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Rethinking the basic conservation unit and associated protocol for augmentation of an 'endangered' caribou population: An opinion

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Abstract: Use of the subspecies as the basic unit in the conservation of endangered caribou (*Rangifer tarandus*) would produce a "melting pot" end-product that would mask important genotypic, phenotypic, ecological, and behavioral variations found below the level of the subspecies. Therefore, we examined options for establishing the basic conservation unit for an endangered caribou population: use of subspecies based on taxonomy, subspecies based solely on mtDNA, Evolutionarily Significant Units, and the geographic population. We reject the first three and conclude that the only feasible basic unit for biologically and ecologically sound conservation of endangered caribou in North America is the geographic population. Conservation of endangered caribou at the level of the geographic population is necessary to identify and maintain current biodiversity. As deliberations about endangered caribou conservation often involve consideration of population augmentation, we also discuss the appropriate augmentation protocol for conserving biodiversity. Management of a critically endangered caribou population by augmentation should only be initiated after adequate study and evaluation of the genotype, phenotype, ecology, and behavior for both the endangered caribou and the potential 'donor' caribou to prevent the possible 'contamination' of the endangered caribou. Translocation of caribou into an endangered population will have failed, even if the restocking efforts succeed, if the donor animals functionally alter the population's gene pool or phenotype, or alter the ecological and behavioral adaptations of individuals in the endangered population. Most importantly, a seriously flawed restocking would risk irreversibly altering those functional characteristics of caribou in an endangered population that make them distinct and possibly unique. It might even result in the loss of the endangered population, thus eliminating a uniquely evolved line from among the caribou species.

Key words: augmentation, behavior, ecology, genotype, geographic population, phenotype, *Rangifer tarandus*, translocations.

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Introduction

There is considerable public relations value in the perception of doing something for conservation by capturing large animals and moving them to different locations to increase or reestablish populations. Historically, there have been many reasons for translocating animals, including aesthetic, commercial, and mitigative. For example, Griffith *et al*. (1989) report several hundred translocations per year from 1973–1986 in Australia, Canada, and the United States of America, with the number of translocations doubling over that period. For endangered caribou, population augmentation (restocking) is a commonly considered management tool (e.g., Audet & Allen, 1996; Almack, 2000; Vanderstar & Keim, 2000). However, appropriate augmentation protocols for conserving biodiversity have not been implemented to date. Most likely, this is because management agencies have been forced by sociopolitical pressure to consider first retaining or increasing the number of caribou when a caribou population is at proximate risk of extirpation.

In this paper, we address the use of translocations for the purpose of augmenting geographic populations of critically endangered caribou for the sole purpose of conserving that population. Such augmentations would emphasize the long-term maintenance of the population's biodiversity, while allowing naturally occurring gene flow over time–and not just conserving the species' range of occupancy. To do this, we must first establish a basic conservation unit that will allow the identification and separation of biological and ecological groupings that represent variation in genetics, phenotypes, ecology and behavior, which we believe forges the functional characteristics that we wish to conserve.

The attributes of an ecosystem depend predominantly on its biodiversity in terms of the functional characteristics of organisms present in the ecosystem and the spatial and temporal distribution and abundance of those organisms (Hooper *et al*., 2005). We believe that the primary goal of all conservation efforts should be the maintenance of biodiversity. This can be addressed at the start by detailed examination of the available evidence, including pertinent publications and agency reports plus ongoing work. This will aid initially in determining what feasible level of animal grouping and the associated land unit best identifies the lowest, most refined, division of separation for maintenance of biodiversity within the species under consideration. In this paper, we first consider four possibilities for a basic unit of conservation for endangered caribou; we then present our views on selecting the basic unit of conservation that recognizes the most appropriate (i.e., refined) division for applying conservation measures to caribou; and then we develop our associated reasoning and the procedure that we believe is necessary for a biologically and ecologically sound augmentation protocol for endangered populations of North American caribou.

Definitions of terms

The biological literature is full of examples of imprecise terminology leading to misunderstanding and division among different natural science disciplines. As an example, Wells & Richmond (1995) offer a non-exhaustive list of 13 definitions of 'population' and present 20 terms for different kinds of populations. Failure to unambiguously define important terms has hampered both clear communication and comparative evaluation of studies. Important terms should be defined explicitly and then used discerningly in a way that makes us fully aware of their implications (Wells & Richmond, 1995). We recommend that any biologist interested in the conservation of endangered caribou populations and the use of *ex situ* conservation actions become familiar with the definitions of pertinent terms and their functional meanings (see Wells & Richmond, 1995; Stockwell *et al*., 2003; DeYoung & Honeycutt, 2005; Hooper *et al*., 2005 and the references therein). We describe below our understanding and use of the key terms that we apply specifically for caribou in this paper.

Basic conservation unit (BCU)

The BCU for caribou is the smallest feasible grouping that can be used consistently for all North American caribou as an identifying unit to recognize and maintain the differences in their existing biodiversity. Working at any less refined level above the BCU would mask much of the variation in existing functional biodiversity and would prevent obtaining the primary conservation goal–maintenance of the current level of existing biodiversity.

Geographic population

Wells & Richmond (1995:461) define a 'population' as "–a group of conspecific individuals that is demographically, genetically, or spatially disjunct from other groups of individuals," and they suggest that spatial disjunction is probably the most important because it is easiest to detect. Lane (1976:618) and Wilson (1980:8) define a 'population' in terms of the delimited land area (geographic region) occupied by a group of conspecific organisms. We place special emphasis on 'spatial separation' for a geographic population, whether physical (e.g., islands) or through the lack of intermixing as the result of learned behavior where no physical barriers exist (traditional seasonal and annual range occupancy). It is the known annual home range boundaries of a caribou population that define the fixed land unit of the geographic population. Thus, a geographic caribou population is all of the caribou found anywhere within the boundaries of a clearly defined fixed land unit during the 'caribou-year' (July to June).

Augmentation (also known as restocking, reinforcement, and supplementation)

Augmentation, as we use it, involves the addition of individual caribou from a viable free-ranging population to an existing remnant population of endangered caribou, with the intention of increasing the number of individuals in the endangered population in their original habitat, without meaningfully altering the functional characteristics of future individuals in the endangered population.

Four possibilities for the BCU for conservation of endangered caribou

We examine four possibilities for establishing a BCU for an endangered caribou population: subspecies based on taxonomy, subspecies based solely on mitochondrial DNA (mtDNA), the use of Evolutionarily Significant Units, and the geographic population.

Subspecies based on taxonomy

Banfield (1961:6) noted that 55 species and subspecies of caribou and reindeer have been described since Linnaeus' 10th edition of *Systema Natura* (Linnaeus, 1758). However, in his revision of the genus *Rangifer*, Banfield (1961) recognized only four extant forms of North American caribou and three extant forms of Eurasian reindeer. The four North American forms are the Canadian barren-ground caribou (*R. t. groenlandicus* Linnaeus, 1767), the Alaskan barren-ground caribou (*R. t. granti* Allen, 1902a), the Peary caribou (*R. t. pearyi* Allen, 1902b), and the woodland caribou (*R. t. caribou* Gmelin, 1788). The taxonomic nomenclature of North American caribou has indeed been fluid: scientific names of the currently recognized four extant forms were assigned 92 times between 1767 and 1961, resulting in 52 variations of those names (Table 1). If classification changes were debated on a taxonomic basis in the early 1900s, the debate would have had to start at the species level. Now, with only the single Holarctic species *tarandus* recognized in the genus *Rangifer*, the debate falls first to the subspecies level.

The transitional nature of the taxonomy for *Rangifer* was discerned early on: Banfield (1961:103) remarked that the single Holarctic species of *tarandus* and its several subspecific forms did not readily fit into the classical species or subspecies categories but that a precise fit should not be expected as evolution is a dynamic process. Banfield (1961:106) concluded in his revision of the genus *Rangifer* that "Many of the demes mentioned in the report will reach subspecific rank." Should his predictions materialize, a major regrouping of any BCU based on the current four subspecies would be required as it would confound or undo any earlier conservation efforts based upon the original four. Identification of new subspecies, as was predicted by Banfield (1961:106) for tundra reindeer (*R. t. groenlandicus* and *R. t. pearyi*) and woodland caribou (*R. t. caribou*) would make it obvious that the variation in their genetics, morphology, and ecology was ignored in the past when the new subspecies were ranked below the subspecific level.

It is possible that groups of caribou that have both unique geographic ranges and recognizable appearance can be treated as different from each other (O'Brian & Mayr, 1991). However, the assumption that *only* recognizable appearance will allow meaningful separation among groups of caribou does not hold. The phenotypic expression of an animal that is supposedly inherited is not always clear-cut. Two or more groups of animals can share the same or similar phenotypic expression without having common ancestry (convergent evolution) while other animal groups can exhibit differences in appearance but have a common ancestry (divergent evolution). Apparently, this disconnect holds true for caribou, as mtDNA demes described by Dueck (1998), which are presumed to reflect ancestry, only partially support the demes described by Banfield (1961), upon which our current subspecies designations are based. Thus, although we seek to conserve natural patterns of diversity, when it is argued that distinctive appearance or behavior is a manifestation of diversity, we have to be careful that we do not assume that similarities or dissimilarities indicate something they do not.

For example, even though one woodland caribou assigns to the Southern mtDNA clade and a second from the same population assigns to the Northern mtDNA clade (Dueck 1998), their phenotypic appearance cannot be told apart. On the other hand, caribou from the Canadian Arctic Islands classified as *R. t. pearyi*, and *pearyi* x *groenlandicus*, Dolphin and Union caribou on southern and eastern Victoria Island, Canada, classified as *R. t. groenlandicus* (*groenlandicus* x *pearyi* below the subspecies), and Canadian mainland barren-ground caribou (*R. t. groenlandicus*) can be easily separated from each other on the basis of their respective appearance even though they all form part of the same mtDNA group (Dueck, 1998; Eger *et al*., in press). Phenotypic and genetic traits do not evolve at equivalent rates, which therefore challenge the sole use of recognizable differences in appearance to indicate meaningful separations. The above examples emphasize the importance of differences among environmental settings in forging phenotypic diversity.

DNA evidence exists that allows separation of North American caribou well below the subspecific level (Zittlau, 2004). Thus, the subspecies level masks much, if not most, of the functional biological and

Table 1. Number of classification assignments and name changes in the taxonomic nomenclature for North American caribou between 1767 and 1961: derived from Banfield (1961).

North American Caribou	Time span (yr)	Number of changes			Classification assignments
		Genera	Species	Subspecies	(name changes)
R. t. groenlandicus	1767–1961	3	4	3	23 (9)
R. t. granti	1902–1961	2	5	2	9 (6)
R. t. pearyi	1902–1961	1	3	1	7 (3)
R. t. caribou	1788–1961	3	11	13	53 (34)

ecological differences that indicate biodiversity within, between, or among different populations. When both Manning (1960) and Banfield (1961) did the taxonomic classification of caribou at the subspecific level on the Canadian Arctic Islands, they recognized the considerable variation that existed below the subspecies level between and among caribou on the Canadian High Arctic Islands (north of 74ºN), collectively known as the Queen Elizabeth Islands, and those caribou on the Canadian Arctic Islands to the south of 74ºN latitude.

The melting-pot composition of *R. t. pearyi* is exemplified by the 'umbrella use' of the subspecies. *R. t. pearyi*, as described by Manning (1960) and Banfield (1961), was based on relatively few samples, without a complete examination of the entire range across which those caribou were believed to occur, thus resulting in a diversity of caribou lumped into the same taxonomic group. In his revision of the genus *Rangifer*, Banfield (1961) based his assessment of *R. t. pearyi* on 113 specimens (107 from Canada and 6 from northwest Greenland). Only 73 of the 107 Canadian specimens were identified as "Typical *pearyi*." Those 73 were all from the Queen Elizabeth Islands, with the exception of 7 specimens from Prince of Wales Island. Those last seven caribou were all large adult males collected and used by Manning & Macpherson (1961) to describe the 'ultra *pearyi*' of Prince of Wales Island. Banfield (1961) then used the same seven caribou, drew the same conclusions as Manning & Macpherson (1961), and called them a 'super deme of *pearyi*.' Neither Manning & Macpherson (1961) nor Banfield (1961) examined any of the smaller caribou on Prince of Wales Island (or any caribou from Somerset Island or Boothia Peninsula) and they assumed that the smaller caribou type on Prince of Wales Island was the same type as those on Banks Island (i.e., "Intergrades *pearyi* x *groenlandicus*"). Thirty-three of the 34 remaining specimens representing caribou from the Canadian Arctic Islands south of 74ºN latitude were actually all from Banks Island and the remaining one was a migrant collected on Cape Dalhousie, Mackenzie District, on the Canadian mainland. All 34 were identified as "Intergrades *pearyi* x *groenlandicus*." To lump all of these sampled caribou at the subspecies level for the purpose of their conservation prevents an adequate evaluation of the biodiversity found among these caribou below the subspecific level.

mtDNA genetics

Dueck (1998) showed that there were two mtDNA clades of North American *R. tarandus.* These groups represent northern and southern refugial origins during the Wisconsin Glaciation. It has generally been thought that phenotypic, ecological, and behavioral differences that form the basis of current subspecies designations were derived from isolated northern (barren-ground) and southern (woodland) refugia (Banfield, 1961:41). Therefore, the subspecies designations should coincide with mtDNA differences. However, the mtDNA clades do not always separate according to present-day designations of subspecies. Phenotypic differences evolve at a faster rate than mtDNA if selection pressure is strong, and thus degrees of similarity based on each measure are not equivalent. MtDNA is most useful for examining genetic differences at or above the subspecies level and would not detect a relatively recent difference below subspecies that had been established within the past few thousand years. We should reconcile this lack of agreement between the four extant North American caribou subspecies determined taxonomically and the two "subspecies" demonstrated by mtDNA before we get into *ex situ* conservation efforts that involve the mixing of caribou from two or more populations.

Although usually only one genetic line exists within a geographic population, the genetic situation can be complex in many instances. In Arctic Canada, for example, the Prince of Wales-Somerset-Russell islands-Boothia Peninsula geographic caribou population is (or was: see Gunn *et al.*, 2006; Miller *et al.*, 2007) represented by four ecotypes: the arctic-island ecotype, the 'ultra *pearyi*' ecotype, the Boothia Peninsula ecotype, and the mainland ecotype (Banfield, 1961; Manning & Macpherson, 1961; Miller *et al.*, 2005; 2007). The most complicated geographic populations solely in terms of their genetics exist among populations identified as woodland caribou. Within such populations, some individuals assign to the Southern mtDNA clade, and represent caribou with a southern refugial origin, while other individuals assign to the Northern mtDNA clade, representing caribou with a northern refugial origin, indicating that caribou from different genetic ancestry can occur in a single geographic population (Dueck, 1998).

Many of the caribou sampled by Dueck (1998) and currently identified as woodland caribou from Yukon to Labrador were found to belong to the Northern mtDNA clade. That is, if there were a genetic basis for the woodland caribou subspecies, they all would have been assigned to only the Southern mtDNA clade and vice versa for barren-ground caribou. However, proportionately many individuals were assigned to the Northern mtDNA clade in 12 of 15 woodland caribou populations sampled while 3 of 7 barren-ground caribou populations contained individuals that were assignable to the Southern mtDNA clade. All four of the woodland caribou populations sampled in Yukon were assigned 100% to the Northern mtDNA clade and only the critically endangered Pukaskwa National Park woodland caribou population north of Lake

Superior in Ontario and the Humber and Middle Ridge woodland caribou populations in Newfoundland were assigned 100% to the Southern mtDNA clade. Although it is possible that larger samples from those populations could change the proportional representation of the two mtDNA clades, it does not lessen the importance of the fact that those populations contained individuals belonging to both mtDNA clades.

Therefore, if conservation measures are based solely on mtDNA genetics, the Canadian and Alaskan forms of barren-ground caribou, all caribou on the Canadian Arctic Archipelago, and many of the caribou in populations currently recognized as woodland caribou, would not be considered as separate. Obviously, this would be illogical–but it could happen under strong socio-political support for using transplants from essentially any source to reestablish harvestable populations, despite the lack of biological or ecological support for such actions.

Most importantly, the mtDNA differences reported here reflect subspecies-level genetic differences and may not represent any recent (~ <10 kybp) phenotypic, ecological, or behavioral adaptations that form the basis for the functionally meaningful differences among caribou populations. Thus, when we wish to conserve the existing biodiversity of caribou and to protect the natural pathways for continued gene flow between and among populations, we must work below the subspecific level based on mtDNA (or on taxonomy).

Evolutionarily significant units

The concept of the 'Evolutionarily Significant Unit' (ESU) was first developed by Ryder (1986). Crandall *et al.* (2000) noted that as a new concept, the definition of an ESU has received considerable alteration, emphasizing reproductive isolation rather than the maintenance of adaptive differences. Ryder (1986) first suggested that any population that actually exhibited significant adaptive variation as demonstrated by sets of data obtained by different techniques qualified as an ESU. Waples (1991) added a further restriction and focused on populations that are reproductively separate from other populations as well as having unique or different adaptations as the standard for an ESU. Then Moritz (1994) made the definition even more restrictive by suggesting the populations had to be 'reciprocally monophyletic' for mtDNA and show significant divergence of allele frequencies at microsatellite loci. The reciprocal monophyly standard presents an obstacle for evaluating populations with paraphyletic histories (Crandall *et al.*, 2000).

When Moritz's (1994) definition is accepted for establishing ESUs, it seems to negate or at the very least seriously confound the possible application of the ESU to the North American caribou that have been reported to have a polyphyletic origin. Gravlund *et al.* (1998) concluded from mtDNA sequence analysis that the three forms of small-bodied high-arctic *tarandus* (Peary caribou, *R. t. pearyi;* the now extinct East Greenland caribou, *R. t. eogroenlandicus*; and the Svalbard reindeer, *R. t. platyrhynchus*) had a polyphyletic origin. Those authors suggested that the three forms were ecotypes of relatively recent diphyletic origin (*pearyi* and *eogroenlandicus*, versus *platyrhynchus*) that likely evolved convergently as a result of exposure to similar climatic conditions and levels of nutrition.

Also, based on mtDNA analyses, none of the North American caribou subspecies have a monophyletic origin (Dueck, 1998; Eger *et al.*, in press). Eger *et al.* (in press) show that Peary caribou from Bathurst Island within the Queen Elizabeth Islands are genetically different from caribou populations on Eglinton Island to the west, on the more southerly Arctic Islands of Prince of Wales, Victoria, and Banks islands, and also at Coppermine (Kugluktuk) and Spence Bay (Taloyoak) on the mainland. In fact, they indicate that monophyly does not hold true even for individuals from a single Arctic Island. The range in environmental conditions across the Canadian Arctic Islands varies from "extreme" north of 74°N to more "benign" south of 74°N latitude, with much diversity between. Presumably, this environmental range has led to ecological and morphological divergence that is not reflected by mtDNA diversity. These findings suggest that the role of environmental variables is great in forging successful individuals and bring concerns for variations in phenotype, ecology, and behavior to the forefront, especially when both mtDNA clades described by Dueck (1998) are present in the same populations. That is, the genome would set the limits for adaptability but the environment would mold the successful adaptations and the variations in those adaptations among different populations in different environmental settings.

Crandall *et al.* (2000) point out that the conceptual framework of the ESU demands a decision–ESU or not–that is based on a continuum of genetic diversity, variation in habitat types, and differences in selective pressures across populations. Thus, the application of ESUs to polyphyletic populations would be highly questionable, especially if there were more than two possible origins. Vogler & DeSalle (1994) concluded that no generally accepted definition existed for an ESU that would serve as a basis for its use in practical conservation situations.

Geographic population

Fixed land boundaries for a geographic caribou population should first be determined by the known history of the population's annual range occupation (including seasonal migrations) compiled over a series of years and with further study where necessary. All caribou found within an annual home range boundary should be considered as a single geographic population. This condition holds even if some caribou subunits within the geographic population exhibit different demographic performances, with more than one calving ground and rutting area possibly occurring in the same year. It should be expected that as evidence is accumulated over time, the need for changing at least some boundaries of some geographic populations will become evident.

Although fidelity to calving grounds is a criterion for defining many populations (Thomas, 1969; Gunn & Miller, 1986; Nagy *et al.*, 1999), there are many exceptions, especially among caribou on the Canadian Arctic Archipelago and also among woodland caribou populations. Thus, while relying on calving grounds serves well as the focus for identifying some geographic populations (mostly for mainland Canadian and Alaskan barren-ground caribou) it is not always useful for determining other geographic populations.

The most conservative and easiest approach to the conservation of endangered North American caribou is to initially treat all populations as unique from each other and worthy of being conserved as discrete entities regardless of their relative complexities or lack of complexity and known fidelities to different calving areas, until proven otherwise. We would do this by first identifying the annual land boundaries of each population and then treat all caribou that occur within each of those fixed areas as a single geographic population. These geographic populations are the potential BCUs. Then, we can begin a 'lumping and splitting process' only after a satisfactory amount of supporting data allows us to objectively conclude that it is or is not justifiable to combine or further divide those geographical populations.

Selecting the best BCU for endangered caribou

The most satisfactory BCU for caribou should be a naturally occurring one, such as a free-ranging population. Miller & Gunn (2003) concluded in their discussion about caribou on the Canadian Arctic Archipelago that the most basic and consistently workable caribou conservation unit is the geographic population. We agree and apply the geographic population as the best choice for endangered caribou throughout North America. We believe that while a BCU should rely on genetics and morphology, it also should rely heavily on ecology, which includes behavioral adaptations. As has already been shown (Zittlau, 2004), it is most likely that further study will reveal a high degree of complexity among caribou populations below the subspecies that now is obscured by the subspecies classification. Therefore, recognition of the geographic caribou population as the BCU would provide a much more meaningful biological and ecological approach to the management and conservation of endangered caribou than could be realized by any approach based on the subspecies or the ESU.

Many geographic populations have been functioning as distinct units for numerous generations according to comparisons of microsatellite DNA (Zittlau, 2004). This forms the basis for adaptations within the populations, leading to meaningfully functional differences. By recognizing geographic populations as functionally distinct in their respective contribution to the evolutionary lines of caribou within a region, the need for affording protection to the natural pathways for the flow of genes between populations should also be appreciated. This protection strategy should promote and preserve adaptive diversity among caribou. However, access to movement corridors can have a down side, including the possible spread of disease, and much more investigation and evaluation of associated pros and cons is needed (Simberloff *et al.*, 1992; Hogg *et al.*, 2006).

Working at the subspecific level would produce a "melting pot" end-product that would mask important variations in genotype, phenotype, and in ecological and behavioral differences found well below the level of the subspecies. This could lead to the unwitting loss of functional biological and ecological differences that indicate ongoing contributions of biodiversity between or among different populations. Thus, relying solely on the subspecific level of taxonomic classification is unsuitable for the conservation of endangered caribou populations. In addition, the use of an ESU for a polyphyletic species like caribou is questionable and should not be used as a BCU because of the extremely low likelihood of collecting adequate data within a reasonable time for all of the caribou populations that we can already recognize by other standards. We believe this limitation in the use of subspecies and ESUs applies equally to all caribou throughout North America.

The three possibilities rejected above are all markedly less discriminating and well above the level of the geographic population. If any one of these three that we reject was accepted, it would allow the corruption of thousands of years of evolution through human-induced manipulations of caribou populations. Such a superficial standard would permit the capture and release of caribou from any location within the subspecies' range into other populations, with total disregard for the variation in genetics, morphology, ecology, and behavior that exists among those populations. Such actions would obviously defeat any attempt to maintain current biodiversity through the distinctive and unique evolutionary lines of these endangered populations of caribou.

We recommend that the geographic population be used as the standard for the BCU in the conservation of endangered North American caribou. The only possible shortcoming that we currently can discern for the use of the geographic population as the BCU for endangered caribou is in not adequately collecting the necessary information for each geographic population to accurately describe its geographical land base. However, we view this as much less of a problem to deal with than the shortcomings that we have described above for working at the level of the subspecies or the use of the ESU.

Augmentation of endangered caribou populations

We have considered the four possibilities for a basic unit of conservation for endangered caribou and have reviewed our reasoning for the selection of the BCU that recognizes the most appropriate (i.e., refined) division for applying conservation measures to caribou. We now develop our associated reasoning and procedure that we believe is necessary for a biologically and ecologically sound augmentation protocol for endangered populations of North American caribou.

What needs to be considered

Our position is that we do not currently have enough detailed information on genetics, phenotypes, ecology, or behavior of critically endangered caribou populations or on candidate donor caribou populations to proceed with translocations at a satisfactory level of biological confidence. Our primary aspiration is that no human-induced actions are taken that risk causing detrimental outcomes, especially irreversible ones, for the endangered caribou. Among all the probable management and conservation prescriptions, translocation of caribou has the greatest potential for causing negative results, and the greatest potential for contamination of a critically endangered caribou population would come from augmentation with incompatible donor caribou from a viable population.

The dichotomy between management-orientated wildlife biologists and conservation biologists is real: it starts with each having differing basic philosophies, leading to the divergence of their respective objectives and goals. Therefore, it is extremely important when evaluating the use of translocations to keep in mind the difference between introductions, reintroductions, and restocking solely for management purposes versus augmenting critically endangered caribou populations solely for conservation efforts. The primary aim for management purposes is to retain or expand a species' range of occupancy and population size, and to avert further population declines by preventing populations from occurring in isolated habitat patches (Storfer, 1999). These management-orientated translocations are not based on the preservation of biodiversity created by distinct evolutionary lines. Rather, they are often driven by hunter incentives for game animals (Bergerud & Mercer, 1989) or by eco-tourists for non-consumptive viewing opportunities (e.g., aesthetics and photography). They also often occur as last-ditch efforts without concern about genetic dissimilarity.

We are proposing guidelines that are concerned with the conservation of biodiversity through augmentation for the sole purpose of sustaining a genetic line of endangered caribou that are more naturally adapted to their surroundings than are caribou from elsewhere. Even if human-induced manipulation that alters functional characteristics of an endangered caribou population results in more animals or an "improved animal," it would defeat the stated purpose of the conservation of a distinct group of endangered caribou and cause the loss of any unique contribution that the group previously made to the biodiversity of North American caribou.

The augmentation of the Selkirk Mountains woodland caribou population in northern Idaho between 1987 and 1992 with 60 caribou from British Columbia serves as an example of the need to reconcile differences in what is judged an acceptable protocol for conservation efforts with the stated purpose of preserving an endangered caribou population. This is also a good example of what we consider a geographic population. The Selkirk caribou population was listed as endangered in 1984 under the U.S. Endangered Species Act. Although the stated purpose of the translocations was "to assist in the recovery of the endangered Selkirk population" (Compton *et al.*, 1995:490); the augmentations were carried out without knowledge of the possible differences between the genetics of the endangered caribou and the donor caribou. There was no mention of concern about possible phenotypic differences or the known differences among ecotypes and their respective ecology and behavior. Some of the donor caribou came from the 'Interior Plateau region' of west-central British Columbia and represented 'northern ecotype' caribou that rely primarily on terrestrial lichens in winter, while the other donor animals came from the 'Interior Wet Belt region' of southeastern British Columbia and represented 'mountain ecotype' caribou that rely primarily on arboreal lichens in winter, as do the Selkirk caribou. It was known that the "Mountain ecotype caribou exhibit different habitat use patterns, seasonal migrations, and winter diet selections than northern ecotype animals…" (*in* Compton *et al*., 1995:494). As they knew they were mixing caribou ecotypes, and as they did not know the genetics of the caribou they were working with, it is likely that there was little concern for retaining the functional characteristics of the caribou in the endangered Selkirk population to truly aid in the recovery and maintenance of the Selkirk population *per se*.

From a purely management position, these augmentations could be viewed as justifiable efforts. The augmentation program would have been judged successful if the translocated animals survived and established a stable population within the Selkirk range–this did not happen. However, from a conservation position where maintenance of the functional characteristics of the caribou already in the Selkirk population is the primary goal, the augmentation efforts cannot be considered valid, regardless of the outcome. Later augmentation efforts were made between 1996 and 1998, translocating northern and southern ecotype caribou from four regions in British Columbia into the Selkirk Mountains of Washington (Audet & Allen, 1996). These later augmentations attempted to use donor animals that were likely to be as genetically similar as possible to the original Selkirk population, where the degree of genetic similarity was assumed–but neither measured nor proven at that time–to correspond with geographic proximity of the potential donor populations, which is not supported by subsequent limited microsatellite DNA analysis (Zittlau, unpublished data).

The consideration of genetic similarity may be most difficult for management biologists to accept or appreciate as a primary concern. That is, the potential benefits of improvements in reproduction, survival, and fitness-related traits in maximally outbred individuals in small isolated populations could make it appealing to overlook the potential negative aspects of introductions (Hedrick, 2005)–if one ignores the need to keep human intervention from unnaturally altering contributions from different evolved lines of caribou. The conundrum created by these alternative outcomes serves to emphasize the need for establishing and clearly stating the primary long-term goal of any human-induced manipulation.

Unless management-orientated efforts are not allowed to interfere in any way with the biologically and ecologically sound conservation of an endangered caribou population, 'optimal strategies' will not be kept within the bounds of 'natural change'. We must determine what degree of genetic deviation, if any, is acceptable between an endangered caribou population and the donor caribou population, or what is the latitude for causing genetic change before we are "playing God." We must also pay more attention to the importance of the environment in shaping variation in phenotypic, ecological, and behavioral adaptations of caribou. These questions cannot be answered with complete confidence until considerably more studies are made.

We must keep in mind that the current lack of detailed information about the various endangered caribou populations makes augmentation of endangered caribou populations extremely risky. Working with critically endangered caribou populations does not allow us the luxury of initial 'trial-and-error' efforts. Until we increase the necessary data for the populations under consideration, our efforts should be directed first at obtaining adequate information that will allow us to make objective decisions about moving caribou from one population to another without disrupting or corrupting the endangered population or the natural system within which that population lives. We must remember that what works in one case will not necessarily work in another. We should consider first exhausting *in situ* conservation efforts (e.g., habitat protection, harvest restriction, and predator maintenance) before turning to *ex situ* actions (e.g., augmentation, reintroduction; and or captive breeding, rearing, and release into the wild).

The exception

We believe the one exception to our considerations above is the preventive measure of capturing caribou from an endangered caribou population while the population still has enough animals to spare them (Caughley & Gunn, 1996), and then raising them in captivity for potential release back into that endangered population when conditions are favorable. However, using captive-raised animals after long periods in captivity has its own set of problems that need to be clarified and resolved.

The apparently large number of captive caribou needed to promote a successful release back into the wild seriously limits the use of captive rearing. When deciding to augment a population, consideration must then be given to the 'effective population size' for caribou and how the effective size may vary among different caribou populations due to differences in their biotic and abiotic environments. Genetic considerations must be combined with many other factors that could or would influence the effective population size (Franklin, 1980; Lande, 1988; Caughley & Gunn, 1996; Franklin & Frankham, 1998a, b; Lynch & Lande, 1998), and thus the conservation of endangered North American caribou. Proposed effective population sizes currently range from as few as 50 individuals up to 5000 (Franklin & Frankham, 1998a).

Extremely endangered caribou populations that have been augmented or that are being considered for augmentation are each already below 100 individuals (Compton *et al.*, 1995; Audet & Allen, 1996; Almack, 2000; Vanderstar & Keim, 2000).

However, captive-rearing could be of value in special cases where *in situ* efforts have failed. Even if the animals raised in captivity are not released back into the wild, there is considerable public relations value in displaying endangered animals in a pleasant setting where they can be viewed by the public with educational materials provided; thereby, keeping the endangered animals' plight before the public. Free-release introduction of endangered caribou to areas beyond their known past range should not be considered as a valid *ex situ* conservation effort.

What needs to be done

Prescriptions for conservation should focus on the long-term goal of conserving caribou populations by maintaining biodiversity that results from naturally occurring evolutionary lines. We recommend a precautionary approach for the conservation of caribou, where investigators should step back and carefully assess their knowledge to avoid implementing actions that may lead to irreversible results. Our intent is to take only those actions that will allow evolutionary development to continue along natural pathways and to prevent any corruption of endangered caribou populations by human manipulations (Fig. 1).

Although the logic of first controlling or reversing the original cause(s) of a population decline before initiating an augmentation effort is abundantly clear, in reality it is seldom possible for caribou populations. In many cases, the cause of a decline is not even known. Even if the cause is known, it may be beyond our ability to reverse or even mitigate. Often our inability to do so is governed by socio-political pressures: e.g., hunters disbelieving population survey results, public objection to the control of predators, on-going pressure from nonrenewable and renewable resource development companies on caribou range, et cetera. In reality, the complexity and uncertainty of an unfavorable socio-political atmosphere can make all aspects of what would normally be a relatively simple planning and implementation recovery effort from a technical standpoint into a task burdened with unnecessary challenges and delays or even abandonment.

We must first determine what we can justifiably do and what we must avoid before human-induced manipulations become commonplace and especially before augmentation becomes the prominent part of any conservation effort. Otherwise, we run the risk of committing detrimental and possibly even irreversible acts. Many actions that might now be seen as beneficial and not intrusive based on our current limited knowledge may subsequently prove not only to have been unbeneficial but also seriously intrusive in the natural process of change. In addition, an all-important initial procedure for all translocations is to make every effort to determine that the donor animals are disease-free before being used.

There are many problem areas in conservation biology that need more work before augmentation becomes commonplace (Frankham, 1995:306; 1999:238; Stockwell *et al.*, 2003). We need to learn much more about individual variation within a population and between or among populations (Hayes &

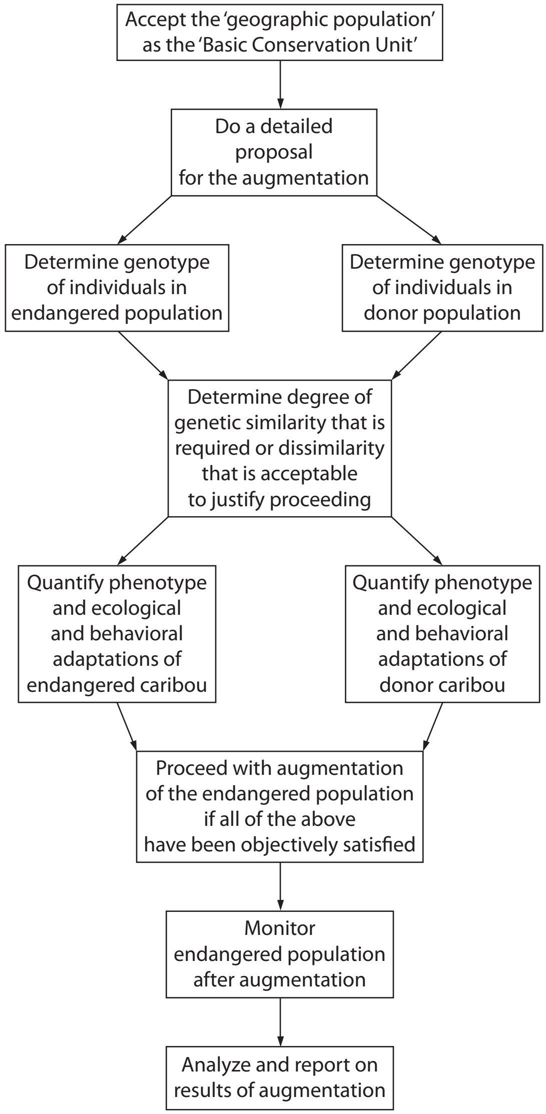

Fig. 1. Protocol for augmentation of an endangered caribou population with caribou from a viable wild population.

Jenkins, 1997; Holmes, 1997; Lacy, 1997). We need to learn much more about 'contemporary evolution' where evolutionary changes take place within a few hundred years and often even within decades (Stockwell *et al*., 2003). To the best of our knowledge, no one has considered the effects of translocation on the historical phylogeographic structure of caribou (Stephen *et al*., 2005).

We must develop consensus as to what actions must be taken before, during, and after the transplanting of caribou into an endangered population. Specific augmentation guidelines will have to be developed on a case-by-case basis. Then, specific detailed augmentation plans will have to be developed, each starting with an unambiguous statement of purpose. The proposal should consider the potentially negative as well as the potentially positive outcomes, as well as an adequate accounting of the original cause(s) of the decline or at least an objective acknowledgement that the root cause(s) of the decline is not known.

Augmentation of an endangered caribou population demands strict adherence to the accepted protocol and uncompromising attention to the predetermination of all four areas of concern: genetics, phenotypic expression, ecological (physiological and morphological) adaptations, and behavioral repertoires. We must give detailed consideration to the above in terms of their respective inheritable linkages that were forged by the respective group's environmental setting–both biotic and abiotic (Vogler & DeSalle, 1994; Craven *et al*., 1998; Miller *et al*., 1999; Fischer & Lindenmayer, 2000). We believe this approach will deal with the important biological and ecological distinctions between or among caribou populations. Each case must include a complete work-up for both the endangered caribou and the potential donor candidates (Fig. 1) to prevent 'contamination' of endangered caribou by incompatible donor animals, to avoid the risk of potentially irreversibly altering functional characteristics of resident endangered caribou, and to avoid corrupting and thereby removing a distinctly evolved line from among the region's caribou–forever.

Conclusions

The geographic population is the most refined and consistently workable BCU for the conservation of endangered populations of North American caribou, as it is spatially disjunct and thus relatively easily recognized. Therefore, it is not reasonable to lump caribou in a large and biologically or ecologically meaningless BCU at the level of the subspecies, as such an action would ignore the considerable biodiversity that exists among groupings of caribou in geographic populations well below the subspecfic level.

The conservation of endangered caribou requires attention to the biology and ecology of the caribou under consideration at the smallest possible scale. It is reasonable to assume from marked biotic and abiotic differences in their respective environments that physical adaptations and behavioral repertoires acquired by caribou are important to their long-term survival and that these differences further separate the geographic populations into their particular niches on a meaningful ecological basis. Therefore, conservation efforts should identify the fundamental interdependency of genetic and non-genetic processes affecting viability among geographic populations.

It is our position that before any augmentation of an endangered caribou population occurs, there is a great need to review our knowledge base to prevent actions that could result in negative outcomes and, most importantly, could create irreversible results. It should be a prerequisite in any conservation program that there be prior determination that both the endangered and donor caribou are indeed genetically, phenotypically, and ecologically the same. In the absence of a match, even out of desperation or even if highly similar caribou exist, no augmentation should proceed until we know with a high level of biological confidence that the functional characteristics of the caribou being augmented will not be lost. We recommend that this subject be given in-depth consideration–at the level of the geographic population.

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