genetic diversity of peripheral populations (Mayr 1970; Lewontin 1974).
3. Peripheral populations, because of their position at the edge of the range, are more isolated than central populations and will receive fewer immigrants than central populations (Mayr 1970; Brussard 1984). Fewer immigrants make it less likely that an allele lost because of genetic drift or intense selective pressures will be replaced by immigration.

However, while these expectations of low viability and low genetic diversity in peripheral populations are reasonable, they rest on patterns or assumptions that have been accepted uncritically. A closer examination of these patterns or assumptions is necessary if predictions produced from them are to be used to guide conservation. The expectations of low viability and low genetic diversity in peripheral populations are themselves subject to testing.

While many studies have suggested that a species is more abundant near the center of its distribution than at the periphery, the generality of this pattern across different regions and taxonomic groups is still in question. In a study of 32 British passerines, Blackburn et al. (1999) found no general pattern of greater abundance near the center of a species' distribution. In a meta-analysis of 145 separate tests of the hypothesis of greater central abundance, Sagarin and Gaines (2002) found that only 56 (39%) of those tests demonstrated greater abundance near the center of the species' distribution. The results of these two studies suggest that larger central populations and smaller peripheral populations may not be a general pattern. In addition, these results suggest that we should question the use of the assumption of larger central populations to guide conservation planning.

The lack of generality of this pattern has implications for the expectations that peripheral populations have low viability and will maintain less genetic diversity. If populations at the periphery of a species' distribution are not consistently smaller than populations near of the center of its distribution, then the extinction probability of the central and peripheral populations may also not differ. If populations at the periphery are not consistently smaller than populations near the center, then the capacity of central and peripheral populations to preserve genetic diversity may be similar.

Beyond testing the assumptions that peripheral populations are of low conservation value, we can directly test the expectations that those populations have low viability and low genetic diversity. Do populations near the center of the species' distribution persist longer than populations at the periphery of the species' distribution? Do populations near the center of the species' distribution have greater genetic diversity than populations at the periphery of the species' distribution?

Few studies have examined the persistence of species across their geographic ranges; however, those that exist suggest that species persist best at the periphery of their distribution or in areas isolated from the rest of their distribution. Towns and Daugherty (1994) found that many species of amphibians and reptiles from New Zealand persisted in areas at the edge of their historical distribution, especially on smaller isolated islands. Lomolino and Channell (1995) found that many mammals persisted better at the periphery than at the center of their historical distribution. Using a much larger dataset, Channell and Lomolino (2000a, 2000b) found that species persisted better at the periphery of their historical distribution than near the center, and that the pattern of higher peripheral persistence held across diverse taxonomic groups and geographical regions. Lomolino and Channell (1995) suggested that the pattern of greater persistence at the periphery of the species' historical range was the result of the spatial dynamics of environmental changes that had precipitated the species' decline. Regardless of where the changes to the environment start, the most secure populations will be those last exposed to the spread of the environmental change—i.e., those populations along the edge of the historical distribution of the species.

The literature on the distribution of genetic diversity within the geographic range of a species is growing rapidly; however, there are difficulties in interpreting this literature when evaluating whether peripheral populations are genetically depauperate compared with central populations. A major difficulty in interpreting this literature is due to the use of marginal populations. Peripheral is used to describe the geographic position of a population. Marginal is used to describe not only the geographic location of a population but also the size of the population, the immigration into the population, and the ecology of the population (Lewontin 1974; Brussard 1984; Shreeve et al. 1996). Many researchers examining genetic diversity limit their selection of peripheral populations to populations that are also marginal (small populations that receive few immigrants from other populations) (Lewontin 1974); however, not all peripheral populations are marginal populations (Lewontin, 1974; Brussard 1984). As discussed above, there is no clear pattern of population size relative to position within the geographic distribution of a species; thus, by limiting investigations of peripheral populations to populations that are also marginal (small, isolated, and ecologically marginal), there is a serious risk of associating the effect (low genetic diversity) with the wrong cause (either location, size, isolation, or ecology). Thus, studies of the genetics of marginal populations are unlikely to provide solid information that we can extrapolate to peripheral populations in general. To determine the influence of geographic position, it is important that the periphery be sampled at random without regard to the size, isolation, or ecology of the population. Moreover, the distinction between peripheral and marginal is not merely academic. If scientists and policy makers are trying to decide the conservation value of populations based on their geographical position, then there needs to be a strong relationship between geographical position and the viability or genetic diversity of the populations.

A review of the literature that compares the genetic diversity of central and peripheral populations shows that a strong relationship between the position of a population and its genetic diversity does not exist (Table 1). Out of the 45 species that I reviewed, 18 had greater genetic diversity near the center of their distributions; however, 5 of these 18 species were sampled only at peripheral sites that the researcher considered to be marginal (i.e., sites that were peripheral, small, and isolated). Most of the other researchers did not tell how they defined a peripheral population. More importantly, 27 of the species (60% of those reviewed) showed no significant difference between the genetic diversity of central and peripheral populations (Table 1); thus, most species do not show greater genetic diversity near the center of their distributions.

Table 1. Tests of greater genetic diversity near the center of the species' distribution.

Species name/ Common name[1]	*Greater genetic diversity near center of distribution?*	*Citation*
Angiosperms		
Arabidopsis thaliana Mouseear cress (Wall-cress)	Yes	Kuittinen et al. 1997
Camellia japonica Camellia	No	Wendel and Parks 1985; Chung and Chung 2000
Cirsium acaule Stemless thistle	Yes	Jump et al. 2003
Cirsium arvense Canadian thistle	No	Jump et al. 2003
Cirsium heterophyllum Melancholy thistle	No	Jump et al. 2003
Corrigiola litoralis Strapwort (European corrigiola)	Yes	Durka 1999
Decodon verticillatus Swamp loosestrife (Hairy swamp loosestrife)	Yes	Eckert and Barrett 1993
Erythronium montanum Avalanche Lily (Glacier fawnlily)	No	Allen et al. 1996

[1]Names in parentheses are those listed by NatureServe Explorer (version 4.0, July 2004).

Table 1. Tests of greater genetic diversity near the center of the species' distribution (cont'd).

Species name *Common name*[2]	*Greater genetic diversity* *near center of distribution?*	*Citation*
Gleditsia triacanthos Honey locust (Honey-locust)	No	Schnabel and Hamrick 1990
Gysophila fastigiata	Yes	Lonn and Prentice 2002
Helonias bullata Swamp pink (Swamp-pink)	No	Godt et al. 1995
Lilium parryi Lemon lily	Yes	Linhart and Premoli 1994
Lloydia serotina Alp lily (Common alpine lily)	No	Jones et al. 2001
Lychnis viscaria German catchfly (Clammy campion)	Yes	Lammi et al. 1999; Siikamaki and Lammi 1998
Phlox drummondii Garden phlox (Drummond phlox)	No	Levin 1997
Quercus suber Cork oak	No	Jimenez et al. 1999
Silene nutans Nottingham catchfly (Nodding catchfly)	No	Van Rossum et al. 2003
Gymnosperms		
Picea abies Norway spruce	No	Lagercrantz and Ryman 1990
Pinus contorta Lodgepole pine	Yes	Yeh and Layon 1980; Fazekas and Yeh 2001
Pinus edulis Pinyon pine (Two-needle pinyon pine)	No	Betancourt et al. 1991
Pinus jefferyi Jeffrey pine (Jeffrey's pine)	Yes	Furnier and Adams 1986

[2]Names in parentheses are those listed by NatureServe Explorer (version 4.0, July 2004).

Table 1. Tests of greater genetic diversity near the center of the species' distribution (cont'd).

Species name *Common name*[3]	*Greater genetic diversity* *near center of distribution?*	*Citation*
Pinus rigida Pitch pine	No	Guries and Ledig 1982
Pinus sylvestris Scots pine (Scotch pine)	No	Dvornyk 2001
Pseudotsuga menziesii Douglas-fir	Yes	Li and Adams 1989
Invertebrates		
Coenonympha hero Scarce heath	No	Cassel and Tammaru 2003
Drosophila buzzati	Yes	Barker and Mulley 1976
Drosophila obscura	No	Lakovaara and Saura 1971
Drosophila pachea	No	Rockwood-Sluss et al. 1973
Drosophila persimilis	No	Prakash 1977a
Drosophila pseudoobscura	No	Prakash 1977b
Drosophila robusta	No	Prakash 1973
Drosophila subobscura	No	Saura et al. 1973
Drosophila willistoni	No	Ayala et al. 1972
Echinometra mathaei	Yes	Palumbi et al. 1997
Isognomostoma isognomostoma	No	Van Riel et al. 2001
Macoma balthica Baltic clam	No	Hummel et al. 1997
Paruroctonus mesaensis Desert sand scorpion	Yes	Yamashita and Polis 1995
Vertebrates		
Acrocephalus arundinaceus Great reed warbler	Yes	Bensch and Hasselquist 1999
Alectoris chukar Chukar	No	Safriel et al. 1994

[3]Names in parentheses are those listed by NatureServe Explorer (version 4.0, July 2004).

Table 1. Tests of greater genetic diversity near the center of the species' distribution (cont'd).

Species name *Common name*[4]	*Greater genetic diversity* *near center of distribution?*	*Citation*
Dipodomys stephensi Stephen's kangaroo rat	Yes	Metcalf et al. 2001
Hyla arborea European tree frog	Yes	Edenhamn et al. 2000
Lynx canadensis Canada lynx	Yes	Schwartz et al. 2003
Rana latastei Italian agile frog	No	Garner et al. 2004
Rana pretiosa Spotted frog (Oregon spotted frog)	Yes	Green et al. 1996

In fact, it may be a bit naïve to believe that there should be any relationship between the genetic diversity of a population and the population's position in the species' distribution. While genetic diversity is influenced by factors that act in ecological time (e.g., immigration, population size, selection), it must also be influenced by accumulated historical events (e.g., mutation, bottlenecks, immigration) (Brussard 1984; Vucetich and Waite 2003; Schmitt and Hewitt 2004). Of the papers that I reviewed (Table 1), 11 (24%) suggested that historical factors (e.g., Pleistocene glaciation) had a strong influence in shaping the distribution of the species' genetic diversity. The current position of a population does not inform us about the historical events that shaped its genetic diversity; therefore, position cannot be a complete gauge of the population's genetic or conservation value. We might choose to conserve a population that currently is near the center of the species' distribution, and in the future, that distribution may shift so our population is now at the edge of the species' distribution. Will its genetic diversity and its conservation value have declined? We cannot assume that the current distribution of the species or the distribution of its genetic diversity is unchanging, or that they are described completely by current conditions.

The general recommendations that have directed conservation biologists to conserve central populations at the expense of peripheral populations because of the former's perceived greater viability and greater genetic diversity seem baseless. These recommendations, however, have limited the conservation options that mangers have considered and that have influenced species conservation. While it cannot be proven that policy based on these recommendations has harmed any species, conservation managers are likely to develop better conservation plans when they are allowed a greater list of choices (i.e., the possible inclusion of peripheral populations).

[4]Names in parentheses are those listed by NatureServe Explorer (version 4.0, July 2004).

Conservation biologists should consider both central and peripheral populations when developing conservation plans.

The Value of Peripheral Populations to Conservation

If the viability and genetic diversity of peripheral populations are not inherently inferior to those of central populations, then central and peripheral populations both have roles to play in conservation. In this regard, peripheral populations may be important in certain aspects of conservation.

Peripheral populations may represent valuable opportunities to conserve biodiversity that is threatened by global climate change. Thomas et al. (2004) estimated that 15–37% of all species will be threatened by global warming in the next 50 years. Many studies have already documented poleward shifts in many species' distributions (Parmesan 1996; Parmesan et al. 1999; Parmesan and Yohe 2003; Root et al. 2003; Channell, unpublished data). While there may be difficulty in predicting shifts in species' distributions in response to global warming (Davis et al. 1998; Crozier 2002), poleward peripheral populations may represent our best chance to conserve those species threatened by global climate change. The loss of peripheral populations will reduce our choices in developing conservation plans to deal with the threat posed by global warming.

One of the major goals of conservation biology is to preserve the evolutionary potential of species (Frankel 1983). The adaptation of peripheral populations to different environments is often seen as a stepping stone to speciation (Mayr 1970). These adaptations also allow peripheral populations to persist in stressful environments and may be preadaptations to future changes in the environment (e.g., Johansson 1994; Lomolino and Channell 1995; Volis et al 1998; Lammi et al. 1999; Jones et al. 2001; Pedersen and Loescheke 2001; Van Rossum et al. 2003). Peripheral populations often display higher levels of differentiation than central populations (e.g., Linhart and Premoli 1994; Jones et al. 2001; Lonn and Prentice 2002; Jump et al. 2003; Taylor et al. 2003). The peripheral isolates model is often cited as one of the main modes of speciation (Mayr 1970; Lesica and Allendorf 1995; Lammi et al. 1999). The loss of peripheral populations may reduce the ability of a species to adapt to future changes in the environment and may reduce its potential for speciation.

Peripheral populations often persist longer than central populations (Lomolino and Channell 1995; Channell and Lomolino 2000a, 2000b). Lomolino and Channell (1995) suggested that this greater persistence was the result of the geographical distribution and spread of anthropogenic changes to the environment. They further suggested that populations persist in areas where these changes do not reach, reach last, or are of lower intensity (Lomolino and Channell 1995; Channell and Lomolino 2000a, 2000b). Since these changes to the environment spread contagiously, isolated peripheral populations should persist the longest (Lomolino and Channell 1995). Peripheral populations may be our last opportunity to conserve many species and may represent opportunities to conserve species faced with high intensity and widespread changes to their environment (Towns and Daugherty 1994; Lomolino and Channell 1995; Channell and Lomolino 2000a).

By increasing the options for conservation management, more efficient solutions might be achieved. Araujo and Williams (2001) compared different approaches to positioning nature reserves. They found that nature reserves in the periphery of species' distributions could conserve more species per unit area than nature reserves near the center of the species' distributions (Araujo and Williams 2001). This research suggests that by including peripheral populations in conservation plans, conservationists might be able to make more efficient use of limited conservation resources.

Hunter and Hutchinson (1994) and Lesica and Allendorf (1995) have suggested that even at the edge of their distribution some species will be integral to the communities and ecosystems they inhabit. The loss of peripheral populations of these keystone species might trigger other changes to these ecosystems and communities (Hunter and Hutchinson 1994; Lesica and Allendorf 1995). Such changes could precipitate an extinction cascade. In such situations, the conservation of peripheral populations may be necessary to preserve ecosystem function and other species.

Hunter and Hutchinson (1994) further suggested that peripheral populations of large charismatic species might serve as umbrella species. By conserving the habitat needed for these species, many other species might also be conserved. Thus, conserving peripheral populations might serve as a tool for conservationists to protect other species and ecosystems that otherwise might not be protected.

Conservation Recommendations

This examination of the science behind the assumptions that have relegated peripheral populations to a minor role in conserving species has highlighted several problems in how conservation is conducted. First, conservation biologists need to consider peripheral populations as viable and even valuable for conserving declining species. The traditional assumptions that peripheral populations have low viability and low genetic diversity are contradicted by an examination of the evidence. I am not suggesting, however, that conservationists ignore populations near the center of the species' distribution. Inclusion of both central and peripheral populations in the development of conservation plans will not only increase the number of sites that can be considered, but will also increase the quality of the sites from which to choose.

Second, I would encourage conservation biologists to question generic prescriptions and untested theory. In conservation, we are often faced with a declining species about which little is known. With insufficient data and resources, we often have to use untested ideas to guide species conservation. The urgency of the time justifies the use of untested ideas when we believe that inaction or even delayed action might further risk the loss of the species; however, we should, when we can, test those ideas and their assumptions. Furthermore, I would encourage conservation biologists to avoid proxy variables. If we are interested in persistence, then we should measure persistence. If we are interested in genetic diversity, then we should measure genetic diversity. Proxy variables should be used only when a strong relationship has been documented between the proxy variable and the variable of interest.

Third, I would remind conservation biologists that we live in a dynamic world. Today's peripheral populations may have been central in the past and may be central in the future. Also, changes that threaten one small part of the distribution today may one day threaten the entire species. To develop a conservation plan, we need to know why a species is declining, the spatial distribution of the factors contributing to the decline, and how those factors spread.

Finally, I would urge conservation biologists to be scientists, advocates, and administrators but to draw sharp distinctions between these roles. When speaking in public, conservation biologists need to be clear about what is supported by science when speaking as a biologist, what is influenced by their values when speaking as an advocate, or what is limited by the available resources when speaking as an administrator. In conservation, science must lead advocacy and administration, but all three are necessary for conserving biodiversity.

Conclusion

I am not arguing that all populations must be protected, but that our selection of populations for conservation should be based on sound science, and that the general exclusion of peripheral populations is not scientifically justified. Limited conservation resources will require that scientists and administrators prioritize which species and populations receive special protection or management; however, wise use of those resources would require consideration of both central and peripheral populations for conservation.

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