SCALING UP THE ROLE OF PREDATION IN CARIBOU DECLINES IN WEST-CENTRAL ALBERTA (REDWILLOW, NARRAWAY, REDROCK PRAIRIE CREEK, A LA PÊCHE AND LITTLE SMOKY RANGES)

Final Report, New Results Only (Year 2013), AUPRF project

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<u>Note:</u> core information on activities and key deliverables found in:

For Year 2011: DeCesare, N., C. Semeniuk, M. Musiani, M. Hebblewhite, J. Whittington, and A. Aivaz. 2012. Scaling Up the Role of Predation in Caribou Declines in West-Central Alberta (Redwillow, Narraway, Redrock Prairie Creek, A la Pêche and Little Smoky Ranges). Interim report to the Petroleum Technology Alliance of Canada (PTAC). 99 pages.

For Year 2012: DeCesare, N., Peters, W., C. Semeniuk, M. Musiani, and M. Hebblewhite. 2012. Scaling Up the Role of Predation in Caribou Declines in West-Central Alberta (Redwillow, Narraway, Redrock Prairie Creek, A la Pêche and Little Smoky Ranges). 2012 AUPRF project status update. Interim, internal report to the Petroleum Technology Alliance of Canada (PTAC). 78 pages.

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Preamble

This report relates to deliverables for the Year 2013. Information on activities and key deliverables for previous years is found in:

For Year 2011: *DeCesare, N., C. Semeniuk, M. Musiani, M. Hebblewhite, J. Whittington, and A. Aivaz. 2012. Scaling Up the Role of Predation in Caribou Declines in West-Central Alberta (Redwillow, Narraway, Redrock Prairie Creek, A la Pêche and Little Smoky Ranges). Interim report to the Petroleum Technology Alliance of Canada (PTAC). 99 pages.*

For Year 2012: *DeCesare, N., Peters, W., C. Semeniuk, M. Musiani, and M. Hebblewhite. 2012. Scaling Up the Role of Predation in Caribou Declines in West-Central Alberta (Redwillow, Narraway, Redrock Prairie Creek, A la Pêche and Little Smoky Ranges). 2012 AUPRF project status update. Interim, internal report to the Petroleum Technology Alliance of Canada (PTAC). 78 pages.*

Animal capture and radio-collaring

We captured and radio-collared adult caribou and wolves to monitor movements and survival of individuals across the range of conditions present in the study area. Specifically, we used GPS-enabled collars (Lotek-2200, 3300S, 3300M, 4400S, 4400M, Lotek Wireless, Inc., Newmarket, Ontario, Canada; ATS-G2000, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) to collect location data of high quality and quantity for multi-scale analysis of resource selection, predation and movement patterns.

Winter helicopter net-gunning was used to capture caribou and wolves (Andryk et al. 1983) and we supplemented these efforts with additional summer foot-hold trapping for wolves (Frame and Meier 2007). All animal capture procedures were approved by government and university animal care protocols and permitting processes (Table 1). Full details of animal capture protocols are available upon request from any project personnel.

Literature cited:

Andryk, T.A.; L.R. Irby; D.L. Hook; J.J. McCarthy; G. Olson. 1983. Comparison of Mountain sheep capture techniques: helicopter darting versus netgunning. Wildl. Soc. Bull. 11:184-187.

Frame, P. F.; Meier T. L. Field-Assessed Injury to Wolves Captured in Rubber-Padded Traps. JWM 71: (6) 2074-2078

Table 1.

Research and collection permits, Canadian Rockies.

Alberta Sustainable Resource Development: Fish and Wildlife Division
    Collection Licenses: #21803, #27086, #27088, #27090
    Research Permit: #27085, #27809, #27812
Alberta Tourism, Parks, and Recreation
    Research and Collection Permits: RC08WC014 & Wilka101-07

British Columbia Ministry of Environment: Permit and Authorization Service
    Wildlife Act Permit VI08-31411
    Park Use Permits: 101964

Parks Canada Agency
    Research and Collection Permit: JNP-2007-952
    Research and Collection Permit: LL-2010-4392

University of Montana

> **Animal Use Protocol: 056-06MHECS-010207**
> **Animal Use Protocol: 059-09MHWB-122109**

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University of Calgary
> **Animal Use Protocol: BI-2007-57**

Identifying anthropogenic landscapes of fear and their effects on wildlife using a behavioral agent-based model

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Abstract

Anthropogenic disturbances contribute to the way animals perceive and respond to their environment. These multiple disturbances can additionally act in non-independent ways to shape an animal's landscape of fear, making it challenging to isolate their effects for effective and targeted management. Boreal woodland caribou (*Rangifer tarandus caribou*) populations across Canada are threatened, in part, by intense industrial development that has introduced multiple features on the landscape resulting in increased pressure that has effects similar to predation. Using a spatially explicit behavioral agent-based model (ABM), we conducted a sensitivity analysis with different industry-driven, landscape-of-fear scenarios to test how caribou in west central Alberta differentially respond to industrial features (linear features, forest cutblocks, wellsites) and their attributes such as presence, density, harvest age, and wellsite activity status. The ABM encapsulates predation risk, heterogeneous resource distribution, and species-specific energetic requirements, to recreate the behavioral mechanisms driving habitat selection. To identify industry feature(s) and their attributes with greatest relative influence on caribou habitat use and spatial distribution, simulated caribou movement patterns were compared with those of actual caribou using GPS-telemetry data from thirteen caribou radio-collars deployed in winter

2004. Results revealed caribou have incorporated forestry- and oil and gas features into their landscape of fear that affect their spatial and energetic responses. The presence of roads, pipelines and seismic lines, and, to a minor extent, high-density cutblocks and active wellsites, all contributed to explaining caribou responses. Our findings also indicated that both oil and gas and forestry produced cumulative effects, as they jointly impacted caribou spatial distributions and energetic reserves. There was no clear substitution effect between features. We demonstrate that behavior-based ABMs can be applied to assessing and isolating non-consumptive impacts of cumulative effects, in support of critical habitat planning.

Keywords: agent-based model, animal behavior, landscape of fear, multiple stressors, cumulative effects, caribou, sensitivity analysis

Introduction

Measuring the impacts of anthropogenic activities on the responses of wildlife is crucial for their effective management and population persistence (Leu et al. 2008). Ever-increasing industrial landscape change can lead to consequences beyond habitat loss and amount and arrangement of habitat patches. Anthropogenic features or activities can be perceived by animals as risky habitats or threatening stimuli, respectively, and animals will attempt to minimize their exposure or avoid them (Frid and Dill 2002, Beale 2007). To understand underlying processes driving habitat selection and movement of prey species, the 'landscape of fear' concept has been invoked as a behavioral mechanism explaining how *perceived* predation risk in heterogeneous environments could alter an animal's use of an area as it tries to reduce its vulnerability to predation (Laundré et al. 2001, 2011, Willems and Hill 2009). How animals therefore perceive and respond to anthropogenic features is critical for wildlife management as it will impact their

decisions of where to forage, how much energy to expend, and what habitats to use (Johnson et al. 2005, Krausman, 2011).

Prey rarely find themselves in single-predator environments and must accordingly evaluate the relative predation risk from multiple predators simultaneously (Thaker et al. 2011). With increasing land-use intensification, prey are similarly exposed to multiple anthropogenic features – stressors – that can evoke synergistic, interactive, or unpredictable outcomes that aggregate over time and space (Harriman and Noble 2008). Therefore, an evaluation of how stressors influence an animal's landscape of fear should be examined in a cumulative effects (CE) context. We define here cumulative effects as occurring when the joint effects of features in close proximity are greater or less than the influence of either of the features alone (Riffell et al. 1996). Because anthropogenic CE are characterized by their interdependence between time, space, and activity, this presents a challenging problem in evaluating their relative contributions on wildlife responses (Nitschke 2008). Studies of this kind are limited by the requisite complexity of experimental designs that often require expert guidance (Frair et al. 2008), and use complex statistical analyses for quantifying stressors effects, yet are still unable to adequately quantify interaction terms beyond binary combinations (Glaholt et al. 2012). In addition, studies which examine animal spatial distributions without a behavioral context may also be of limited value, since statistical habitat models parameterized in one area may not be transferable to other areas or conditions in which habitat availability and landscape configuration are different - for example, under future conditions (Beyer et al. 2010). Instead, an integrative modeling framework that allows for the simulation of complex animal movement ecology and behaviors can provide a virtual environment in which to test the interactive, cumulative effects of multiple stressors on an

animal's perception of predation risk and disturbance (Frair et al. 2008, Bennett et al. 2009). Addressing these sources of and pathways to a landscape of fear can resultantly better affect targeted management and mitigation measures (Spaling and Smit 1993).

In view of this, we use a spatially explicit, behavioral agent-based model (ABM) to assess the CE of multiple industrial developments on animal movement, distribution and habitat use by simulating an animal's perception of landscape risk. We parameterized our model for boreal caribou (*Rangifer tarandus caribou*), a useful model species as their populations have been impacted by expanded industrial development over the last few decades (Vors and Boyce 2009, Environemnt Canada 2011). This expansion has resulted in an increased network of seismic exploration, pipelines and roads, and the loss of habitat of older, lichen-bearing forests due to resource-extraction activities of oil and gas and forestry (Peters et al. 2013). Consequently, the decline of woodland caribou is partly based on an indirect interaction between caribou and industry that has increased the caribou's landscape of fear (DeCesare 2013). Habitat change from forestry has increased predator biomass as preferred ungulate prey are attracted to early seral forests (Seip 1992, Wittmer et al. 2005, Peters et al. 2013). Linear features introduced onto the landscape aid in facilitating predator efficiency (Latham et al. 2011, DeCesare 2013). Lastly, caribou can identify industry features as disturbance and predation-risk events, either directly through physical footprint, or indirectly through sensory disturbance, and respond similarly as they would to natural predators, minimizing their exposure (Vistnes and Nelleman 2008). Due to these higher levels of predation pressure and disturbance, the evolved predator-defense strategies of caribou - avoidance/ separation behaviors - have augmented the allocation of habitat caribou deem as 'risky'/'fearful' (Smith et al. 2000, Dyer et al. 2001, Polfus et al. 2011).

Despite the important impacts of industry activities on caribou fitness, empirical studies face a significant challenge disentangling the relative effects of multiple stressors. Using the ABM, we employ a sensitivity analysis to infer knowledge about caribou responses to different existing industrial features based on characteristics that may affect their relative perception: presence and density of linear features, cutblocks and wellsites; age of harvested forest; and activity status of wellsites. In particular, we test whether industrial features all contribute to a caribou agent's landscape of fear and to what extent, or whether they are substitutable. The resultant landscape configuration that contributes the highest explanatory power to agent habitat-selection behaviors is then evaluated by comparing simulated caribou movement patterns with actual caribou data and with two null models of caribou movement based on random processes (random locations, and undifferentiated responses to industry). The advantages provided by our approach is an understanding of the role of CE on processes governing caribou movements and distributions, and the relative impacts of different industrial stressors, offering a foundation on which decisions and future actions can be evaluated (Nitschke 2008).

Methodology

Study area

The area chosen for the study was the range of the Little Smoky (LS) herd demarcated by the Alberta Fish and Wildlife Division (ASRD 2010), covering 3,100 km^2 in the foothills of west-central Alberta (Fig. 1). The LSM range is located in the upper foothills ecoregion of west central Alberta, Canada (54°N, 119°W), with the lands primarily managed by the government for multiple uses including forestry, oil, and natural gas industries. Because the Little Smoky is such

a dynamically changing landscape due to industrial development, we confined our study to a single time period, during winter 2004-2005. The LS range has the highest level of industrial development of any boreal caribou herd in Canada, with 95% of its range in proximity (500 m buffer) of anthropogenic activities (Environment Canada 2011), and as such provides an ideal case study to evaluate the cumulative effects of the caribou's landscape of fear. Specifically, the activities of four forestry management agreements and numerous petroleum-company operations (WCCLPT 2008) have generated an estimated 0.45 km/km^2 of infrastructure (roads and pipelines), 3.5 km/km^2 of seismic lines, 439 oil/gas well sites and 9.1 ha/km^2 of cutblock densities in the LS c. 2005. There also continues to be considerable development pressure and increases in allocations to industrial users within the caribou range (Robichaud 2009).

Agent-based model overview

Our current work expands on the ABM we developed that simulates winter habitat selection and use of female woodland caribou in the LS (Semeniuk et al. 2012). The underlying premise of the ABM is that an individual's internal state influences how it perceives its environment and hence drives its decision-making process (Houston and McNamara 1992). The model consists of one category of agents, the caribou, represented as a cognitive entity. It has a mental representation of its environment, can plan its activities, and has a memory of profitable and safe patches in the study area. Specifically, the caribou agent can balance its needs to meet its daily energetic requirements and minimize its energetic loss in order to ensure its long-term goal of reproductive success. The caribou also considers its predation risk since relatively safer locations are not always the most profitable in terms of energetic resources. The major findings of the ABM allowed us to determine the processes driving habitat selection. Namely, when navigating their

environs, our model suggested caribou make context-dependent decisions, and respond to the pervasive predation risk of their environment when they can afford to (and in doing so, incur additional energetic costs). Energetic needs for daily maintenance have priority. From a behavioral ecology point of view, our approach indicates that humans and infrastructure might be perceived equivalent to predators. In our original model, however, we did not distinguish between forestry and oil-and-gas industrial features, although it was demonstrated that general industry effects on caribou habitat-selection strategies were highly significant.

In recognition that movement characteristics and energetic constraints influence the availability and accessibility of habitat, and that the attributes, distribution, and differential perception of industrial features can influence animal movements in turn (Martin et al. 2008), the current ABM seeks to improve upon the former by disentangling the confounding effects of multiple industrial features and their attributes, to increase overall model fit, and to enhance its predictability for novel environmental conditions such as modelling augmented or mitigated future development scenarios.

Caribou agent decision-making heuristics
The caribou agent is provided fitness-maximizing rules: to tradeoff the competing goals of energy acquisition and conservation (i.e., for somatic and reproductive growth) with minimizing predation risk. Accordingly, at each time step in the model (representing 30 min.), the agent first assesses its energetic state; it determines whether it has reached its daily energetic requirements (22-33 MJ day^{-1}, McEwan and Whitehead 1970, Boertje 1985) and by what magnitude, and projects whether it will have enough energetic reserves (and by what magnitude) to have a

successful birth at the end of the season (an energetic loss of no more than 710 - 947 MJ, Bradshaw et al. 1998; 'A' in Fig. 2). At this stage it also senses the immediate risk in its environment as well as the forage availability ('B'). It then determines which fitness-maximizing goal is most important to trade off against the others, and does so by assessing which goal has reached a minimum threshold. Based on this decision-making heuristic ('C'), the agent either forages, ruminates, or moves to a new location ('D' and 'E'). The agent then updates its energy reserves - both gained and lost through its actions ('F'), and commits to memory any profitable or safe locations encountered - to which it returns, should it be energetically stressed and surrounded by inhabitable matrix. ('G'). A more detailed description can be found in Semeniuk et al. (2012).

Landscape representation

Because the environment plays a critical role in the decision-making heuristics of caribou, the ABM includes a spatially explicit representation of the Little Smoky region to ensure biological and ecological realism. For integration with the ABM, four raster data layers at a 45 m resolution were used to represent the physical environment where the caribou agents are located: (1) forage-availability layer, (2) an energetic-content layer, (3) a predation-risk layer, and (4) an elevation landscape. The forage-availability and predation-risk layers were generated from combined land-cover and industry-feature maps composed of habitat classes and industrial features (roads, pipelines, seismic lines, cutblocks and wellsites), respectively, that in turn were assigned both ranked forage and risk scores (Fig. 3).

The land-cover raster map was developed by DeCesare et al. (2012) and contained ten vegetation

classes deemed to be biologically relevant to woodland caribou, ranging from closed conifer forests, to herbs and open water. Individual vector maps of roads, pipelines, seismic lines cutblocks, and wellsites were supplied by Alberta Environment and Sustainable Resource Development (AESRD), and analyzed and updated for accuracy to 2004 (see Appendix A). These AESRD maps included the location of industrial features and associated attributes, such as year of establishment (cutblocks) and activity status (wellsites). The energetic-content layer was produced from combining known caribou daily energetic intake rates and caribou-foraging time budgets with the relative forage-availability of each land-cover class. The elevation layer was represented by a digital elevation model (DEM). To provide an environment to the agents and allow their movement, a virtual grid was overlaid on the four layers described above. Each cell in the ABM spatial environment therefore possesses four values accessible by the agent: a forage-availability score (0-5), an associated energetic content (MegaJoules, MJ), a predation-risk score (1-5), and an elevation (m).

Creating multiple landscape-of-fear configurations

In our original caribou ABM, caribou agents were responsive to only one landscape of fear: habitat land-cover classes (each assigned a risk score from 1 to 5) and industry-feature *presence* (i.e., the actual locations of infrastructure, seismic lines, cutblocks and wellsites). These industry features were randomly given a predation-risk score of either 4 or 5 so as to not overly complicate the model, since deducing the behavioral processes driving overall habitat selection was the original main objective. Nevertheless, the rankings are in accordance with the accepted premise caribou are sensitive to industry features. In this current iteration, we created various fear landscapes with associated risk scores to test the sensitivity of caribou agents to the different

industry types (oil and gas vs. forestry), their features (infrastructure, seismic lines, cutblocks and wellsites), and their associated attributes (either presence, density, harvest age, wellsite activity, or no responsiveness by agents). The predation risk associated with the different habitat land-cover classes remained unchanged.

For the creation of different industry-driven fear landscapes to examine, a four-step process was required (detailed in Appendix B). First, attribute data layers were created for each industry feature: 'presence', 'density', 'age' (for cutblocks only), and 'activity status' (wellsites only). Next, these individual attribute data layers were assigned a high predation risk score. The attribute data layers were then arranged in various combinations via a sensitivity design (Table 1) to generate different configurations of industry-sourced landscapes of fear. An additional response was added to the design: a 'no strong effect', denoting that the industry feature in question (e.g., whether a cutblock or a seismic line, etc.) was not to be deliberately avoided by caribou agents. The last step involved completing the LS landscape representation for input into the ABM. Each of the generated landscapes of fear represented industry-sourced predation risk only, and was subsequently integrated with the land-cover map to represent the complete predation-risk data layer necessary for the ABM (Fig. 3).

Simulation framework

The caribou ABM was simulated with each of the 12 landscapes of fear in separate runs. The ABM comprises one agent assumed to be 132 kg in weight, pregnant, and expected to lose mass over the course of winter (Bradshaw et al. 1998). Accordingly, at the start of simulation, the agent's cumulative energetic loss is set at 0. The simulation is also begun with the agent at a

daily energy intake of 0. Because caribou have distinct summer and winter habitat requirements (including forage), the agent also begins the simulation with no winter locations stored in its memory. Lastly, the start coordinates for the agent corresponds to one of the thirteen initial locations of the actual GPS-collared LSM caribou. To account for environmental stochasticity and for variability in model outputs, simulations are replicated 65 runs per scenario (i.e., fear landscapes). The presented simulation results correspond to the average or median of the values obtained in these replicates.

The model has a reporting mechanism describing the instances of various events at each time step of 30 min. on a 3,100 km^2 grid surface (1786 x 1619 45-m cells). The time and areal step are appropriate temporal and spatial resolutions to capture the variability of foraging behaviors that are characteristic of ungulates at the spatial level of the food patch (Owen-Smith et al. 2010). The ABM simulates over a period of 180 days, the span of winter in Alberta.

The simulation model was developed using the platform NetLogo v. 4.1.2 (Wilensky 1999), and verified for proper programming functioning through progressive debugging and uncertainty testing.

Evaluation of agent responses to different fear landscapes

As caribou agents move across the landscape, the ABM outputs various agent behavioral, bio-energetic, and spatial metrics (patterns). Therefore, each landscape-of-fear (LOF) scenario used in the ABM elicited from agents patterns that could be evaluated and compared. To identify the most ecologically realistic LOF scenario, meaningful patterns were selected from radio-collared GPS location data of actual caribou (Tables 2 and C1). A total of 5225 location points were

obtained at a minimum of 4-hour intervals for 13 female individuals from the Little Smoky in winter (November-April) 2004-2005 (see DeCesare et al. 2012 for more details). The patterns from both actual and simulated data for comparison were industry-related variables that comprised: (1) the median nearest distance (m) between caribou point locations and industrial features, (2) the median lineal density of industrial features within $1km^2$ of caribou point locations (km/km^2), (3) the maximum wellsite density ($\#/km^2$) within $1km^2$ of caribou point locations, (4) the percent difference in nearest-proximity to cutblock ages (old vs. young), and (5) the percent difference in nearest-association with wellsite activity status (inactive vs. active). Two regulating criteria were further added as additional patterns to identify biologically unrealistic model runs: individual-spatial extent (measured as minimum convex polygon – 270 km^2; Semeniuk et al. 2012), and the cumulative seasonal energy lost by the caribou agent (a normal range should be between 710 – 947 MJ; Bradshaw et al. 1998, Semeniuk et al. 2012).

To determine the LOF scenario that best reproduced the *multiple* patterns generated by actual caribou, a multi-response optimization approach was used, known as 'maximum desirability' (see Appendix C). This technique allows for the simultaneous optimization of several patterns, and is analogous to a linear regression model in which the simulated patterns from an LOF scenario are jointly regressed against observed ones, and the degree of 'fit' estimated. Because this analysis can also determine the relative contributions of each industrial attribute to the overall model fit, it can likewise allow for a unique optimized combination of attributes to emerge. Because only a subset of LOF scenarios were evaluated (albeit orthogonal in design), a unique LOF scenario was produced as having the best fit against actual data. This optimized LOF scenario was then incorporated into the ABM, the model run, and agent patterns evaluated.

To further assess the performance of the LOF scenario, we extracted and evaluated additional agent-evoked patterns directly unrelated to industry responses (i.e., not used in the initial evaluations) - the combined spatial extent of individuals and its degree of spatial overlap with the herd range of actual caribou.

Lastly, the robustness of the optimized LOF scenario was tested against two null 'random' models. We used (1) a random distribution of points within the LS boundary meant to represent caribou with no underlying mechanistic habitat selection behaviors (n = 5225, comparable to the number of caribou GPS point locations), and (2) the original caribou ABM (Semeniuk et al. 2012) that did not distinguish oil and gas from forestry but randomly treated the presence of such features as medium-high or high predation risk. This ABM was re-run using the updated industrial feature datasets (Appendix A). We extracted from the two null random models the same suite of patterns and compared them against those of actual caribou as an indirect measure of how well the optimized LOF scenario performed.

Results

Caribou agents generated patterns that best reproduced the multiple response patterns of actual caribou when the presence of infrastructure and seismic lines, the density of cutblocks (>3.8 km km^{-2}), and active wellsites were concurrently considered as the industry-driven landscape of fear (i.e., an optimal fit of 0.26 - see Appendix C; Fig. 4). This optimized LOF was not one of the twelve explicitly modeled during the sensitivity-design process. The twelve LOF-scenarios nonetheless had caribou agents produce patterns that fell within the quartile values of actual caribou (Table 2), although scenarios that ignored the effect of seismic lines caused agents to

generate unrealistic spatial extents and lose uncharacteristically minimal amounts of energy. In comparison, the pattern values elicited from the optimized LOF-scenario either generally fell well within the range of the twelve scenarios or as close to the actual-caribou value as possible (Figs. 5 and 6).

The optimized LOF was robust, outperforming either of the null models more often than the reverse (Table 2). The improvement of the refined caribou ABM over the original is not so drastic as to alter the fundamental patterns that had matched well with actual caribou behavioral patterns derived from the GPS-collar data. Indeed, most patterns remain unchanged, as expected: closed conifer forests, muskeg/wetlands and open conifer forests were still the land-cover classes used most frequently by agents; caribou agents in late winter continued to use lower elevations with reduced daily step-lengths; and the single daily peak in activity levels remained unaffected (present values not reported, although see Semeniuk et al. 2012). However, incorporating the landscape of fear into the ABM increased the realism of the model in that caribou agents, in their quest to minimize exposure to the selected industrial features and their attributes, reproduced individual spatial extents still within the observed actual-caribou range (250-290 km^2), but did so with a smaller and restricted herd range than the original ABM, converging more accurately to the areal coverage used by actual caribou c. winter 2004-2005 (Fig. 7).

Each industrial feature was perceived by caribou to be of high risk – 'no strong effect' was never selected during the optimization procedure to maximize overall fit of the multiple caribou response patterns. There was no possibility of having the quantity of cells apportioned as 'high risk' in the spatial datasets overwhelmingly drive the results: the allocation of cells in the

'presence' and 'high density' data layers were similar for industry feature (within 5%). Moreover, the selected active-wellsite attribute, with fewest number of cells deemed high risk in the data layer, was still capable of eliciting a behavioral response from caribou agents. Caribou agents were also most sensitive to linear features (infrastructure and seismic lines), as evidenced by the sizeable drop in fit estimated as one shifted away from the optimal attribute (Fig. 8). Despite the strength of contribution of linear features in shaping caribou-agent behaviors, there was however no substitution effect: with the exception of seismic lines, overall fit was estimated to approach zero when considering the fit of a sole industry feature (and its optimal attribute) independent of the others. The presence of seismic lines only could explain 17% of the variation in agent responses.

Discussion

Our simulated caribou agents produced behaviors that were similar to those observed in this study for actual caribou. The sensitivity analysis that we performed also elucidated caribou responsiveness to different anthropogenic features, which we described as different scenarios of Landscape of Fear (LOF). These findings indicate how modeling approaches using ABM are adequate in simulating real-world wildlife agents and to recreate the response of these agents to human impacts. Our findings revealed that in addition to resource distribution, the responsiveness of caribou agents to the multiple industry features affects the extent to which caribou distribute themselves on the landscape as well as their energetic reserves (the caribou agent's seasonal energy loss was slightly higher when compared to the null ABM model; Table 2). Furthermore, no one industrial feature is substitutable for another when invoking anti-predator responses in caribou – there is no redundancy. In fact, they interact in a way to produce

cumulative effects, as can be evidenced in their ability to jointly and non-independently impact a variety of caribou habitat-selection responses even though predators are not explicitly modeled in the ABM. These findings are comparable not only to LSM-specific caribou, but are also consistent with what is known about caribou sensitivities to industrial features in general. They contribute to our knowledge of how cumulative effects impact an animal's decision making, specifically, and landscape of fear, generally. These points are discussed below.

The results of the caribou ABM sensitivity analysis are consistent with statistical findings from other habitat-selection studies of boreal caribou: our agents represent a herd established in an area (and thus to 3rd order, finer scale resource selection), and were found to be less responsive to cutblocks and active wellsites than to linear features. These results coincide with two independent resource-selection studies at a herd-specific and regional (western Canada) levels. In the former, Neufeld (2006) found caribou occupancy in winter habitat was influenced only somewhat weakly by the proportion of $1km^2$ area that is cutblock, was not affected by wellsite distance or density, but was strongly influenced by the distance to seismic lines (but not density). Similarly, DeCesare et al. (2012) found woodland caribou herds in western Canada to be responsive to cutblocks at first- and second-order selection, respectively - the population and individual home ranges. Within an individual caribou's home range, caribou were sensitive to lineal density (when compared to forestry cutblocks) at third-order caribou selection (i.e., the individual). Our similar model results can be explained by examining the spatially explicit distribution of agents: high cutblock density formed a contiguous movement barrier in the northern portion of the herd range (Fig. 4). Agents, therefore spending more of their time in the central area, were exposed to a higher frequency of occurrence of infrastructure and wellsites

(seismic lines are ubiquitous), and thus demonstrated an increased sensitivity to linear features that included seismic lines, roads and pipelines, as these were the features most often encountered.

The stressors examined in this study have been shown to commonly co-occur in boreal caribou ranges and to elicit responses from caribou (Environment Canada 2011). While CE impact models for caribou exist, they are either characterized by future scenario analyses of i) habitat availability (e.g., Schneider et al. 2003), caribou population dynamics (e.g., Weclaw and Hudson 2004), and female reproductive value (e.g., Russell et al. 2005); or ii) current analyses of habitat loss (e.g., cumulative zones of influence; Polfus et al. 2011). In the former instance, a drawback to these studies is in the inability to generate spatially explicit landscapes of actual caribou habitat use, a necessary element for conservation planning of critical habitat (McLane et al. 2011). In the latter instance, the CE models are based on habitat use, occupancy, or intensity, but do not determine the behavioral process of choosing habitat (i.e., habitat *selection*), resulting in limited value when applied to conditions and areas that differ from the ones considered for parameterization (Beyer et al. 2010). In addition to being able to accommodate both spatial and behavioral contexts of CE, the greatest utility of a model like ours lies in its ability to isolate and jointly test the effects of one stressor from and against the other. We show that the non-independent relationship between stressors is considerable, thus filling the gaps in cumulative stressor research.

Another advantage of ABMs over traditional habitat-selection models is their usefulness as an experimental system in which hypotheses regarding the effects of contrasting environments on

animal distribution patterns can be evaluated (Jespen and Topping 2004). As such, our model equally isolated stressors from landscape context. First, the ABM models habitat selection behaviors of agents since they are capable of trading off goals of energy acquisition with predator-risk minimizations in a spatially explicit environment. This means that agents' decisions are influenced by the landscape in terms of forage availability, travel cost, and predation risk. Next, the use of the 'no strong effect' option in the sensitivity design forced agents to ignore industry and use habitat-mediated cues to assess their environment. Taken together, the model was capable of teasing apart the confounding accessibility vs. preference (or avoidance) space-use of animals (Matthiopolous 2003). For instance, the separation distances measured between actual caribou point locations and industrial features could not be explained in our model by features simply being in areas too forage-poor or too costly to access; otherwise, habitat characteristics alone would have been enough to explain agent distributions and their seasonal energetic losses. Indeed, habitat-mediated (not industry) avoidance was revealed to be the least informative attribute in explaining landscape-level distributions as it resulted in unrealistically small individual-agent spatial extents, energetic losses, and other improbable spatial patterns. To sum, our model suggests caribou are perceiving industrial features as akin to threatening stimuli, and responding accordingly.

On a final note, our study emphasizes the importance of understanding how anthropogenic landscapes of fear shape animals' perceptions of habitat quality. While predator–prey dynamics are typically examined by quantifying changes in the numerical abundance of prey populations as a consequence of direct consumption by predators, non-consumptive effects - like those precipitated by landscapes of fear - can also affect patterns in prey distribution and survivorship

(Matassa and Trussell 2011). Prey respond to predation at the landscape level using temporal and spatial changes in activity in addition to the selection of safer habitats, which can conflate or confound estimates of prey mortality (Peckarsky 2008). The use of habitat cues rather than predator presence is a pervasive strategy in terrestrial predator-prey systems. A meta-analysis by Verdolin (2006) revealed habitat characteristics to have a stronger effect on prey behavior as correlates of predation risk than the presence of live predators and associated cues; and more specifically, in a study of African ungulate species, Thaker et al. (2011) found that the selection and avoidance of habitats by animals was stronger than avoidance of areas characterized by high predator activity. For wildlife species that rely on spatial-separation strategies to avoid predators, gauging habitats that are risky rather than of high predator density/activity – such is the case for boreal caribou – is the first line of defense. As such, anthropogenic stressors associated with high risk and/or perceived as a disturbance could play a large role in shaping how an animal uses its habitat, how much energy it expends, and its ability to minimize exposure to predation, thus having consequences for effective planning and interpretation of conservation measures and outcomes.

Conclusion

Annual population growth rates and calf recruitment of caribou have been shown to be significantly highly impacted by a combination of natural and anthropogenic disturbances (Sorensen et al. 2008, Environment Canada 2008, 2011). Consequently, the Canadian Federal Government has undertaken a scientific assessment to inform the identification of critical habitat for the woodland boreal population, defined as the percentage of range needed to maintain or return that herd at or to a self-sustaining rate (Environment Canada 2011). As this study represents the first to apply a behavior-based, spatially explicit approach to isolate the

contributions of anthropogenic stressors driving the statistically inferred 'industry avoidance' of caribou, it can provide important information for decision-makers regarding factors influencing the species' distribution and its bio-energetic consequences, and contribute to our state-of-knowledge of caribou conservation beyond numerical management.

First, any future increase in actual and functional habitat loss (i.e., removal of prime caribou habitat and increased industrial development) can energetically tax caribou as they respond to risk effects imposed by their landscape of fear combined with reduced forage availability. Because relatively small shifts in mass result in relatively large changes in caribou parturition rate (Cameron and Ver Hoef 1994), caribou fecundity can be negatively impacted. In the ABM, agent caribou experienced an average mass loss of 18%, approaching the hypothesized 20% failed-reproduction threshold (using calculations presented in Bradshaw et al. 1998), and thus demonstrating that energetic effects of LOF are not insignificant.

Second, as increasing industrial development can create semi- to fully impermeable barriers to caribou movement, animals should have within their extant range areas to which they can retreat with relatively smaller industrial footprints. While range contraction is often seen as a consequence of population decline and vice versa (Schaefer 2003), the spatial extent of caribou agents revealed their distribution to be a behavioral consequence of minimizing exposure to risk, a finding otherwise unfeasible in other habitat models. The attention to biological realism, in combination with our validated sensitivity analysis, provide confidence in the predictive ability of the ABM to explore caribou spatial distribution and bio-energetic expenditure to future changes in the LS landscape - an asset to critical-habitat planning, and the next focus of our

research.

Acknowledgements

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Preferred habitat and effective population size drive landscape genetic patterns in an endangered species

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Abstract

Landscape genetics provides a framework for pinpointing environmental features that determine the important exchange of migrants among populations. These studies usually test the significance of environmental variables on gene-flow, yet ignore one fundamental driver of genetic variation in small populations, effective population size, N_e. We combine both approaches in evaluating genetic connectivity of a threatened ungulate, woodland caribou. We used least-cost paths to calculate matrices of resistance distance for landscape variables

(preferred habitat, anthropogenic features, predation risk) and population-pairwise harmonic

means of N_e, and correlated them with genetic distances, F_{ST} and D_c. Results showed that spatial

configuration of preferred habitat and N_e, were the two best predictors of genetic relationships.

Additionally, controlling for the effect of N_e increased the strength of correlations of

environmental variables with genetic distance, highlighting the significant underlying effect of

N_e in modulating genetic drift and perceived spatial connectivity. We therefore provide empirical

support to emphasize preventing increased habitat loss and promoting population growth to

ensure metapopulation viability.

Key index words or phrases

Canadian Rockies, genetic drift, habitat fragmentation, landscape genetics, least-cost paths,

Rangifer tarandus caribou

Introduction

Maintaining wildlife habitat connectivity amidst the mosaic of human impacted landscapes has

become a global conservation priority [1]. A lack of connectivity, particularly in the small

isolated populations that typify many endangered species, leads to a multitude of demographic

and genetic consequences. These include inbreeding depression [2], compromised immune

response [3], loss of adaptive potential [4] and heightened susceptibility to demographic and

environmental stochasticity (e.g. [5]). Landscape genetics methodologies address the interactions

between environmental features and the evolutionary processes such as gene flow, genetic drift

and selection, and thus the mechanisms by which negative genetic impacts can be manifested.

These methodologies are increasingly coupled with landscape resistance models to guide

management decisions in identifying where best to set aside corridors, construct habitat linkages and otherwise promote connectivity [1,6,7].

Landscape resistance is a hypothesized measure of a landscape feature's impediment to gene flow. Studies using landscape resistance models often lack empirical data and instead rely heavily upon expert opinion to identify habitat variables important to resistance [6,7]. However, this qualitative approach has been shown to suffer from lack of repeatability and poor performance in describing actual landscape costs [8]. Some studies have begun to incorporate radio-telemetry data to identify key environmental metrics for constructing more objective landscape resistance surfaces [7,9]. A common method in studies of terrestrial animal ecology is to build models of resource selection functions (RSFs; e.g. [10]) to infer a species' preferred habitat. Shafer et al. [9] have recently demonstrated the superiority of RSFs over null isolation-by-distance and isolation-by-barrier models in predicting genetic structure. Prior limitations in landscape genetics research may be circumvented by utilizing advances in empirically derived landscape resistance models.

While landscape genetics can enhance conservation planning, it cannot ignore the fundamental evolutionary processes that underlie metapopulation dynamics at spatial and temporal scales. For example, few studies have taken into account the potential impact of population size on patterns of genetic diversity and the potential for genetic drift to obstruct resistance models from identifying important landscape genetic relationships, particularly when dealing with endangered species. Genetic drift is an evolutionary process with important applications to conservation biology due to its sensitivity to changes in population demographics, including population size and temporal and geographic isolation [11-13]. The leading parameter that reflects evolutionary changes in population dynamics is the effective population size (N_e),

defined as the size of an idealized population exhibiting the same rate of random genetic drift as the population under consideration [14], and which can roughly be seen as the number of breeders that contribute genes across generations. The loss of genetic diversity caused by genetic drift is inversely proportional to N_e, following approximately $H_t/H_0 = [1-(1/2N_e)]^t$, where H_t/H_0 is the reduction in heterozygosity after t generations. Consequently, knowledge of N_e can be a powerful tool in conservation as a predictor of genetic diversity loss, inbreeding and, perhaps most important to landscape genetics studies, population differentiation.

In this study, we conducted a detailed landscape genetics analysis that incorporates the effect of N_e among the factors determining patterns of genetic diversity. Specifically, we analyze the primary environmental and demographic variables that drive ungulate population substructure in endangered woodland caribou (*Rangifer tarandus*). Our *a priori* landscape models were chosen to test specific hypotheses regarding the factors thought to have the greatest conservation impact on threatened species, including caribou. We test four hypotheses that population genetic structure is influenced by: 1) preferred habitat availability, 2) anthropogenic barriers, 3) predation risk, or 4) reduced effective population size, N_e. If small populations are experiencing rapid genetic-drift due to small N_e, this may explain a large variance component in population pairwise genetic distances and obscure the signal from landscape variables. Woodland caribou offer an ideal species to explore these hypotheses as their ecological and conservation challenges are well documented in the literature (e.g. [15-17]) and genetic and spatial telemetry data are available for many populations [10,18].

Methods

Study Area

The study area encompassed a ~70,000 km^2 region in west-central Alberta and eastern British Columbia, Canada, (figure 1) that lies within the central Canadian Rockies ecosystem, and includes ~16,000 km^2 and 12,000 km^2 of federally and provincially protected areas, respectively. The remaining area is primarily managed by provincial governments for natural resource extraction, including forestry, oil and natural gas industries. The topography is typified by the rugged slopes of the Rocky Mountains (400-3937 m) enveloping flat valley bottoms. The climate is characterized by long winters and short, dry summers, and habitat types include montane, subalpine, and alpine ecoregions that correspond to increasing elevation and decreasing annual productivity. Protected areas tend to be located in the more mountainous regions, in contrast to the areas of highest human impact occurring predominantly in the boreal foothill regions in the eastern portion of the study area. Roads, seismic lines, well pads, and forestry cut blocks were more prevalent in the eastern portion of the study area.

We studied caribou herds representing eight spatially distinct populations (figure 1; A la Pêche, Banff, Brazeau, Little Smoky, Maligne, Narraway, Redrock-Prairie Creek, and Tonquin) that included both Central Mountain and Boreal ecotypes. The study area represents the area historically available to these specific caribou herds [10]. Census herd size estimates (N_c; table 1) were based upon population data from 2006-2009 [19].

Genetic Data

The 207 individuals analyzed represent those herds previously analyzed [18] for which validated habitat data were also available [10]. The genetic data used here are from individuals PCR-amplified and genotyped at 14 polymorphic microsatellite loci, following Weckworth et al. [18]

(DRYAD entry doi:10.5061/dryad.gn22271h). DNA was derived from blood samples collected through agency monitoring efforts over the past decade.

Analysis of genetic data

For comparison to population pairwise resistance distances (see below), we calculated standard pairwise estimates of F_{ST} [14] in Microsatellite Analyzer v3.0 (MSA, [20]). We also used MSA to calculate pairwise chord distance (D_c, [21]). D_c emphasizes genetic drift over mutation, reflects decreases in populations better than other genetic distance metrics, and thus may be particularly suited for microsatellites and fine-scale landscape genetic analyses such as those used here [21,22]. Significance for F_{ST} was calculated using 10,000 randomizations, correcting for type I errors using sequential Bonferroni adjustment. We also estimated deviations of observed heterozygosities from those expected under Hardy-Weinberg equilibrium (HWE), using population inbreeding coefficients (F_{IS}) using FSTAT 2.9.3 [23], where $F_{IS} > 0$ indicates greater inbreeding than expected under HWE and $F_{IS} < 0$ indicates greater heterozygosity than expected [2].

To calculate the effective number of breeders within each studied population, we estimated N_e using the linkage disequilibrium (LD) method in LDNe [24]. We report analysis results after excluding alleles with frequency < 0.02 (as suggested by Waples and Do [12]) and with 95% confidence intervals derived from a jackknife approach. Additionally, N_e was used to provide a quantitative, non-landscape factor that may affect patterns of genetic differentiation among populations. We constructed a population pairwise matrix of the harmonic mean of N_e between each population pair.

Finally, herds were assessed for genetic effects of rapid reduction in population size using the program BOTTLENECK [25]. A two-phase model of mutation (TPM) was assumed with multistep mutations accounting for 5%, 10% and 20% of all mutations. We used the Wilcoxon signed rank test, which is suggested to provide the most robust statistical results for tests of bottlenecks for datasets with fewer than 20 loci [25].

Landscape resistance for caribou

We considered four landscape variables to be potentially biologically important in determining gene flow between caribou populations. These include a combination of ecological and anthropogenic factors that are explained below.

Habitat loss and fragmentation has been cited as one key driver in caribou population declines [17]. We used a resource selection function (figure 2A, RSF; [10]) model that included multiple topographic (elevation, slope, aspect, topographic position, distance to water), climatic (percent snow cover, distance to tree line) and vegetative (land cover type and normalized difference vegetation index) variables that are recognized as important predictors of caribou habitat suitability [15,16]. DeCesare et al. [10] estimated an RSF for the same caribou populations as considered here, including a "baseline" RSF that excluded anthropogenic effects. For this analysis, we spatially applied the baseline RSF to our study area to estimate preferred habitat under "pristine" conditions, that is, the resistance imposed by natural landscape heterogeneity alone (i.e. all contemporary human features removed; figure 2A).

Caribou use a strategy of spatial separation from wolves (*Canis lupus*) as a mechanism to avoid predation [26]. As such, we assessed the potential role of predation as a driver of landscape

resistance using a previously developed spatial model of predation risk that integrated both the probabilities of encountering and being killed by wolves within our study area (figure 2C; [27]). Similar to our treatment of preferred habitat availability, we excluded the effects (coefficients) of anthropogenic features when applying the predation risk model to our study area to characterize predation-based resistance due to baseline natural conditions alone. Additionally, we treated three types of anthropogenic footprints (figure 2B), each as potential sources of landscape resistance, including: forestry cut-blocks, roads, and other non-road linear features (seismic lines and maintained hiking trails).

Finally, we evaluated the null hypothesis of a completely homogenous landscape of resistance by assessing the role genetic drift, via geographic distance alone, in isolation-by-distance analysis (IBD). It is important to note that while IBD is a common null model in landscape genetics studies that addresses one source of genetic drift, it does not account for the potential influence of genetic drift via demographic episodes of bottlenecking or founder events that are specifically related to population size.

To determine if landscape resistance has influenced past gene flow, and thus genetic differentiation among population pairs, we calculated accumulative cost distance of least-cost paths (LCP) between all pairwise population combinations for each hypothesized landscape resistance surface (figure 3). LCPs are modifications of geographic distances that reflect the hypothetical effects of landscape characteristics on promoting or impeding movement along a single pathway [28]. These movements represent dispersal, and so by comparing genetic divergence among individuals between cost distances, we can test hypotheses on the effects of landscape features and other environmental variables on gene flow [7]. The details of the LCP simulations and modeling are available in APPENDIX D.

Landscape genetic analyses

To evaluate caribou connectivity in this framework, we used simple and partial Mantel tests [29,30] to calculate the correlation between genetic distances and geographic distance, landscape resistance distances and harmonic means of N_e. A review of the literature shows a recent emergence of diverse and computationally complex methodologies offered for landscape genetics analysis (reviewed in Balkenhol et al. [31]). However, the utility of these new analytical techniques remains unclear until further simulation studies can standardize their application. We used Mantel tests because they are easy to interpret, are widely used, retain a high level of power that is demonstrated to be appropriate for distance data [32,33] and are shown to correctly identify drivers of genetic diversity [34]. The statistical software package XLSTAT v. 2012.1.01 was used to perform all simple Mantel and partial Mantel tests to calculate Mantel's *r*. Significance of Pearson product-moment correlations was assessed using 10,000 permutations of the data. We used the Monte Carlo *p*-value to determine significant correlations.

We first tested for a pattern of IBD where genetic differentiation is predicted to increase with geographic distance as expected under mutation/migration/drift equilibrium [35]. We then tested for patterns of resistance for each of the landscape variables from the pairwise LCP analyses. Finally, we calculated partial Mantel's *r* between genetic distances and landscape resistance distances after accounting for the effects of geographic distance (IBD) and the effects of N_e. This correlation provides a measurement of the strength of the environmental relationships after removing the influence of pure geographic distance and effective population size.

Results

Genetic Analysis

F_{ST} and D_c population pairwise genetic distances ranged from 0.021 to 0.213 and 0.227 to 0.603, respectively (table 1, APPENDIX D). As would be predicted, F_{ST} and D_c were highly correlated ($r = 0.849$, $p < 0.0001$). F_{IS} results (table 1) show a large negative value for BNP, which indicates an excess of heterozygosity. Most other populations trended towards heterozygosity expected under random mating.

Estimates of effective population size, N_e, were unclear in two herds (BNP and MAL) as 95% confidence intervals included infinity. These results are likely due to the small sample sizes of these herds (table 1). In order to obtain values for constructing the pairwise matrix of effective population size, we considered the results of the similarly sized population of BRZ, calculated the ratio of individuals estimated as effectively reproducing over the census population (N_e/N_c) and made the assumption that BNP and MAL had a similar ratio and from that calculated an N_e to use in the pairwise comparison matrix. For all other populations, the general trend showed that N_e was always lower than N_c, and usually N_c was not included within the 95% N_e confidence intervals (table 1).

After correction for multiple comparisons (strict Bonferroni), significant excess heterozygosity (one-tailed Wilcoxon test for H excess) at TPM of 20% was detected in RPC and BNP herds. As the TPM converged towards a purely Stepwise Mutation Model (TPM of 10% and 5%), only BNP continued to show significant heterozygosity excess ($p < 0.003$) expected under bottleneck scenarios.

Landscape Analysis

In the simple Mantel tests, all variables had positive significant correlations with both F_{ST} and D_c (table 2), except N_e, which was negatively correlated. Correlations were stronger (Mantel's r) in tests using D_c over F_{ST}. Although there was a significant pattern of isolation-by-distance (i.e. a correlation between genetic and geographic distances; figure 4), the strongest correlation for both F_{ST} and D_c was with the resistant distances based on the RSF ($r = 0.856$ and 0.900, respectively, and $p < 0.0001$ for both; table 2, figure 4). Effective population size (N_e, table 2) had second highest correlations with genetic distances ($r = -0.627$, $p < 0.0001$, and -0.767, $p < 0.0001$, respectively; figure 4).

Partial Mantel tests that controlled for the effect of geographic distance (GEO) gave different results (table 2). Again, in all correlations, the Mantel r values were greater in tests using D_c than F_{ST}. After accounting for geographic distance, only the RSF-calculated distances and pairwise harmonic means of N_e remained significant. Although the correlation with RSF decreased slightly for both genetic metrics, the correlation with N_e increased, and surpassed the RSF, for D_c.

In analyses that controlled for the effect of N_e, partial Mantel r values for all variables were significant. The r values decreased for F_{ST} and increased for D_c, except for RSF, which decreased for both genetic metrics (table 2). Nonetheless, the best correlation was consistently the RSF.

Finally, given the predominant relationship of genetic distance to the RSF distance matrix, we performed *ad-hoc* partial Mantel tests on all variables, this time partialing out the variability explained by the RSF (table 2). In this case, the only variable significantly correlated was effective population size (N_e) with D_c ($r = -0.596$, $p = 0.0003$; table 2). Therefore, preferred

habitat and effective population size were consistently the most important drivers of connectivity.

Discussion

Our study is one of the first to assess the impact of effective population size (N_e) in a landscape genetics framework. We found that after accounting for geographic distance preferred habitat availability (figure 3, RSF) and N_e were the most significant explanatory variables in determining genetic distances between herds (table 2). This pattern was further supported when we controlled for RSF based resistance and the partial Mantel r-values approached zero for most landscape variables (table 2), indicating, with one exception (N_e), that no other variables explained genetic variability after accounting for preferred habitat availability. RSF models have only recently begun to be applied in landscape genetics, but are already demonstrating superior results to traditional landscape models (e.g. [9]).

After accounting for the effects of geographic distance, only the RSF and N_e were significant in explaining the variability among genetic relationships in both F_{ST} (RSF was best followed by N_e) and D_c (N_e was best, followed by RSF; table 2). Similarly, in tests controlling for the variability explained by the RSF, only N_e (as measured by D_c) was a significant explanatory variable. Interestingly, after controlling for N_e, the genetic distance correlations with the anthropogenic variables increased for D_c (table 2). This effectively reveals the relentless effect of random genetic drift that, in conjunction with other dominant landscape features, affects the genetic relationships among populations. The interactive effects of drift and habitat fragmentation likely result in even stronger landscape fragmentation effects in small populations

where drift is strongest; a detail that cannot be ignored in the precariously small populations that typify many endangered species [1].

The use of parameters related to population size have largely been absent from landscape genetics projects. However, ecological research on caribou found that censused population size was one of the key variables explaining genetic relationships [36,37], but did not explicitly test for landscape resistance at the same time. In arctic char, Wollebæk et al. [38] found genetically-assessed N_e to be the major cause of contemporary population differentiation. Thus, the effects of genetic drift due to small populations, rather than by geographic distance (i.e. IBD), can be a major explanatory variable of population genetic relationships, and in some cases this may obfuscate the strength of relationships between genetic structure and landscape variables. This emphasizes that landscape genetics studies conducted without accounting for the effects of N are likely erroneous and could result in misleading conservation recommendations.

In our study, ratios of effective population size (N_e) and census population size (N_c) varied from 0.16 to 0.48 (table 1) and were higher at lower census size, which has been suggested to indicate an intrapopulation mechanism of increased individual reproductive success at low breeding densities that can 'compensate' and buffer against the genetic consequences of low N_e [11]. The 50/500 rule often cited by conservation practitioners [39] postulates that a minimum of $N_e = 50$ is necessary to prevent a damaging rate of inbreeding in the short term, but that an N_e of 500-1000 is required for long term genetic integrity [40]. Our figures of N_e were therefore concerning. Results from assignment tests [41] provide evidence of recent historical metapopulations in these caribou, a pattern that is also supported at the continental scale [18]. It is likely these same metapopulation dynamics that allowed for the maintenance of genetic diversity through gene flow among demographically viable populations across unfragmented

habitats. Given the persistently small populations sizes for these caribou, management strategies to protect them should emphasize fostering connectivity among caribou herds [18,41] and rebuilding past metapopulation relationships.

The model of isolation by distance (IBD) was significant (table 2), indicating that pairwise genetic distance was highly correlated to geographic distances between populations. Interestingly, in partial Mantel tests that controlled for N_e the relationship between genetic distance and geographic distance increases, and vice versa (table 2). This elegantly reveals the antagonizing relationship between drift and gene flow, a tug-of-war which is often theorized [14,39], but difficult to demonstrate in nature [1].

Despite the documented decline in population sizes for all caribou populations [19], tests for excess heterozygosity, as an indicator of recent bottlenecks, was detected consistently only for the Banff (BNP) population, and is corroborated by a negative F_{IS} value that is also indicative of heterozygosity excess (table 1;[2]). The Brazeau (BRZ) and Maligne (MAL) populations were of similar size, but there is some evidence that these two herds have recently exchanged migrants, which would effectively buffer them from the potential impacts of a population reduction [13], and explain non-significant heterozygosity excess. The Banff population suffered local extinction from an avalanche in 2009 [5]. Barring an increase in population size, both BRZ and MAL are at immediate risk of similar stochastic extinction [42].

Predation by wolves has been noted as the most important proximate threat to the persistence of threatened caribou populations [43]. Caribou natural history characteristics describe anti-predation behaviour through geographic spatial separation [26, Latham et al. 2011]. As such, a historic pattern of avoiding specific regions that provide good habitat for wolves could provide a natural barrier to gene flow. However, in our study the correlation of predation

risk to genetic distances was highly auto-correlated with geographic distance (table 2). Thus, predation by wolves may be too ephemeral to become a permanent landscape barrier that would influence gene flow. Alternatively, our model of predation risk may reflect wolf occurrence on a human manipulated landscape that is too recent to show up in genetic signatures. Anthropogenic barriers are frequently cited as major concerns for connectivity of fragmented populations [1,6]. With caribou, human-mediated landscape changes are predicted to be a major influence on population structure [43], particularly in Alberta [19]. However, similar to wolf predation in our study, after accounting for geographic distance, the relationship between anthropogenic features and genetic distance mostly disappeared (partial Mantel tests, table 2). The lack of a strong relationship independent of geographic distance may be due to the time lag of a genetic response to the anthropogenic features [44, Anderson et al. 2010]. In caribou, a detectable numerical response to human land use changes have been documented to take several decades [45] and the potential negative impacts of anthropogenic features, even at the low density revealed here, cannot be dismissed.

The implications for endangered species such as woodland caribou are twofold; 1) in the threatened populations analyzed here, modern anthropogenic features do not appear to yet have significant impacts on gene flow by themselves, but have been shown to reduce population size [36], thus leading to increased drift; 2) conservation efforts should focus on preserving preferred caribou habitat to maintain the natural pattern of landscape resistance in caribou metapopulation dynamics.

Conclusions

Promoting connectivity among populations of threatened species in heterogeneous landscapes impacted by human disturbance is further complicated by the fact that most species already exist within discontinuous mosaics of preferred habitat [1,9,36]. Here we demonstrate that the greatest predictor of genetic connectivity in caribou of west-central Alberta is preferred habitat availability. The distribution of preferred habitat demonstrated in figure 2A and the associated resistance surface of that habitat (figure 3) exhibit the classic matrix of suitable habitat interwoven within a matrix of unsuitable space on which we would expect metapopulation dynamics to operate [46].

Metapopulation theory dictates that throughout the metapopulation, localized extinctions take place at the population level, only to be recolonized in the future. A reduction in connectivity (e.g. by habitat destruction or landscape barriers) lowers per patch immigration rate, thus inhibiting the rescue effect [46] and resulting in declines in abundance and occupancy of remaining patches [47,48]. For caribou, telemetry data (for females) indicated little movement between populations [36,41], suggesting a breakdown in such metapopulation dynamics. The Banff population illustrates the danger of decoupling metapopulation dynamics, as exemplified by its persistent isolation for decades with no new migrants, which ultimately resulted in stochastic localized extinction [5] and loss of that patch's genetic contribution to the metapopulation. Our results therefore emphasize the importance of habitat within and between population ranges for the viability of the metapopulation and its discrete elements.

The correlation that we found between genetic differentiation and low population numbers provides an empirical link between habitat loss and fragmentation [1,6]. The failure of demographic rescue in local populations points to lack of preferred habitat between populations and to a paucity of effective migrants, which in turn may be due to a synergistic relationship

between declining caribou numbers and population density-dependent dispersal behaviour [36].

Little is known about the dispersal patterns of male caribou, but the lack of female dispersal in

caribou is directly correlated with small isolated subpopulations throughout the Canadian

Rockies [36,41]. In our study, after preferred habitat, the second variable that best explained

levels of gene flow was effective population size (table 2), and if drift (from both small

population size and geographic distance) continues in these declining and isolated populations,

barring any demographic rescue, we would predict that N_e will ultimately explain most of the

variability.

Population size, and in particular effective population size, is an important variable that

tends to be neglected in most landscape genetic studies [49]. Genetic drift due to small, isolated

populations can lead to spatial structuring in markers such as microsatellites that are frequently

used in landscape genetic research. A failure to account for multiple components of genetic drift

(i.e. other than IBD) may lead to erroneous inferences of population structure strictly based on

landscape features and, as a result, will fail to pinpoint crucial demographic processes important

to conservation.

Acknowledgments

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