Plagued by a Plethora of Peripherals: Refining Guidelines for Peripheral Taxa

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Abstract: The size, location, and topography of British Columbia encourage incursions of taxa that are more widespread and abundant elsewhere. The periphery of the range of at least 1400 taxa extends into British Columbia. Over 900 of these appear on the Red and Blue Lists prepared by the Conservation Data Centre. Conversely, less than half of British Columbia's endemic taxa or taxa for which the province has significant global stewardship responsibility appear on the Red and Blue Lists. We examine why we conserve and list species, concluding that a primary scientific or practical reason is to sustain genetic variability. We consider two broad kinds of peripheral species—disjunct (geographically marginal) populations and politically peripheral (often ecological marginal) populations that straggle irregularly across provincial boundaries. We document the degree to which each enters provincial Red and Blue Lists. The Conservation Data Centre generates the Red and Blue Lists using seven ranking factors. These factors are correlated in a fashion that biases politically peripheral populations towards rankings of artificially high risk. Thus, the lists have little utility in guiding conservation priorities. Recovery plans for most politically peripheral species appear doomed to failure for sound biological reasons. We note alternative approaches to evaluating species for conservation action and recommend that conservation efforts for peripheral species be focused on disjunct populations, rather than politically peripheral populations.

Key Words: British Columbia, conservation priorities, range periphery, disjunct populations, species ranking

Introduction

British Columbia (B.C.) hosts an abundance of taxa for which < 10% of their range occurs within the province. In fact, such 'peripheral' taxa represent over 70% of species that are red- or blue-listed within the province. The province also hosts many taxa for which it has 30–100% of global stewardship responsibility. The literature provides conflicting advice on the degree to which conservation effort should be assigned to peripheral taxa. We first review reasons why we conserve and list species, then provide an operational definition of peripheral in terms of British Columbia, and note why we, in British Columbia, must be particularly mindful of peripheral taxa. After describing some features of peripheral taxa, we offer specific suggestions for assigning

conservation effort to them. We argue that some disjunct populations will prove to be the most worthwhile investment.

Why We Conserve and List Species

We conserve species because we are concerned about their loss. Workers have classified the nature of this concern using 5 to 8 categories (Ehrenfeld 1976; Bunnell and Williams 1980a) but these can be grouped effectively into two broad classes (Bunnell 1990): one that is primarily aesthetic and moral, and one that is primarily practical. We can ignore legal or policy-driven rationales because they are a response to the deeper concerns. Aesthetic and moral issues obviously influence policy, but they can be remarkably divergent. The practical rationale merits more attention because it helps clarify how we should assign priorities to our efforts to conserve species. That rationale begins with the scientific reason for conserving biological richness.

We use 'biological richness' instead of 'biological diversity' deliberately. Delong (1996) and Bunnell (1998a) reviewed about 90 definitions of biological diversity. None were the same. The reason for this diversity of definitions is simple: biological diversity is a cluster of concepts (many of which we understand poorly) rather than a thing, subject to measuring, probing, and prodding. The diversity of definitions reflects the theoretical nature of concepts imbedded in the term, but leaves practitioners in a quandary. If our concern for sustaining biological diversity is genuine, we cannot await scientific clarification. The major danger, well illustrated by Delong (1996), is that we can subvert the scientific content of our definitions by defining them in terms of operational measures. One solution is "…to clearly distinguish interim operational criteria from slowly developing scientific consensus on the meaning of…biological diversity" (Bunnell 1997). An initial and scientifically credible operational measure is to focus on species, thus species richness.

Namkoong (1998) and Bunnell (1998b) present the argument in detail. Most simply, a fundamental scientific and practical reason for sustaining biological diversity is to sustain genetic variability. Genetic variability permits continued adaptability, continued creation of biodiversity, sustained productivity in a changing environment, and thus sustained resources. Indeed, the Convention on Biological Diversity makes a clear and specific distinction between biological diversity ("variability among living organisms"; Convention, Article 2. Use of terms) and entities or biological resources ("genetic resources, organisms or parts thereof, populations, or any other biotic component of ecosystems"; op. cit.). In short, neither the scientific rationale for sustaining biological diversity nor the Convention on Biological Diversity argues for sustaining species. They argue explicitly for maintaining variability. But, there is no practical ability and little theoretical guidance for creating targets of requisite genetic variability. Species are a credible (and publicly favored) surrogate for sustaining genetic variability. Bunnell and Williams (1980b) argued that subspecies also were a tractable surrogate because they often represent visible genetic variation. Moreover, species and subspecies are the only self-replicating packages of genetic

variation. Both Namkoong (1998) and Bunnell (1998b) concluded that species and subspecies are the most useful interim surrogate for sustaining the values embraced by the term 'biological diversity'. Note that the convention was careful not to argue for sustaining all species, but states that "each contracting party shall identify components of biological diversity important for its conservation and sustainable use…" (Article 7a).

In summary, we conserve species primarily to meet aesthetic and moral concerns of the public. Species also represent a useful interim surrogate for attaining the practical values we hope to derive from sustaining biological diversity. In recognition of regional differences in history, social conditions, and economic states, the Convention on Biological Diversity does not stipulate which species to conserve. Instead, that choice is ours, as are decisions about peripheral taxa.

We list taxa to assist our efforts to conserve them. To attain this goal we create lists for three primary reasons: (1) to contribute to regional and broader estimates of a taxon's status, (2) to rank species according to some measure of threat, such as risk of extinction or rarity, and (3) to rank species according to priority for conservation.

Two broad problems have arisen from listing processes. The first problem has resulted because lists created for the first and second reason have been used for the third. A few species that have declined to very low numbers have consumed the bulk of resources for recovery at the expense of many less threatened species with higher chances of recovery. For this reason, the U.S. Fish and Wildlife Service has two systems for listing species—one for ranking species according to threat and one for ranking species according to priority for conservation. Criteria in both processes are the same—degree of threat and taxonomic distinctness—except that to rank species by conservation priority, recovery potential is also considered.

The second problem arises when measures of rarity, used as an index of threat, are applied locally, according to the location of political borders. Measures of local rarity result in lists that simply and accurately rank species into categories of local rarity, but inaccurately rank species into categories of threat. When such lists are used to prioritize conservation effort, this problem results not in too much expenditure on critically threatened species, but in the same level of expenditure on species *that are not even threatened*.

A critical question is, can one approach to listing serve all purposes? A corollary question is: does our current listing process in B.C. adequately guide conservation efforts for peripheral species?

Defining Peripheral

Creating an operational definition of a 'peripheral population' is simple, though there are practical challenges. An initial definition is easy—populations at the margin or periphery of a taxon's geographical range. It also is relatively easy to define disjunct populations as those removed by distance from more continuous populations; however, distinguishing disjunct

populations from populations that inhabit the margin of a more continuous population can be more difficult when the taxon's range is not accurately described.

Not all peripheral populations are equal, especially when viewed from the perspective of a political unit. Political boundaries almost always are different from those created by nature. Questions arise relevant to the conservation value of those peripheral populations found within a political unit for which a list is constructed. Is the range of the entire taxon expanding into or contracting away from the unit? If the population is disjunct, how far is it from the continuous population? Do a few organisms creep irregularly across the political boundary, or is the periphery comprised of well established populations? How long have they been established? Does what we know of their natural history suggest they are generating a quite different genetic composition, or not? Is the population in British Columbia part of a larger disjunct population that may be genetically distinct? Is the global range of the species small relative to other species in the taxonomic group, implying higher conservation concern than peripheral species with large global ranges?

This list of questions, and others like them, illustrate a crucial point: not all peripheral populations are equally amenable to conservation efforts or have equal conservation value. Both amenability to success in conservation effort *and* the potential value, if successful, are completely dependent on answers to these questions. We have recognized these questions in the list of peripheral taxa that we have created for British Columbia (see www.forestbiodiversitybc.ca). For example, disjunct populations occurring only in B.C. are distinguished from those occurring in B.C. and elsewhere.

To determine which taxa are peripheral to British Columbia, we use one criterion and a modifier. The criterion is simple: no more than 10% of the taxon's range occurs within the province. The modifier is intended to exclude extremely widespread species, such as the fisher (*Martes pennanti*), American marten (*Martes americana*), or American robin (*Turdus migratorius*). Less than 10% of these species' ranges occur in the province, but it also is true that less than 10% of their range occurs in many provinces or states in North America throughout their large range. Such species are excluded because simplistic application of the criterion (< 10 %) makes them peripheral everywhere. In practice, the modifier works by ensuring that the taxon's range extends over less than 30% of the landbase in British Columbia. When we provide numbers for peripheral taxa, it is this definition of peripheral (criterion plus modifier) that applies.

Why Should We Worry?

Why should we, in British Columbia, worry about peripheral taxa? There are two broad reasons: (1) we have a surprising number of them, and (2) many of them appear on the provincial Red and Blue Lists, which implies conservation concern. British Columbia is uncommonly rich in species, even without all those for which < 10% of their range extends across provincial boundaries (Bunnell and Williams 1980b). The underlying reasons for this richness are simple.

The province sits at the nexus of three continental climate regions, contains much more up and down than sideways topography, and the up and down is oriented perpendicular to prevailing weather systems. As a result, there is great variety in the regional climate (the highest number of terrestrial climate regions of any jurisdiction in North America except Mexico; 7 of the 10 growing regions recognized by the United States Department of Agriculture for North America), in the vegetation (broad ecosystem types ranging from desert to coastal rain forest), and in the number of species inhabiting that array of vegetation (Bunnell 1990). For example, the province contains 66% of Canada's butterfly species, 70% of its freshwater fish species, 76% of its bird species, 60% of its conifer species, 56% of its fern species, and 41% of its orchid species (see www.forestbiodiversitybc.ca). This richness is outstanding if you delight in natural history. It is a daunting challenge if your task is to sustain it all.

It is equally clear why peripheral species contribute so much to this richness. The arrangement of landforms in the province makes it easy for species to forge or straggle across our borders. The Puget Sound lowlands encourage incursions from species much more common farther south, as do the Okanagan Valley and the Rocky Mountain Trench. The Peace River lowlands allow easy access for species much more abundant to the east; the Tatsenshini-Alsek triangle welcome visitors from the north. When taxa encounter these gateways into the province they enter—more than 1400 of them. Most of them become red- or blue-listed in the province once they have crossed the border (Table 1).

Table 1. Incomplete summary of peripheral taxa or populations occurring in British Columbia and their status as determined by the B.C. Conservation Data Centre.

Group	*Total*	*% Red- and blue-listed*	*No. of red-listed*	*No. of blue-listed*
Mosses	238+?	?	49	189
Vascular plants	711	67.7	226	255
Odonata	25	60.0	7	8
Butterflies	138	41.3	10	47
Fish	30	63.3	8	11
Amphibians	9	77.8	5	2
Reptiles	10	80.0	3	5
Birds	141	41.8	31	28
Mammals	99	31.3	12	19

Two broad points are evident from the data presented in Table 1. First, a large number of taxa meet our operational definition of peripheral in B.C. (1401 from an incomplete listing). Second, many of these species are red- or blue-listed. About 70% of all red- and blue-listed species in the province are peripheral, having < 10% of their range within the province and occurring over less than 30% of the province. Those facts inspire a significant question when assigning conservation priorities: what do we do about all these listed peripheral taxa? Elsewhere in these proceedings we noted that at least 100 endemic taxa occur in the province, for which the province has 100%

of the global stewardship responsibility (Bunnell et al. 2005). There are an additional 138 taxa for which the province hosts 50% or more of the world's population either year-round or in specific seasons (Bunnell et al. 2005). What portion, if any, of scarce conservation funds should go to taxa having < 10% of their range in the province, especially given that there are so many taxa for which the province has significant global responsibility?

The data in Table 1 also expose another question that has received recent attention in the conservation literature: can biodiversity 'hotspot' analysis guide the allocation of conservation efforts? A large number of taxa in the province are peripheral and locally rare, as we expect most peripheral species to be. 'Hotspot' analyses of species richness and rareness in B.C. tend to glow hottest where peripheral species commonly enter the province, particularly in the south and east. Other workers have pointed out various failings of hotspot analysis to effectively guide conservation efforts, specifically, the allocation of land to reserves (e.g., Reid 1998; Araújo and Williams 2001). In the case of British Columbia, the failing could be exacerbated because effort would be assigned to areas where many species are ecologically marginal (see next section).

At least one further question arises from the data in Table 1: why is such a high portion of peripheral taxa red- and blue-listed? The answer is simple. Conservation Data Centres throughout North America and beyond create their listings using seven factors developed by The Nature Conservancy:

- estimated number of existing occurrences;
- viability of these occurrences;
- trend in population, size, number, number of occurrences;
- overall estimated population size;
- geographic distribution (range);
- number of occurrences adequately protected and managed; and
- actual or potential threats facing the species or its habitat.

Classes for each factor can be found in Harcombe (2000). The web site for the B.C. Conservation Data Centre (CDC) notes that "the number of occurrences is key to the status of many species, since those with very few occurrences are vulnerable to both predictable and unpredictable influences. The score for number of occurrences usually determines an initial rank, which is then modified sequentially based on the scores for other factors." The great value of this approach is that it is standardized to the extent possible across a number of jurisdictions (50 states, 10 provinces, and 12 Caribbean and Latin American jurisdictions). It thus contributes significantly to the broad picture of the geographic range and overall conservation status of species.

Bunnell et al. (2004) described how such a system deals with a peripheral taxon for which some individuals irregularly straggle across the provincial borders, perhaps as seldom as once every two or three years. The taxon would not have many occurrences—it would be locally rare in B.C. It necessarily would have low viability in the province, be erratic in trend, have a small

provincial population size, and small provincial range. A responsible agency would not have committed funds to adequately protect and manage habitat for the taxon. Each of these correlated features that are intended to *modify* local rarity serve to *emphasize* rarity within the province and increase its apparent risk of endangerment. For peripheral taxa, the system is strongly biased in an unhelpful direction. We noted at the outset that there are least three broad reasons for listing taxa. The approach taken by Conservation Data Centres fulfills the necessary task of estimating the relative rarity of species within B.C.; however, the listing process provides little appropriate guidance on how to assign conservation priorities. Nor is it intended to. Conservation priorities for peripheral taxa are best assigned by considering the ways in which taxa are peripheral.

Ways of Being Peripheral

Among peripheral populations there is a gradient in the degree of continuity with the larger population. There also is a strong gradient in the degree to which the population has adapted to conditions at the periphery of its range or how well established it is. It is these two broad features—isolation and potential for genetic change plus population vigor or viability—that determine a population's value to conservation effort. For simplicity, we have broken these continua into two broad groups that we term disjunct and politically peripheral (Fig. 1). We note additional features that modify the conservation value of each group.

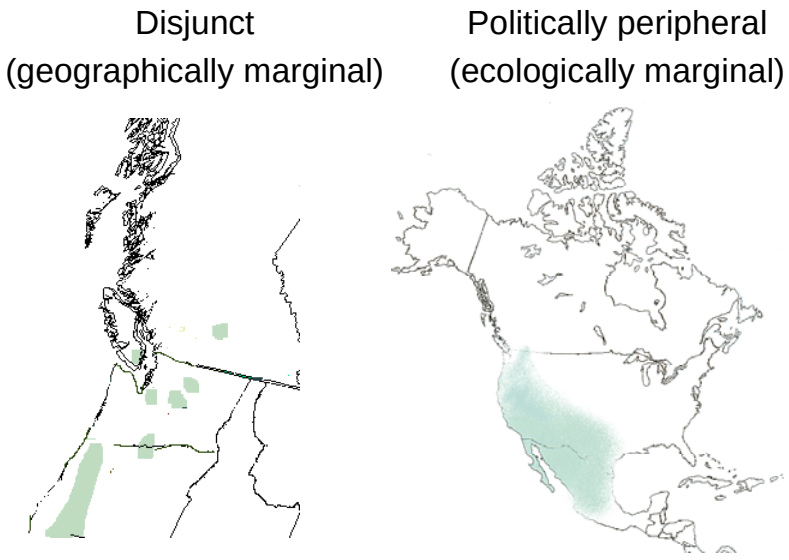

Figure 1. Example ranges of disjunct (sharp-tailed snake) and politically peripheral (pallid bat) taxa in British Columbia.

Disjunct Populations

Shumaker and Babble (1980) and Soulé (1973) define 'geographically marginal' populations as peripheral populations that are separated from central ones by spatial distance. Such populations are commonly termed 'disjunct'. They tend to occur in less suitable environments and are isolated or disjunct from the central, more continuous populations (Lesica and Allendorf 1995). In his review, Mayr (1997) noted almost universal agreement that the prevailing process of speciation is allopatric—derived from geographical separation. When discussing why we conserve species we noted that the fundamental scientific rationale is to conserve genetic variability. The conservation value of disjunct populations depends upon their divergence from other conspecific populations through isolation, genetic drift, and natural selection (Lesica and Allendorf 1995).

Bunnell et al. (2004) reviewed the major features that can be used to determine the conservation value of peripheral populations:

1. Spatial Distance: The more distant or disjunct populations are from the more continuous range, the more divergent they are likely to be due to the random effects of the founder principle (e.g., Yeh et al. 1985; Gould 2002). Populations isolated by distance, also can suffer a greater loss of genetic variation than larger populations with greater potential for genetic exchange (Nei et al. 1975). Divergence induced by distance is one mechanism by which new species are created, and which the conservation of biological diversity is intended to promote.
2. Life History: Species with life history attributes that cause reduced gene flow between populations are more likely to form evolutionary significant peripheral populations by enforcing a form of isolation. Pond-breeding amphibians in dry climates, for example, show greater inter-population genetic differences than does the stream-breeding tailed frog (*Ascaphus truei*) (Ritland et al. 2000). Similarly, species with short generation times will diverge more quickly, once isolated, than species with longer generation times (Niklas et al. 1985), so require shorter periods of isolation for genetic divergence. Other aspects of population viability are as important as gene flow.
3. Time: The longer a population is isolated from parent populations, the greater the likelihood for the evolution of genetic differences. The period of isolation required for genetic divergence is shorter for species with shorter generation times.
4. Ecological: Genetic divergence also can occur when populations occupy habitats that are very different from, or more stressful than, habitats in the species' more continuous range, thereby providing stronger selection pressure on populations with lower diversity than that across the entire species' range (reviews in Lesica and Allendorf 1995 and Gould 2002). Selection may be stronger in peripheral populations or it may just be different—acting on different traits or selecting traits in different directions.

Bunnell et al. (2004) noted that these features are not tidily discrete, but interact. For example, lower effective population sizes will encourage greater genetic drift (thus greater genetic differentiation due to random forces) but will weaken the efficacy of selection (thus decreasing the potential for adaptation). The fundamental point is that species must have genetic variability to evolve; therefore, the most genetically distinct populations should be protected (Beardmore 1983; Millar and Libby 1991). Because populations become isolated near the periphery of a species' range, the periphery or margin is one of the most active regions of genetic divergence and speciation (Mayr 1954; Gould 2002). In his review, Mayr (1997) noted near universal agreement that new species have arisen primarily from disjunct or isolated populations. These often are at the periphery of a range. Unfortunately, these small, isolated populations also are more likely to be at risk than more continuous populations.

Politically Peripheral Populations

Disjunct populations are geographically separated by distance from the more continuous range of the species, whereas politically peripheral populations are those that extend across a political border but retain their connection to larger, continuous populations. The simple schemata of Figure 1 is not the way nature usually works. Very few organisms have a continuous range. In fact, many songbirds are rare throughout most of their range (when we map that range by drawing a line around the edge of occupied area; Mehlman 1994). If we actually could map those ranges at the level of habitat, they all would be speckled by holes where the species was absent. But the major point holds—there are disjunct populations that are well removed from more continuous populations, and those are peripheral. Also, there always are populations at the margins of larger ranges. When these extend across a political boundary, we term them politically peripheral.

Most politically peripheral populations also are ecologically marginal. Unless restricted to an island or by some other topographic feature, the edge of any species' range is fuzzy and variable from year to year or generation to generation. That occurs naturally because conditions at the edge of a range usually are less favorable to the species than conditions near the center. The unfavorable condition includes stronger selection pressure that speeds genetic divergence, but also puts small populations at risk. Stated differently, there is a band of variable width around most species in which λ (estimated growth rate) is less than 1. Populations in this band, termed 'land of the living dead' by Wolf et al. (1996) or 'black-hole sinks' by Gomulkiewicz et al. (1999), are ecologically marginal. This is a natural condition, and there usually will be an area of a species' range that is ecologically marginal, in which individuals must struggle more fiercely to survive.

The challenge to setting conservation priorities occurs when this wavering band crosses a political boundary, and the taxon is politically peripheral. Efforts to conserve species that are locally rare but globally common often simply ignore the ecologically marginal nature of habitat and population. They engage in a fight with nature. As well as being wasteful, this fight has a

charmingly whimsical aspect. Consider that had the United States prevailed in the "54°40′ or fight" argument of 1846, sage thrashers (*Oreoscoptes montanus*) and white-headed woodpeckers (*Picoides albolarvatus*) would not be 'critically imperiled' in British Columbia, but Pacific treefrogs (*Pseudacris regilla*) and Brewer's blackbirds (*Euphagus cyanocephalus*) would be. That change of status would have occurred with no change in abundance or distribution of the species.

Disjunct populations also can be ecologically marginal populations, but they are more likely to survive and diverge because they have been isolated from the center of their ranges for some time. They may harbor unique alleles, genotypes, or phenotypes. Unlike politically peripheral populations, the persistence of disjunct populations indicates survival through the founder stage and successful exposure to new selective pressures. Ecological marginality for a disjunct population may, in fact, lead to genetic innovation through new alleles or new adaptations (Bunnell et al. 2004).

Table 2 summarizes numbers and proportions of disjunct and politically peripheral populations in British Columbia. Three significant points are apparent: (1) among the groups examined, for all but fish, 50–100% of red- and blue-listed taxa are peripheral (< 10% of their range occurs within the province), (2) the vast majority of these are politically peripheral and likely ecologically marginal, and (3) for most groups the proportion of red-listed taxa that are peripheral varies between about 30–100%. It is apparent that listings of provincial status as compiled by the CDC, while contributing importantly to some objectives, are not appropriate to assign conservation priorities. Too much conservation effort would be spent on the 'land of the living dead' or 'black-hole sinks'.

Table 2. Peripheral taxa in British Columbia listed by the B.C. Conservation Data Centre and COSEWIC, with proportions that are red-listed, red- and blue-listed, politically peripheral, and disjunct.

Group	*COSEWIC*[a]	*CDC*[b]	*Red-listed*[c]	*Red- and blue-listed*[d]	*Politically peripheral*[e]	*Disjunct*[f]
Mosses	2	238	58.3	66.3	59.3	7.0
Vascular plants	22	481	83.1	79.5	76.4	3.1
Odonata	0	15	87.5	65.2	52.2	13.0
Butterflies	4	57	83.3	85.1	77.6	7.5
Fish	4	19	27.6	43.1	38.6	4.5
Amphibians	7	7	100.0	77.8	66.7	11.1
Reptiles	6	8	100.0	100.0	87.5	12.5
Birds	12	59	74.8	68.6	60.5	8.1
Mammals	9	31	40.0	50.8	50.8	0

[a]Number of peripheral taxa or populations that are listed by COSEWIC.

[b]Number of red- and blue-listed peripheral taxa or populations.

[c]Percent of red-listed taxa or populations that are peripheral.

[d]Percent of red- and blue-listed taxa or populations that are peripheral.

[e]Percent of red- and blue-listed taxa or populations that are politically peripheral.

[f]Percent of red- and blue-listed taxa or populations that are disjunct.

How Can We Assign Conservation Priorities?

An obvious question arises: how can we effectively assign conservation priorities when so many of our listed species are peripheral? This question becomes more compelling when we recall that British Columbia hosts at least 100 endemic taxa for which the province has 100% of the global responsibility. Many other taxa have significant portions of their global range in the province, and still more have shown long-term decreasing trends but are not yet rare enough to appear on the Red or Blue Lists (Bunnell et al. 2005).

There are both practical and scientific challenges. Practically, we have at least 1401 peripheral taxa (Table 1), and 915 of these are red- or blue-listed. Attention to all of these would consume our budget many times over and leave nothing for taxa for which we have more stewardship responsibility. Scientifically, there is little evidence of success in recovery of peripheral populations. Success in recovery of any species in North America has proven limited. Recent reviews of recovery programs in the United States indicate that of over 1350 taxa listed in 1992, only 0.3% had been downlisted as a result of recovery plans (GAO 1992). Data for Canada are nearly identical. Of 425 taxa that have been listed by COSEWIC as Endangered, Threatened, or Special Concern, only 6 or 1.4% have been downlisted as a result of recovery plans (data from COSEWIC species database available online at www.cosewic.gc.ca). We expect delisting or downlisting to be easier in Canada because regulations in the United States require 'proof' that adequate protection will be provided to the taxon once it is delisted (Doremus and Pagel 2001). We are aware of no reviews of the recovery process in Canada, but at least seven reviews are available for the United Sates (e.g., Stafford 1995; Kirkland and Ostfeld 1999; Abbitt and Scott 2001; Elphick et al. 2001; Restani and Marzluff 2001; Clark et al. 2002; Taylor et al. 2003). One conclusion is that efforts are likely to succeed only where suitable habitat is available in most of the surrounding area, not simply in one direction (e.g., to the south or east).

Our failure rate in both nations approximates 99%. For a larger area, Canada allocates about 5% of the funding to species recovery as is allocated in the United States ($19.6 million in 2003 [RENEW 2003] compared to $495.3 million in the United States in 2000 [USFWS 2003]). We do not have such ample funding that we can waste 99% of it, so we must allocate our resources where they are most likely to be successful. On the basis of their review of peripheral taxa, Lesica and Allendorf (1995) emphasized, "…our findings do not lend themselves to hard and fast rules for constructing priorities". Hunter and Hutchinson (1994) arrived at the same conclusion. In short, a blanket policy for peripheral species has no scientific credibility. What is reasonably clear is that there is at least theoretical merit in attempting to sustain isolated, disjunct populations that have been reproducing in isolation long enough to become genetically divergent. Whether they should receive scarce conservation resources instead of declining populations of a taxon for which a political unit has much larger global responsibility requires thoughtful scrutiny. Fraser (2000) presented arguments without consistently distinguishing forms of peripheral populations. Bunnell et al. (2004) noted at least six additional issues that should be considered before allocating conservation resources to geographically marginal populations.

Among peripheral taxa, conservation priority should be given to populations that are clearly established in the province. Many populations have survived within the province for 10 or more generations and are unlikely to be ecologically marginal. They have proven they can survive. We can assess the relative conservation value of disjunct populations, even where we have no genetic fingerprint. The conservation value of well-established disjunct populations depends upon their divergence from other conspecific populations through isolation, genetic drift, and natural selection. The amount of that divergence can be estimated by considering the factors governing genetic change noted earlier (e.g., spatial distance, time, life history, and ecological features). Note that these factors lead to the creation of new species. In allocating scarce resources, we are making a wager with nature that populations with satisfactory combinations of these factors will survive and continue to evolve. Because disjunct populations are likely to be the most genetically distinct, these should receive highest conservation priority.

There may be candidates for our resources among politically peripheral species as well. That is less likely, because more of these species are likely to be ecologically marginal. Factors influencing conservation priority among politically peripheral species include whether the range is expanding or contracting, and whether or not there is evidence of collapse towards the periphery of the range.

There are obvious caveats to a simplistic dichotomy between disjunct and politically peripheral that favors the former. One is that it is not always clear which populations are well established and which are ecologically marginal. An easy way to assess whether a bird species in B.C. is represented by an ecologically marginal population is to calculate the proportion of years that the species has been present in the province over the past 30 years or so. If it wanders erratically in and out, it likely is ecologically marginal in the province. On this basis the spotted owl (*Strix occidentalis*) is a potentially more useful investment than the sage thrasher or white-headed woodpecker. A second caveat is that some politically peripheral populations are newly arrived and expanding rapidly. With growing evidence of climate change it is easy to assume that the numbers of such populations could expand. There is little scientific evidence to address the issue, though Davis and Shaw (2001) suggested that confronted with rapidly changing environments, leading edge peripheral populations (the advancing front of a species' distribution) are likely to fare much better than lagging edge populations, and to be key to founding new populations as ranges shift. If that condition is general, then taxa expanding from the south into British Columbia may merit more attention than incursions from the north or east. Although scientific evidence is scant, empirical evidence is available. As long as such populations continue to expand, we need not invest resources other than monitoring. These populations are in the process of revealing whether or not they are ecologically marginal.

There are two more caveats that are less easily defined. First, there are politically peripheral populations whose much larger range outside of British Columbia is under threat. Species of sagebrush habitats are a classic example (Knick et al. 2003), and in B.C., include the sage thrasher and Brewer's sparrow (*Spizella breweri)*. Generally, these peripheral species will not

profit from the study a recovery plan often invokes because their movements in and out of the province frequently are too erratic. Nonetheless, where habitat degradation is widespread, resources for habitat acquisition, even at the periphery of populations, may be a helpful investment (e.g., Taylor et al. 2003). That could be particularly true where constellations of species are in widespread jeopardy. Unfortunately, habitat acquisition is expensive and caution is especially warranted given theory regarding the marginality of peripheral populations within a continuous range. Garcia-Ramos and Kirkpatrick (1997) suggest that species' ranges are prevented from expanding by asymmetric gene flow from core to peripheral populations. Peripheral populations cannot adapt to new conditions outside the current range and expand the range because they are swamped by gene flow from core populations. Such a mechanism would help explain the irregular nature of incursions of many taxa into British Columbia. It is noteworthy that disjunct populations have the advantage that they do not receive high gene flow and thus can diverge and adapt (as long as effective population sizes are large enough to maintain adequate genetic variation for adaptive traits).

There also is apparent evidence for species collapse towards the periphery of their range (Lomolino and Channell 1995; Channell and Lomolino 2000a,b). That evidence must be viewed very cautiously. Generally most species are rare throughout much of their range showing isolated pockets of abundance (e.g., Rabinowitz et al. 1986; Schoener 1990; Mehlman 1994). Even cursory examination of Figures 3 through 5 of Lomolino and Channell (1995) reveals that their algorithm for determining the center of the range and their index of centrality have greater capacity to mislead than to inform. There is no way it can accommodate naturally occurring pockets of abundance, and the retreat may be to areas of initial population concentration rather than away from concentration (although still away from the geographic center of the range). For related reasons, the hypothesized form of demographic collapse of Channell and Lomolino (2000a) is unlikely to be realized in nature. Nonetheless, the patterns reported in many instances do support the role of 'contagion' or spread of extirpation. We agree with Channell and Lomolino (2000b) that "…anthropogenic extinction forces…render historical density patterns irrelevant." We simply suspect their index does not adequately represent historical distribution patterns. We know of no examples, but in some instances peripheral populations in British Columbia may represent a retreat from anthropogenic forces of extinction. We need to be mindful that their suggestion that "…remote islands and mountain ranges often provide valuable opportunities for conserving endangered species" is not generally applicable to British Columbia. Many of our peripheral populations occur exactly where anthropogenic forces are greatest—in the densely populated areas of the Puget Sound lowlands or Okanagan Valley. Note also, that given the relatively crude nature of the maps which Channell and Lomolino (2000a,b) use, those persistent populations at the periphery of ranges may well have been disjunct.

A first and necessary step in dealing with conservation of peripheral species is to marshal the kinds of data that could help guide allocation of conservation effort. We have begun that (e.g., Tables 1 and 2) cooperatively with the Wildlife Data Centre and the B.C. CDC. We gradually are

working our way through the list of taxa, recording features such as apparent time of isolation for disjunct populations. Such lists do not assign priorities, but they can help to guide them.

Conclusions

The location and topography of British Columbia encourage a large number of peripheral taxa (Table 1). A large portion of peripheral taxa are red- or blue-listed (Table 1), and a surprisingly large portion of red-listed taxa are peripheral (Table 2); however, lists of provincial status assigned these taxa by the B.C. CDC were never intended to determine conservation priorities. Nor should they be, because in many instances the populations are ecological marginal and the funds would likely be wasted and withdrawn from taxa where there is greater chance of success. In another paper in these proceedings, we have proposed criteria that could be used to set conservation priorities for species (Bunnell et al. 2005). Those criteria do not directly address the more troubling issue of peripheral taxa, which comprise the majority of red- and blue-listed taxa within the province. Consideration of the genetic basis for evolution and conservation leads us to conclude that among peripheral taxa, emphasis should be placed on disjunct populations. Conservation effort for politically peripheral species will less often be successful and should be focused on habitat acquisition.

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