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SYNTHESIS & INTEGRATION

Lines on a map: conservation units, meta-population dynamics, 1 and recovery of woodland caribou in Canada

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Abstract. Delineating conservation units is a fundamental step in recovery planning for endangered species. 3 Yet, challenges remain in the application and validation of scientifically evaluated conservation units 4 in management practice. The Canadian government makes use of Designatable Units (DUs) as the primary conservation unit under their Species-at-Risk Act. DUs must be ecologically discrete and have demonstrated evolutionary significance, which, in the case of woodland caribou (*Rangifer tarandus caribou*), has led to the definition of multiple DUs across Canada. Simultaneously, Environment and Climate Change Canada has released two recovery strategies affecting four DUs, wherein DUs are subdivided into smaller conservation units. However, the two recovery strategies adopt different definitions for the conservation unit. For the Boreal DU, the Local Population is considered the conservation unit for recovery management, whereas for Southern Mountain DU, the conservation unit for recovery is the subpopulation, which may or may not be comprised of several Local Populations. The scientific rationale for the difference between recovery strategies is unclear, not necessarily supported by genetic or demographic evidence, and highlights a policy challenge facing caribou conservation. We argue that the current emphasis on protecting subpopulations within a DU might be inconsistent and unviable for recovery planning. Instead, the recognition and emphasis on maintaining meta-population dynamics within DUs is essential and currently underutilized in the long-term recovery of woodland caribou in Canada.

Key words: conservation units; designatable units; endangered species; *Rangifer tarandus;* recovery planning; species-at-risk act; woodland caribou.

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Introduction

Delineating biologically meaningful conservation units is important when considering conservation action, a concept accepted theoretically and enforced by law (Crandall et al. 2000, United States Government 2004). The era of legislated conservation units began in 1973 with the passing of the Endangered Species Act (ESA) in the United States. The Act provided a commitment and legal obligation to protecting species from extinction, while also catalyzing an era of science and policy meant to scientifically evaluate, quantify, and validate units within species upon which endangered species legislation would act. Conservation units are groupings of organisms below the species level containing the biodiversity necessary for the generation of new species, persistence of species following environmental change, and local adaptation (Mee et al. 2015). Internationally, the value of subspecific conservation is recognized by the World Conservation Union's (IUCN) Red List of Threatened species and appendices in the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), among others.

Classifying units below species is intrinsically difficult (Wilson and Brown 1953, Waples and Gaggiotti 2006). There is no scientific consensus on defining subspecific units, and so a precautionary approach is warranted in their application. Moreover, the concept of conservation units themselves is often scale-dependent, or hierarchical, such that larger units (e.g., subspecies) may themselves be comprised of smaller units worthy of conservation (Moritz 2002). While there has been frequent debate about relevant conservation units under the ESA (Pennock and Dimmick 1997, Crandall et al. 2000), other global endangered species legislation has not received the same attention in the published literature.

In 2003, Canada passed the Species-at-Risk Act (SARA). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is the legislated body under SARA charged with assessing the conservation status of Canadian flora and fauna. Given SARA's inclusion of subspecies, varieties, or geographically or genetically distinct populations, COSEWIC recognizes Designatable Units (DUs; Table 1; COSEWIC 2015) to encompass those entities that may warrant receiving federal protection (Green 2005). Consequently,

Table 1. Units referenced in manuscript either generally or specifically those adopted and defined in various Canadian woodland caribou assessment and recovery documents under the Species-at-Risk Act (as cited).

Name	Definition	Source
Conservation unit	Used generally in text to refer to either Evolutionary Significant Units (ESUs) as historically isolated and independently evolving sets of populations; or Management Units, which represent the demographically independent populations that make up the functional components of ESUs.	Moritz (1999)
Nationally significant populations	Predecessor to COSEWIC DUs. A population considered either genetically distinct (via genetic analysis, taxonomy, or other compelling evidence) or geographically distinct (representing either a significant portion of the historic range in Canada or is the sole representative of a species within any of Canada's biogeographic zones), and has clear assignment to one particular ecotype.	COSEWIC (2002)
Ecotypes	Classes of populations adapted to different landscapes or environments as expressed primarily by their movements, feeding behavior, and climate.	COSEWIC (2002)
Designatable Unit (DU)	Designatable Units should be discrete and evolutionarily significant units (similar to ESUs above) of the taxonomic species, where "significant" means that the unit is important to the evolutionary legacy of the species as a whole and if lost would likely not be replaced through natural dispersion	COSEWIC (2011, 2015); http://www.cosewic.gc.ca/default.asp?lang=en&n=DD31EAEE-1
Local Population	A group of boreal caribou occupying any of the three types of boreal caribou ranges (conservation unit, improved conservation unit, local population unit†)	Boreal woodland caribou Recovery Strategy (2012)
Subpopulation ("herd")	A group of caribou occupying a single caribou range.	Southern mountain caribou Recovery Strategy (2014)
Local Population Unit	Larger historical subpopulation that has since declined and that has been fragmented into the currently recognized subpopulations	Southern mountain caribou Recovery Strategy (2014)

† Environment Canada (2012) identified three types of ranges based on the degree of certainty in the boundaries; conservation units had low certainty, improved conservation units had medium certainty, and local population units had high certainty in delineation.

COSEWIC assesses DUs in the case where a single status applied to the entire species does not accurately reflect the risk of extirpation of unique sub-units of that species. COSEWIC outlines criteria for evaluating first the discreteness and second the significance of a proposed DU prior to its evaluation for protection status (i.e., endangered or threatened). Then, under SARA, recovery planning occurs within each DU at both federal and provincial levels. Sometimes this involves the identification of finer-scale conservation units as the focus for recovery actions, taking into consideration various demographic and biodiversity principles. Further complexity is often added because provincial definitions for management scale conservation units often differ within and across federally defined DUs. Indeed, the sheer number of, and redundancy among, terms to describe intra-species groups, for conservation purposes or otherwise, impairs effective conservation management (Cronin 2006; Table 1).

A current and ongoing example of the challenges of identifying conservation units is in caribou (*Rangifer tarandus*). Decades of anthropogenic disturbance have led to rapid declines in many caribou populations across Canada (Festa-Bianchet et al. 2011, Hervieux et al. 2013), requiring recovery planning both at and within the level of DUs. Prior to 2011, large-scale conservation units of caribou were defined as Nationally Significant Populations, based primarily on differences in taxonomy, movement and feeding behaviors, and climate (COSEWIC 2002; Table 1). However, given SARA's adoption of DUs and with the opportunity provided by caribou research programs, especially molecular studies, a revision of caribou conservation units into DUs was adopted by COSEWIC in 2011 (COSEWIC 2011). This 2011 revision exposed the difficulty in integrating evolutionary criteria to differentiate DUs, particularly for the woodland caribou subspecies (*R. t. caribou*), which we expand on in section "Challenges in identifying DUs…" below. Furthermore, there are apparent discrepancies in how conservation units are defined within recovery strategies for the Boreal DU versus several Mountain DUs (Fig. 1). Considering that COSEWIC's conservation evaluation recommended "Endangered" status for Southern Mountain and Central Mountain DUs (Fig. 1; Ray et al. 2015, COSEWIC 2014, legal adoption by ECCC still pending), there is great need to address the challenges of defining conservation units for effective recovery policy and enactment of efficient management strategies.

In this Synthesis and Integration paper, we examined the challenges of woodland caribou conservation in Canada via a review of the mechanisms of species conservation under SARA, with an emphasis on how conservation units are delineated and managed. We perform this examination under the same hierarchical logic flow as done for any new species under review in Canada. First, we dissect the challenges in identifying DUs in woodland caribou in western Canada. We then review the subsequent process of recovery planning within DUs, notably for Boreal and Southern Mountain woodland caribou, including provisions and challenges added by SARA's technical feasibility clause and recent extirpations. We compare and contrast the hierarchy of caribou conservation units defined by these recovery plans (ranging in scale from the Local Population to the DU; Table 1) to the units supported by published scientific evaluation of the same caribou (Weckworth et al. 2012). We then propose a path toward a policy solution by using scientifically validated meta-populations as the focal unit for caribou conservation. We finish by summarizing insights from the examination and discussion to elucidate broader policy implications across scales of conservation, which are applicable for caribou and in other species and contexts.

Challenges in Identifying Designatable Units (DUs) in Woodland Caribou in Western Canada

In 2011, COSEWIC released a reassessment of caribou DUs (COSEWIC 2011) based upon a review of the literature, including, for the first time, genetic evidence (summarized in Ray et al. 2015). While the power of genetic data to aid in defining conservation units is well established, the provisions for its formal use in delineating DUs are not as straightforward as other lines of evidence (COSEWIC 2015), one of the challenges encountered in making any defined conservation unit conform to real-world conservation management (Paetkau 1999, Palsbøll et al. 2007). Given this is the first extensive use of genetic evidence in defining caribou conservation units, and its

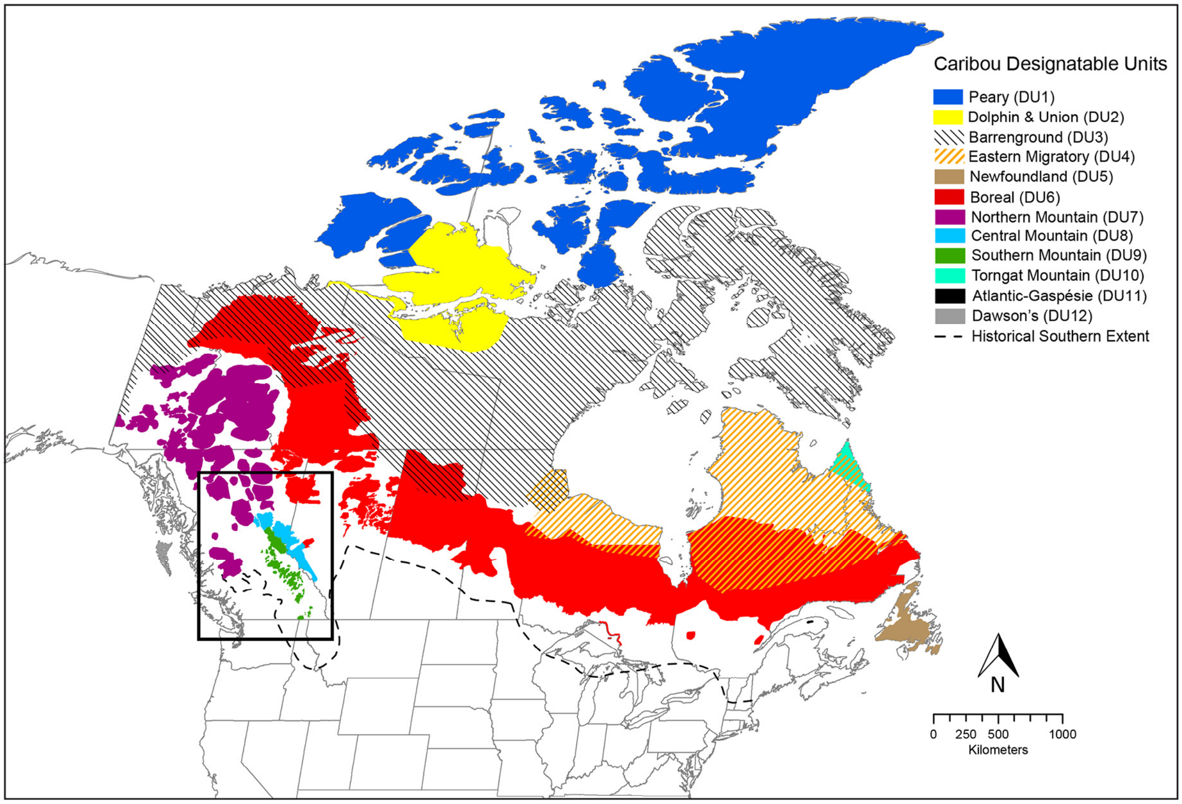

Figure 1. Designatable Units (DUs) for Caribou (*Rangifer tarandus*) in Canada as developed by the Committee on the Status of Endangered Wildlife in Canada (figure adapted from COSEWIC 2011). The area denoting the Southern Mountain Caribou Recovery Strategy (2014) is within the black rectangle.

relative weight in determining DUs compared to other lines of evidence, we focus primarily on the ambiguities and difficulties in interpreting genetic data.

The universal COSEWIC DU guidelines (revised in COSEWIC 2015, but consistent with version used for COSEWIC 2011) for the use and application of genetic data in DU designations are often unclear or contradictory, which may have implications for accurately defining caribou (or any other) DUs. For example, the DU criteria for discreteness and significance are determined based on "one or more criteria" among an evaluation of behavioral, morphological, ecological, geographic, and genetic lines of evidence (COSEWIC 2015). Yet, in the Some Practical Considerations section of the document describing how to define DUs (COSEWIC 2015), it states that "genetic distinctiveness by itself is not sufficient for DU designation," obfuscating whether or not all genetic data are insufficient as a single criterion for qualifying a proposed DU. Moreover, inconsistencies in patterns of genetic variability will arise given that each genetic marker provides a different evolutionary perspective (e.g., mtDNA, microsatellites, genomics). The DU guidelines generalize that a number of genetic data types can fulfill requirements for discreteness, but that evolutionary significance requires "qualitative genetic differences at relatively slow-evolving markers" and that "microsatellites, generally would not be sufficient to meet this criterion" (COSEWIC 2015). However, no range of mutation rates is given to provide context or guidance of what is meant by "slow-evolving markers" as compared to relatively rapid-evolving microsatellites.

The COSEWIC caribou DU report (2011) laid out the lines of evidence used specifically to test for discreteness and significance in proposed caribou DUs. In concert with the COSEWIC guidelines on defining DUs (COSEWIC 2015), the report referenced phylogeography as a primary means of determining significance. Thus, the previously described phylogeographic caribou lineages of Beringian–Eurasian and North American origin (Cronin et al. 2005, McDevitt et al. 2009), as well as the hybrid swarm of both lineages (McDevitt et al. 2009), were three possible lines of evidence used to validate the significance of a DU. Any detectable phylogenetic patterns outside of these three would require additional evidence for DU distinction. However, conflict between COSEWIC 2011 and the COSEWIC DU guidelines emerges when evaluating genetic diversity and structure using neutral genetic markers (e.g., microsatellites). The distance statistic F_{ST} was chosen as the universal metric for comparison, with a threshold of $F_{ST} > 0.05$ "as indicative of significant difference between groups of caribou" (COSEWIC 2011). This departs from the COSEWIC DU guidelines on appropriate genetic markers used for determining significance, where no thresholds are specified and multiple markers are suggested (COSEWIC 2015). Additional ambiguity is added in the caveat that if individuals in neighboring DUs were sampled within a single study and differences at microsatellites were statistically significant ($P < 0.05$), then $F_{ST} < 0.05$ was acceptable (COSEWIC 2011). Further, in the report, if $F_{ST} < 0.05$ but individuals were assigned to separate clusters in Bayesian assignment tests (e.g., STRUCTURE, Pritchard et al. 2000), this could support a DU, but only in combination with at least one other discrete trait. No threshold for assignment statistics is provided. These criteria are sometimes vague or inconsistent and, given non-uniform geographic sampling across genetic studies, effective meta-analysis cannot be easily considered. These details all underscore the difficulty in accurately using genetic data for DU determination in a piecemeal approach and emphasize the need for revised analysis with uniform sampling and genetic markers.

The report (COSEWIC 2011) described 12 caribou DUs across Canada (Fig. 1). Among the 12 DUs were four in western Canada: Northern Mountain, Southern Mountain, Central Mountain, and Boreal (not occurring exclusively in western Canada). In general, although many DUs utilized genetic criteria to demonstrate discreteness, evidence for significance was typically related to underlying evolutionary principles of ecological adaptation that were inferred from the best available science, perhaps because of the challenges noted above. One exception where phylogeography came into play as a major criterion was with the Central Mountain DU (DU 8, Fig. 1). Their geographic distribution, seasonal elevational migrations, and population genetics provided discreteness, but evolutionary significance was determined chiefly by the unique gene pool that was a product of the hybrid swarm reported by McDevitt et al. (2009). The local adaptation of this hybrid gene pool in a different biogeoclimatic zone (with caribou ranges encompassing boreal forest, mountainous, and also alpine tundra environments) from neighboring DUs finalized the justification for the distinct Central Mountain DU.

Among the other western Canada caribou DUs, distinctions had primarily an ecological, not genetic, basis. The distinction between Southern Mountain and Central Mountain (DUs 8 and 9, respectively, Fig. 1) emphasized the local deep snow adaptation in the interior, old growth temperate rainforests of the Southern Mountain range (COSEWIC 2011, Ray et al. 2015) where these animals forage on arboreal lichens in old growth conifer forests, a unique strategy among caribou. Clear genetic differentiation with adjacent DU's was not always apparent (Fig. 3). For example, in east-central British Columbia at the interface of the Southern Mountain and Central Mountain DUs (Figs. 2, 3A), there is not only close spatial proximity and overlap of the Parsnip subpopulation (Southern Mountain) range with Quintette and Kennedy subpopulations (Central Mountain), but also no significant genetic differentiation (Weckworth et al. 2012; Fig. 3B). Nevertheless, the distributions of Boreal, Southern Mountain, and Central Mountain DUs of caribou are mutually exclusive during the breeding season, hypothetically preventing interbreeding and indicating unique ecogeographic distributions that provided the validating set of criteria (along with microsatellites) for consideration of Boreal, Southern Mountain, and Central Mountain caribou as separate DUs (COSEWIC 2011).

Among the wide geographic range of the Boreal caribou DU that spans other significant

Fig 2 Fig 3

COLOR

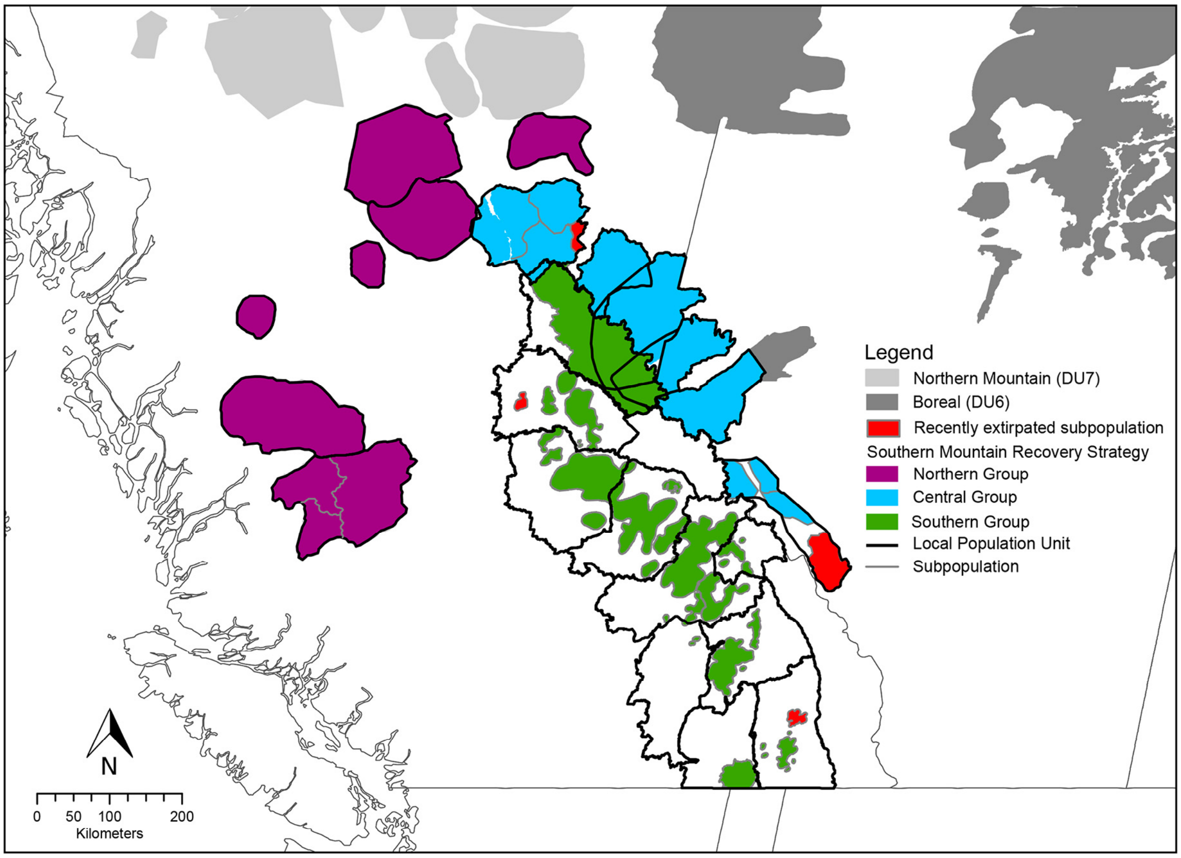

Figure 2. Hierarchical designations of groups of woodland caribou covered under the Southern Mountain Caribou Recovery Strategy (2014; figure adapted from this document). Note that the Northern Group represents a subset of the Northern Mountain caribou DU. The Central and Southern Groups are synonymous with the Central Mountain and Southern Mountain caribou DUs, respectively.

ecological gradients, however, the COSEWIC report did not identify multiple Boreal DUs (Fig. 1). They cited multiple examples of discrete traits, but a lack of criteria for evolutionary significance (COSEWIC 2011), in spite of evidence of mixed lineages for some Boreal caribou herds (Weckworth et al. 2012, draft made available to COSEWIC in 2011 before being published). On a broader national scale, further research is needed to evaluate the possible presence of additional, still undetected (cryptic), DUs. New findings are emerging that similar patterns of differentiation to those described for the Central Mountain DU above occur in other regions of Canada (e.g., as suggested recently in Ontario by Klütsch et al. 2016 and in NWT by Polfus et al. 2017). Overall, the Boreal DU currently used in northern, central, and eastern Canada is possibly being treated as unrealistically homogeneous. Indeed, since the report (COSEWIC 2011), new results have emerged that suggest a need to reevaluate for potentially multiple Boreal caribou DUs, characterized by unique spatial behaviors, migratory patterns, and genetic differentiation (Klütsch et al. 2016, Pond et al. 2016, Yannic et al. 2016, 2017, Polfus et al. 2017).

The use of genetic data in defining conservation units is imperative, yet, for caribou DU designation, it is unclear if the ambiguous criteria for using genetic data, coupled with new genetic, behavioral, morphological, and ecological studies, necessitate a redrawing of DU boundaries. The DU locations and boundaries have implications in the next stage of management, recovery planning within DUs.

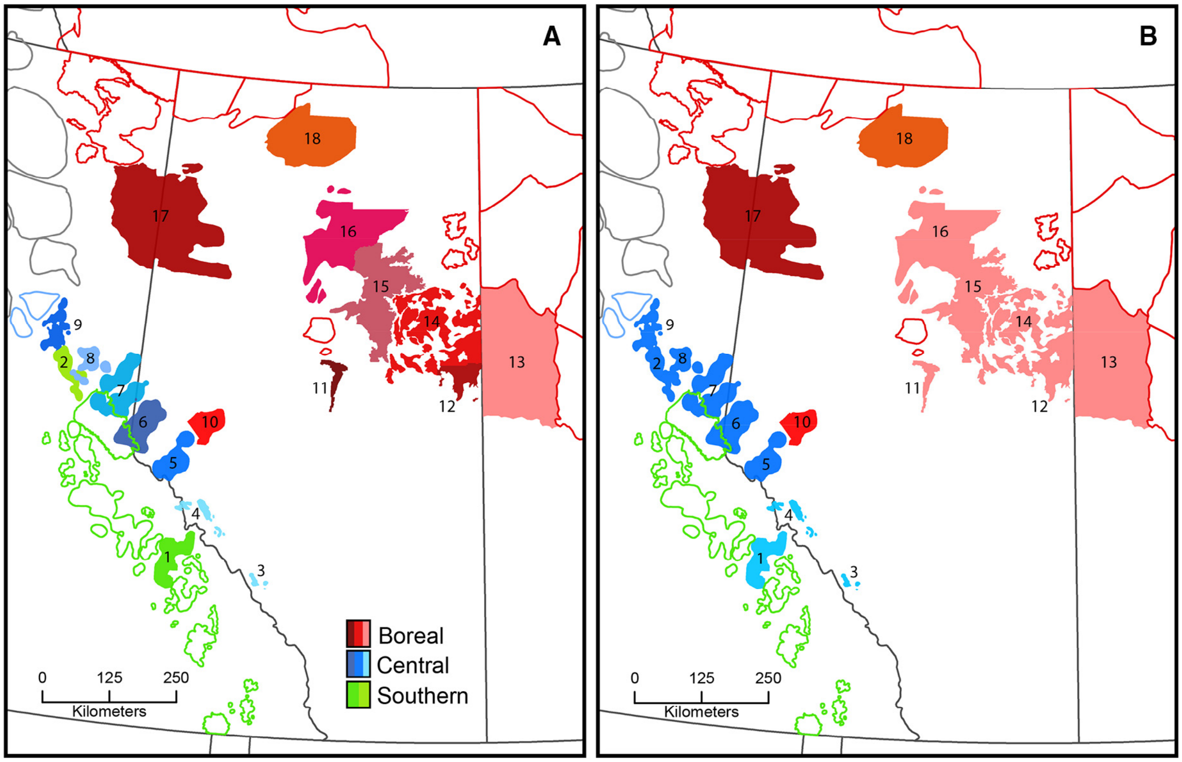

Figure 3. Range of sampling for analysis in Weckworth et al. (2012). Panel A demonstrates the hierarchy of caribou groups; similar color schemes (e.g., reds, blues, and greens) denote different caribou DUs, as per legend. Each distinct color is the Local Population Unit or equivalent for the Southern Mountain and Boreal Recovery Strategies. Each polygon represents individual subpopulations; open polygons were not sampled. Panel B represents the hypothetical meta-populations from assignment tests, as analyzed in Weckworth et al. (2012). Subpopulations: (1) Columbia South, (2) Parsnip, (3) Banff, (4) Jasper, (5) A La Peche, (6) Redrock/Prairie Creek, (7) Narraway, (8) Quintette, (9) Kennedy/Moberly/Pine, (10) Little Smoky, (11) Slave Lake, (12) Cold Lake Alberta, (13) Cold Lake Saskatchewan, (14) East Side Athabasca River, (15) West Side Athabasca River, (16) Red Earth, (17) Chinchaga, and (18) Caribou Mountains.

Recovery Planning within DUs

At provincial levels, and for recovery planning, DUs are further divided into local populations made of social groups (i.e., subpopulations, Table 1; Hervieux et al. 2013); therefore, any DU is in essence a group of populations with common characteristics and presumed connectivity, at least in evolutionary time-frames. This is consistent with the classic definition of a meta-population, a collection of interrelated populations connected by immigration/emigration and gene flow (Hanski et al. 1995). Local populations of caribou are often considered as distinct because of likely demographic independence (e.g., limited or insignificant exchange of individuals with other populations, e.g., van Oort et al. 2011), and thus, in many cases, they are identified by provincial agencies as conservation units, often under the term "herd" (and synonymous with subpopulation), but not to be confused with Local Population, as defined by the Boreal Recovery Strategy (see below; Table 1). For example, to manage and conserve caribou efficiently requires understanding population trends and threats, and this information is gathered most often by radio-collaring adult female caribou at the local population level (Hervieux et al. 2013). This framework is in accordance with conservation biology principles in the theory of meta-population dynamics, which holds that maintaining multiple interconnected populations is important for ensuring long-term persistence of a species and associated biodiversity (Hanski et al. 1995, Funk et al. 2012).

Boreal woodland caribou DU

Under SARA, for every DU listed as threatened or endangered, a Recovery Strategy must be drafted that identifies a recovery goal and the critical habitat required, and recommended actions necessary to achieve that goal. In 2012, after receiving over 19,000 comments on the draft, Environment Canada (now Environment and Climate Change Canada, ECCC) released a revised SARA Recovery Strategy for Boreal caribou (Environment Canada 2012). The primary long-term recovery goal for the Boreal Recovery Strategy is to achieve self-sustaining local populations throughout the entire distribution of [6] Boreal woodland caribou. A local population was defined in the Recovery Strategy as a "group of boreal caribou occupying any of the three types of boreal caribou ranges (conservation unit, improved conservation unit, local population unit)" (Table 1). This definition explicitly acknowledges the uncertainty of present delineations of units within the Boreal DU and appropriately opens the door for future revisions of applicable units within the Boreal Recovery Strategy as more information becomes available. [7] Nonetheless, the working conservation unit within a DU for the Boreal Recovery Strategy is presently defined as the Local Population (Table 1). Although the Boreal Recovery Strategy acknowledges the importance of connectivity, the focus on the Local Population as a conservation unit could lead to micro-managed small-scale policy interventions that do not account for the importance of inter-population relationships and the role of meta-population dynamics in [8] maintaining population viability (Hanksi 1998, [9] Fig 3). The complications with the Boreal DU delineation of conservation units become even more apparent when compared to the Southern Mountain woodland caribou Recovery Strategy.

Southern mountain woodland caribou Nationally Significant Population

In 2014, ECCC released a Recovery Strategy for the Southern Mountain woodland caribou populations that, while acknowledging the new DU structure, retained the old COSEWIC (2002) delineation of Nationally Significant Populations (Table 1). This resulted in a confusing redundancy of similar names (e.g., Southern Mountain Population vs. Southern Mountain DU) describing different conservation units. In this way, the old Southern Mountain Population subsumed the new Southern Mountain and Central Mountain DUs, as well as a subset of the Northern Mountain DU local populations (Figs. 1, 2). Such apparent inconsistencies in delineation were due to the lag time between the proposed DUs being accepted by the Minister via a consultation process versus the caribou entities already on the SARA registry (Ray et al. 2015). Consequently, when the work on the Recovery Strategy started, the new DUs for caribou had not been formulated yet by COSEWIC and the old delineations (Nationally Significant Populations; Table 1) were used, as per COSEWIC 2002 (Environment Canada 2014, Ray et al. 2015). This discrepancy arose because of the separation of COSEWIC and ECCC, and was intended to reduce the potential for political interference in listing decisions, but in this case resulted in disconnected listing and recovery planning. This disconnect exemplifies ineffective and tardy engagement of policy with science in management decisions (Mooers et al. 2010). Thus, the Southern Mountain Recovery Strategy largely ignores current DU designations of these caribou (Fig. 2).

Similar to the Boreal Recovery Strategy, the Southern Mountain Recovery Strategy sets a conservation goal, attempts to identify critical habitat, and proposes recovery actions to achieve the goal. Here we focus again on conservation units within the Southern Mountain Recovery Strategy because of a very different challenge than the Boreal Strategy. The Southern Mountain Recovery Strategy identifies the appropriate conservation unit as a similarly labeled Local Population Unit, but which is defined as likely representing "larger historical subpopulations that have since declined and that have been fragmented into the currently recognized subpopulations" (Table 1). Thus, this Recovery Strategy generally adopts a larger scale (i.e., Local Population Unit) than the Boreal Strategy for the conservation unit (i.e., Local Population). While scientific data exist on how subpopulations might be organized into these units (Serrouya et al. 2012, Weckworth et al. 2012), these were not used in the Southern

Mountain Recovery Strategy, nor is any scientific rationale offered for how Local Populations Units were identified.

Weckworth et al. (2013) demonstrated that within the Central Mountain DU, preferred habitat and effective population size (N_e) were the best predictors of genetic relationships among subpopulations. Similarly, Serrouya et al. (2012) showed for the Southern Mountain DU, and other caribou subpopulations, that census population size was one of the strongest factors affecting patterns of genetic diversity. The implications of these and other studies (van Oort et al. 2011, Weckworth et al. 2012) are that increased levels of isolation among subpopulations will amplify the potential for local extirpation due to higher environmental and demographic stochasticity within any given subpopulation. These studies assert that the long-term viability of subpopulations within the Central Mountain and Southern Mountain DUs is contingent upon not only maintaining critical habitat within each subpopulation's range, but also corridors between them that will allow for the maintenance of critical
10 meta-population dynamics. Because both the Boreal and Southern Mountain Recovery Strategies focus on habitat within Local Populations or Local Population Units, with little to no emphasis placed on connectivity among them, could undermine recovery efforts by allowing for the extirpation of caribou subpopulations, while remaining consistent with SARA's technical feasibility clause as it pertains to the larger DU.

SARA technical feasibility clause and recent extirpations

SARA policy includes a clause (SARA section 40) that dictates that species recovery for a DU must be technically and biologically feasible based on three criteria. First, there must be individuals that are capable of reproducing to increase the population; second, sufficient habitat must be available; and third, the primary threats to the species or its habitats can be avoided or mitigated. Unfortunately, within the range of the Southern Mountain Recovery Strategy, there have already been four extirpations of caribou subpopulations (Banff, Burnt Pine, George Mountain and Purcells Central; Environment Canada 2014; Fig. 2). The recovery steps for these four extirpated subpopulations seem simply to write them off, which can happen without contesting stated recovery plan goals, and thus need not necessarily be addressed by the managing agencies. If the Southern Mountain Recovery Strategy had adopted the same definition and management of Local Populations as in the Boreal strategy, then it is possible that it would be required to demonstrate how these four subpopulations could be technically and biologically recovered within the strategy. Alternately, under the present scheme in the Southern Mountain Recovery Strategy, subpopulations within a greater Local Population Unit can become or remain extirpated, but still meet the strategy's objectives as long as other subpopulations remain. For example, the North Banff subpopulation is subsumed within a Local Population Unit that includes the Jasper National Park subpopulations (Fig. 2), the extirpation of North Banff is allowable because the Jasper subpopulations still persist. Under the Boreal Recovery Strategy definition of conservation unit, North Banff would have been required to be recovered unambiguously. As the population was in a National Park, it has also been explicitly questioned what are the next steps to be adopted by Parks Canada and others after a high profile extinction in a national park (Hebblewhite et al. 2010)? The challenge of local extirpations at or below the conservation unit level is not unique to western Canada, given the recent high profile extirpation of caribou in Pukaskwa National Park, a distinct population in Ontario (Bergerud et al. 2015), and the imminent extirpation of the Val D'Or population in Quebec (Hamilton 2017). Nor is this problem specific to caribou, for example, considering the challenges with salmon recovery in British Columbia (Slaney et al. 1996, Price et al. 2017).

Toward a Policy Solution: Identifying Caribou Meta-populations for Conservation

Meta-population theory provides a demographic and genetic basis for a scientifically defensible definition of a unit at or below that of the DU, but above that of the individual subpopulation (Hanski 1991). Although empirical verification of meta-population dynamics can be difficult, due to the timescales involved, genetic and demographic information for some woodland caribou exists (Serrouya et al. 2012, Weckworth et al. 2012, 2013) to an extent that makes the meta-population framework a realistic and useful scenario for caribou conservation. This can be integrated into recovery strategies, like other criteria in the COSEWIC DU process, in a manner that can provide additional information in our case studies for Boreal and Mountain woodland caribou DUs. In other jurisdictions, such applications are emerging. For example, Yannic et al. (2016) provided an important proposal for integration of ecological and genetic structure of caribou in eastern Canada. Their comprehensive approach optimized unique genetic and ecological characteristics into discrete conservation units that would necessitate individually specific management consideration.

In the case of Boreal and Mountain woodland caribou in Alberta, we illustrate the evaluation of meta-population units using results from molecular genetic analyses of 808 individuals from >36 caribou subpopulations across five DUs in western North America (Weckworth et al. 2012). Discrete genetic units were determined from the results of Bayesian-clustering analysis (Pritchard et al. 2000) of multi-locus genotype data (14 microsatellite loci). Fig. 3B displays the genetic distinction of caribou populations in Alberta and neighboring provinces (Weckworth et al. 2012). This illustrates the difference between the currently defined conservation units from the Recovery Strategies (Fig. 3A), and meta-population structure (based on genetic data; Fig. 3B). Meta-population theory predicts that a decoupling of the demographic exchange among the similarly colored subpopulations (Fig. 3B), which the Recovery Strategy does not mitigate, would increase the risk of local extirpation of the remaining subpopulations (Hanski 1991, Gonzalez et al. 1998).

Serrouya et al. (2012) similarly analyzed molecular data for the Southern Mountain DU and found comparable higher-order meta-population structure that could be used to rationalize the grouping of subpopulations in the Recovery Strategy into defensible Local Population Units. They found, however, that the combination of molecular and radio-telemetry data demonstrated a complete breakdown of historical meta-population dynamics (van Oort et al. 2011, Serrouya et al. 2012). Despite more than a decade of intensive telemetry monitoring between adjacent caribou subpopulations, very little dispersal was identified between subpopulations grouped within the same Local Population Unit or genetic meta-population. They concluded that while historical meta-population structure existed (confirmed by genetic data, reflecting patterns inherited from past generations), current conditions have led to isolated subpopulations with no functioning meta-population structure.

One obvious deficiency in this and most previous caribou telemetry studies have been the focus on females. van Oort et al. (2011)'s findings that there was no contemporary ecological movement between populations are similar to previous studies across Canada, including ours in Alberta (Weckworth et al. 2013). However, we expect gene flow to be male-biased in a strongly polygynous breeder such as caribou, and while few studies have focused on connectivity in general between adjacent caribou herds, none have comprehensively tested for meta-population dynamics using male gene flow. Any argument that cites little present movement of females between adjacent subpopulations might not be the strongest rationale to discount the importance of historical meta-structure in driving units of conservation. Nor does lack of movement of females discount the importance of connectivity for future viability.

It may be that many caribou subpopulations and Local Population Units, particularly on the periphery of caribou range, have never existed at numbers large enough to be self-sustaining over the long term (e.g., North Banff, Pukaskwa). Such groups, as the genetic data suggest, may have relied upon equilibrium of emigration/immigration (as in established meta-population models; Hanski and Gilpin 1997) for long-term persistence (McDevitt et al. 2009, Weckworth et al. 2013). Serrouya et al. (2012)'s data emphasize how the consideration of only contemporary demographic factors in the cases above leads to each subpopulation being considered distinct (because of limited female telemetry movement, for example) from a conservation unit perspective. What this does not capture, however, is that these subpopulations are artifacts of an ongoing extinction process mediated by anthropogenic impacts on caribou populations that were historically larger in number and spread across functionally connected landscapes (Ray et al. 2015). Yet, it is clear that from a practical management standpoint, subpopulations (i.e., herds) are a logical, and at times defensible, unit for which to manage recovery. The challenge now is reconciling practicality with a hierarchical meta-population dynamic that is more likely to recover self-sustaining units, in whatever way they are defined.

Another theoretical construct, the 50/500 rule (Franklin and Frankham 1998), portends that many subpopulation and Local Population Units are destined for extinction. The 50/500 rule hypothesizes that an effective population size of 50 is necessary to prevent a damaging level of inbreeding in the short term, but an effective population size of >500 is needed for long-term genetic viability. While there have been a growing number of studies demonstrating significant negative effects of inbreeding depression in other endangered ungulates (e.g., red deer, Coulson et al. 1999, federally threatened Sierra Nevada Bighorns Sheep, Johnson et al. 2011), there have been no direct studies of inbreeding costs in caribou. Many of the caribou subpopulations in the Southern Mountain and Central Mountain DUs do not have census (let alone effective) populations of 50 individuals (Weckworth et al. 2013). While the 50/500 rule is largely theoretical, the increased risk of stochastic extinction due to small isolated subpopulation size is morbidly real (e.g., North Banff, Hebblewhite et al. 2010, Pukaskwa, Bergerud et al. 2015). Thus, the framework of meta-population dynamics (Serrouya et al. 2012, Weckworth et al. 2012) can explicitly guide strategies to group subpopulations into redefined, hierarchically structured conservation units that approach the population size of 500, with explicit intent to recover the habitat necessary to re-establish connectivity between subpopulations. Then, before a decision to allow extirpation of a subpopulation within a Local Population Unit was allowed, a meta-population viability analysis could be devised to understand the best option for sustaining that unit over time, and under different habitat management strategies. Meta-population structure could also be used to prioritize unique Local Populations for conservation. For example, the Little Smoky population in Alberta (Fig. 3B) is both isolated, and genetically distinctive within its own discrete meta-population unit (Weckworth et al. 2012). Thus, it might warrant higher priority in conservation action because of its uniqueness and isolation, as compared to other meta-population units within which more than one Local Population is nested (e.g., East Side and West Side of the Athabasca River, Fig. 3B). Understanding meta-population structure should guide the decisions about which populations are essential for future connectivity between populations, especially given the grim population trajectories of most Boreal and Mountain populations in Alberta and British Columbia (Hervieux et al. 2013, Wittmer et al. 2013). Currently, connectivity among caribou units has no formal role in recovery planning.

Policy Implications across Scales of Conservation

As demonstrated for woodland caribou, both ecological and genetic data provide important inferences in the delineation of conservation units at broad (DU) and fine (subpopulation/Local Population) scales (Serrouya et al. 2012, Weckworth et al. 2012, 2013, Yannic et al. 2016). Yet, ambiguity from molecular resources arises in two ways. The first is in considering what form of genetic information to consider, with the traditional dualism between mtDNA and microsatellites now being complemented by the added complexity of emergent genomic approaches. COSEWIC (and others; see Funk et al. 2012) recognized that "The emerging science of ecological genomics should be applied to caribou DUs to determine functional gene variation that may help provide more precise delineation of DUs and/or particular ecotypes" (COSEWIC 2011). Genomic analyses can lead to the identification of adaptive genes (genes evolved and maintained as a result of natural selection processes), and this information, in turn, can be used to define conservation units at broader scales (Crandall et al. 2000). Practically, the evolutionary potential and long-term survival of the species will be enhanced and preserved if appropriately defined conservation units are conserved at broad and fine scales.

Ambiguity among genetic markers has already resulted in scientific and political debate in the

United States under the ESA, such as the petition for listing of the Alexander Archipelago wolf (Cronin et al. 2015, Weckworth et al. 2015). Provisions must be decided upon that can provide less ambiguous guidance on the appropriate component of genetic variability used to define conservation units. For example, allowing proposed ecological distinctions to provide the context for choosing the appropriate genetic scale (e.g., phylogeographic versus local adaptation). For caribou, a systematic and uniform geographic sampling scheme could be implemented in a national synthesis of genetic diversity. The haphazard and piecemeal approach to date, with researchers providing independent studies, provides incomplete and often conflicting results that can confound the historical genetic relationships that provide the context for management of population connectivity (Schwartz and McKelvey 2009, 12 Oyler-McCance et al. 2013). At a larger scale, genomic data are emerging, but a number of caribou studies across different regions of Canada have thus far used autosomal microsatellites or mtDNA or a combination of both (Serrouya et al. 13 2012, Weckworth et al. 2012, Yannic et al. 2013, 2016, McFarlane et al. 2014, 2016, Klütsch et al. 2016, Polfus et al. 2017). For inference about population structure, studies have shown that microsatellites in particular generally perform better than, or similar to, a low to moderate number of single nucleotide polymorphisms (see Putman and Carbone 2014). Existing data, synthesized into a new analysis and combined with new systematic sampling, may allow for some meta-analysis and methodical re-evaluation of genetic support for conservation units relevant in future and ongoing recovery strategies.

The fragmentation and decoupling of caribou subpopulations from apparent historically interacting meta-populations will necessitate not only a higher level conservation unit designation (e.g., DU) to implement recovery, but also a consideration of their meta-population dynamics (Hanski 1991). Despite some discussion of the importance of connectivity in both the Boreal and Southern Mountain Recovery Strategies, there was no formal consideration of it as a criteria, nor any quantitative assessment of the degree of connectivity among caribou units. One reason why the meta-population scale may not have been technically addressed yet in caribou conservation in Canada could be due to the difficulty in establishing consensus across provincial boundaries. A second reason may be that, under SARA, both the Southern Mountain and Boreal Recovery Strategies have a goal to recover all caribou units, notwithstanding the unaccounted extirpation of four Mountain subpopulations and one Boreal Local Population (Bergerud et al. 2015). Despite the laudable goal of recovering everything, these extirpations potentially threaten future connectivity and meta-population viability.

The meta-population framework provides a solution to identifying conservation units within DUs that are evolutionarily and ecologically relevant, but also opens the discussion of triage and which units are not technically or biologically viable (a constraint acknowledged by SARA), or, ultimately, socioeconomically feasible to recover (Schneider et al. 2012). The underlying assumption (or perhaps application of precautionary principle) of recovery planning to date is that it is technically and biologically feasible to recover every single caribou subpopulation, but the recent extirpations, including in National Parks, force us to rethink any assessments of feasibility. Moreover, even basic economic analyses in Alberta, where 11 of 14 caribou herds are declining by 5–6% per yr, show that recovering caribou ranges will cost billions of dollars. This has led some authors to suggest triage (Schneider et al. 2010, 2012). Yet, no consideration of genetic structure, connectivity, or meta-population structure was considered as a criterion in the preliminary economic-only model of triage (Schneider et al. 2012). The full set of criteria used for any triage approach has not been clarified, and it seems that consensus would be hard to achieve on whether biological, social, or economic criteria would prevail, nor how to weigh different criteria.

Given this biological and socioeconomic context, the prospects of caribou conservation are daunting. The unrealistic policy directive of the Recovery Strategies to manage every single caribou subpopulation, while time is lost implementing any changes in the real world, may result in losing sight of the greater benefits to meta-population viability of maintaining some degree of natural connectivity. Moreover, we think that redefinition of conservation units under the current post-hoc manner (as done for the Southern Mountain Recovery Plan) allows for unrecoverable subpopulation extirpations in the future as the likely outcome of such an all-or-nothing strategy. Yet, the Recovery Strategies are adaptable whereby ongoing evaluations can allow for appropriate changes. Identifying larger, biologically and ecologically meaningful, metapopulation units, based on genetic and demographic data, that were historically connected (but perhaps no longer, e.g., van Oort et al. 2011, Serrouya et al. 2012), can provide a scientifically rigorous and defensible approach to start the difficult, but urgent conversation on the appropriate actions needed to promote the natural dispersal dynamics that are more likely to recover extirpated and ailing subpopulations and benefit woodland caribou conservation in Canada.

Overall, knowledge gaps remain that need to be addressed to better define conservation units. Lacking this information, caribou are largely managed as separate subpopulations without an understanding of which evolutionary characteristics are at risk should any unit disappear in the future. A scientifically refined definition of caribou conservation units could inform population monitoring of woodland caribou, adding an additional layer of consideration for conservation planning, and better enable the long-term survival of the species and its ecological and evolutionary integrity. Practically, managers could take into consideration trends of subpopulations within DUs as well as trends of DUs within the species. In addition, if captive breeding and herd augmentation programs for specific subpopulations are instituted, wildlife managers will know which populations represent the best choice as a source of individuals. Choosing source populations belonging to the same DUs of sink populations (or similar DUs) will ensure that the correct assortment of characteristics is maintained: including behavioral, morphological, ecological, geographic, and/or genetic distinctiveness.

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