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Demographic responses of boreal caribou to cumulative disturbances highlight elasticity of range-specific tolerance thresholds

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Abstract Conserving species-at-risk requires quantifiable knowledge of the key drivers of population change. Non-linear demographic responses to habitat loss have been documented for many species and may serve to establish quantitative habitat thresholds for management purposes. In Canada, boreal populations of woodland caribou are considered threatened; Environment Canada's empirical model of calf recruitment–range disturbance suggests that at least 65% undisturbed habitat is required to ensure viability. We tested the relationship upon which this conservation guideline is based by pairing demographic estimates with range conditions over a 10-year period for three boreal caribou populations. Our objectives were (1) to evaluate evidence of intra-population demographic responses to fluctuations in range quality over time; (2) to evaluate inter-population differences in

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demographic responses to cumulative range disturbances; and (3) to evaluate the sensitivity of disturbance tolerance thresholds to variation in local population demography. We found strong evidence in support of the disturbance–recruitment relationship for withinpopulation responses over time ($R^2 = 0.77$). Mixed effects logistic regression modeling revealed variations in local population responses to cumulative habitat depletion. Rangespecific disturbance thresholds derived from Monte Carlo simulations were highly elastic in response to observed variation in local population demography, suggesting that 65% undisturbed habitat is insufficient when adult female survival and/or sex ratio is suboptimal. Study populations were determined to be not self-sustaining ($Pr(\lambda \ge 0.99) =$ 37-47%). Adult survival was comparable to estimates reported elsewhere despite Aboriginal harvesting for subsistence purposes. Results underscored potential trade-offs between forest harvesting and wildlife habitat conservation. Protection and restoration of sufficient quantities of undisturbed habitat, particularly via road reclamation, is essential for caribou population recovery.

Keywords Boreal caribou · Canadian boreal forest · Cumulative disturbances · Demographic modeling · Disturbance thresholds · Long-term monitoring

Introduction

Conserving species-at-risk on managed landscapes is one of the most important challenges facing decision makers today. The task is especially difficult for species with large home range requirements because it calls for effective cooperation between multiple jurisdictions, and may require concerted approval by various stakeholders (Festa-Bianchet et al. 2011). In practice, the cumulative effects of disparate resource development activities (e.g. mining, forestry, agriculture, settlement) are seldom mitigated at the landscape scale, and the progressive habitat loss this engenders can lead to population decline or extirpation in wide-ranging species (Laliberte and Ripple 2004).

In the eastern boreal region of North America, large-scale industrial forestry has led to the rarefaction of old forests, such that present-day landscapes fall well outside the historic range of natural variation with respect to forest age and composition (Cyr et al. 2009). The consequent widespread decline of species associated with old boreal forests is well documented (e.g. Drapeau et al. 2016). Over the last century, for example, the semi-continuous range of boreal populations of woodland caribou (*Rangifer tarandus caribou*; hereafter "caribou") has receded in a way that roughly mirrors the northward expansion of human settlement and development (Schaefer 2003; Vors et al. 2007; Festa-Bianchet et al. 2011). Caribou require large tracts of mature undisturbed coniferous forest to facilitate their antipredator spacing-out strategy (Lesmerises et al. 2013). Proliferation of early seral habitats

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on the landscape has led to increased abundances of other cervids [e.g. moose (*Alces americanus*), white-tailed deer (*Odocoileus virginianus*)] and their predators [e.g. wolves (*Canis lupus*), black bears (*Ursus americanus*)] to the detriment of caribou (Seip 1992; Wittmer et al. 2007). This tendency is accelerated by the relentless expansion of roads and other linear networks (e.g. hydroelectric, oil and gas), which generate indirect habitat loss (Polfus et al. 2011). Moreover, roads are known to facilitate predator movement (Lesmerises et al. 2012), increase predator–prey encounters (Whittington et al. 2011) and impact calf (Dussault et al. 2012) and adult survival (Leblond et al. 2013). Similarly, caribou mortality tends to increase in proximity to cutblocks, both for calves (Leclerc et al. 2014) and adults (Losier et al. 2015).

Despite such mounting knowledge on the mechanism behind caribou declines, only in recent years have recovery strategies for boreal caribou identified quantitative habitat objectives offering a measurable likelihood of success. Sorensen et al. (2008) provided first correlative evidence linking functional habitat loss in caribou ranges to the rate of population change. Notably, Environment Canada elaborated a risk assessment framework based on evidence of an empirical relationship between calf recruitment and cumulative range disturbance derived from a set of 24 populations of boreal caribou across Canada (Environment Canada 2008, 2011). Parameters from this disturbance–recruitment model informed the subsequent adoption of a 35% maximum disturbance threshold in the federal recovery strategy (Environment Canada 2012), a target estimated to afford a 60% probability of a self-sustaining population. In practice, however, many caribou populations exhibit vital rates diverging from the average conditions upon which this benchmark is based. Environment Canada (2011) thus recommends additional lines of evidence to support the refinement of range-specific management targets.

The disturbance-recruitment model was derived from multiple populations observed at a fixed point in time across a broad geographical extent. The implicit suggestion that a single population will respond to variation in habitat supply over time according to model predictions has heretofore never been tested. We combined 10 years of land cover data with rangespecific demographic parameters to assess relationships between disturbance and recruitment in three boreal caribou populations previously uncharacterized by Environment Canada (2011) in the managed boreal forest of Northern Québec. We tested whether recruitment rates varied over time in response to changes in undisturbed habitat supply as predicted by the disturbance-recruitment model. We thereby evaluated inter-population differences in demographic responses to cumulative range disturbances in a region extensively transformed by timber harvesting. We hypothesized that distinct range-specific disturbance-recruitment relationships could be detected through long-term monitoring of range conditions and population dynamics. Given that local environmental conditions may shape behavioural adaptations potentially influencing calf survival at a finer scale (for example through calving site selection by females; Faille et al. 2010), we also expected some degree of inter-population variation in demographic tolerance to disturbances. Lastly, we examined the sensitivity of disturbance tolerance thresholds to variation in local population demography. Specifically, we derived range conditions theoretically necessary to support self-sustaining populations when adult survival and/or sex ratio deviated from expected values. We then used empirical data to estimate range-specific tolerance thresholds for caribou populations of Northern Quebec, including and excluding mortalities attributed to Cree Aboriginal subsistence hunting. We expected disturbance tolerance thresholds to be volatile to variation in underlying demographic parameters and predicted that recruitment levels correlated with 65% undisturbed habitat would be insufficient to maintain self-sustaining populations when determinant parameters were suboptimal.

Methods

Ethics statement

Boreal caribou is recognized as threatened in Canada (Environment Canada 2011), a status conveying urgency to more clearly understand the mechanisms linking anthropogenic disturbances to the species' decline. Between 2004 and 2013, 61 female caribou were captured, collared and released by the Ministère des Forêts, de la Faune et des Parcs du Québec (hereafter MFFP). Field procedures were carried out in strict accordance with the recommendations of the Canadian Council on Animal Care, and both captures and manipulations of study animals were approved by the Animal Welfare Committee of the MFFP (certificates # CPA-04-005, 06-00-27, 07-00-04, 2011-03, 2012-03).

Study area

This study is situated within the coniferous boreal forest of Northwestern Québec, Canada (49°–52°N, 70°–80°W; Fig. 1), on the territory subject to the Paix des Braves Agreement (Gouvernement du Québec and Crees of Québec 2002). The agreement ushered in a new forestry regime designed to mitigate impacts on traditional fur harvesting activities via minimum forest retention guidelines within individual trap lines (\sim 270–1700 km²). Small



Fig. 1 Location of the study area in the boreal forest of Northwest Quebec. Shown are the range contours of the three principal woodland caribou populations (Nottaway, Assinica and Témiscamie) forming the Jamésie metapopulation as determined by fuzzy clustering and kernel density estimation using GPS telemetry data (n = 55). Also depicted are natural (≤ 40 years) and anthropogenic (≤ 50 years) disturbances (with 500-m buffer) as of 2013

cutovers (1–150 ha) are spaced at least 200 m apart and separated by retention blocks roughly equal in size that may be harvested once cutovers reach 7 m in height. While beneficial to moose populations (Jacqmain et al. 2008), within a decade this form of dispersed clearcutting has produced a mosaic (checkerboard) of cutover patches across the landscape, generating a continuously expanding road network (St-Laurent et al. 2007). Sport hunting of forest-dwelling caribou is prohibited in Québec since 2001. Despite encouraging a voluntary moratorium on woodland caribou harvesting, the Cree Nation retains its right to hunt for subsistence purposes.

Black spruce (*Picea mariana*) is the dominant tree species in the study area. Jack pine (Pinus banksiana) and balsam fir (Abies balsamea) occur to a lesser extent, in addition to trembling aspen (Populus tremuloides), paper birch (Betula papyrifera), tamarack (Larix *laricina*), and (rarely) balsam poplar (*Populus balsamifera*). Forest understory is dominated by feathermosses and ericaceous shrubs with few herbaceous species. The western part of the region is dominated by large sphagnum bog and fen complexes. Terrain is broad and mildly sloping with occasional topographic relief (45-825 m AMSL). Treed wetlands and upland forest intersperse with bog/fen complexes and lichen or shrub-dominated uplands. The region receives approximately 960 mm of precipitation annually with monthly average temperatures ranging from -19° (January) to $+16^{\circ}$ (July) Celsius. Primary disturbance agents include forest harvesting and fire (mean fire cycle highly heterogeneous in the study area, ranging from 44 years in the north (~52°N) to 712 years in the south (~49°N); Gauthier et al. 2015). Other large mammal species include moose, wolf and black bear. Three subpopulations of caribou inhabit the region, known (from west to east) as the Nottaway, Assinica and Témiscamie local populations (Rudolph et al. 2012; Fig. 1). Caribou densities are estimated to range between 1.5 and $3.5/100 \text{ km}^2$ (Dussault and Gravel 2008; Brodeur et al. 2013; MFFP, unpublished data), with individuals occupying average annual home ranges of 2796 \pm 255 (SE) km² (Bastille-Rousseau et al. 2012).

Demographic survey methodology and data treatment

Sixty-one adult female caribou were monitored from March 2004 to May 2013 (23–31 per year) using GPS collars (Lotek models 2200L and 3300L, Telonics TGW-4680, Vectronic GPSPlus). Individuals were captured and recaptured periodically to retrieve data and change collars, and collars were recovered upon failure or death of an individual. Collars were programmed to acquire locations every 7 h. Monitoring periods varied, resulting in uneven numbers of GPS locations between individuals. The telemetry survey was based on females only due to their strong association with calves, which constitute the most vulnerable portion of the population, making them strongly linked to population dynamics (Leclerc et al. 2014). We used GPS telemetry data to assign individual population identities, estimate local population ranges, and estimate adult female survival. Imprecise fixes (3-D/HDOP > 25; 2-D/HDOP > 8) were filtered out (Dussault et al. 2001). Inspection of caribou distributions revealed several outliers consisting of individuals dispersing far beyond the more-or-less clustered ranges of the populations. Because this behaviour was considered atypical of the boreal caribou, these individuals (n = 6) were removed from the dataset prior to further analysis.

To estimate demographic parameters, we used both GPS telemetry and field data collected by the MFFP between 2002 and 2013 during spring aerial surveys (inventories or composition surveys) (Courtois et al. 2003). Inventories consisted of systematic transects of the territory by fixed-wing aircraft (phase 1) followed by targeted classification of caribou sub-groups by helicopter (phase 2); these took place between January and April of 2002, 2003 and 2013 within varying portions of the Nottaway, Assinica and Témiscamie ranges (Fig. 1). Most frequently conducted were composition surveys (Table 1), analogous in approach to phase 2 except that individuals were principally localized via GPS collar tracking. In both circumstances, the number of males, females and calves in each group were counted. Yearlings (>1.5 years old) were classified as adults since they are expected to reproduce in the coming fall. Females were identified by the presence of a vulval patch and age was ascertained from morphological traits (e.g. coat texture, leg and muzzle length, chest circumference, presence and size of antlers). We presumed that all calves observed during aerial surveys ($\sim 7-11$ months old) survived the winter. Counting and sightability bias were unlikely as groups were sufficiently small in number (11.1 ± 10.8) (SD)) and logistically manageable given relatively flat terrain and the prevalence of open forest stands, barrens and water bodies in our study area.

Population delineation

The local population has been identified as the appropriate ecological unit for conservation and management of wild ungulates (Gaillard et al. 2000), an approach also adopted for woodland caribou (Environment Canada 2011). Local populations are demographically distinct from one another as determined by immigration and emigration rates. Dispersal rates <10% may provide evidence for local population distinction (Environment Canada 2011). Boreal caribou of Northern Québec are considered a metapopulation within which some degree of interchange takes place between individuals of neighbouring populations (Rudolph et al. 2012). The Nottaway, Assinica and Temiscamie populations comprise an important linkage between other populations found in south-central Québec and those in northern Ontario. We used c-means fuzzy clustering of kernel-weighted centroids, one per collared animal (n = 55), in order to assess the statistical evidence for identifying more

Table 1 Origin of demographicestimates obtained between 2002	Population	Year	Survey type	No. of females	No. of calves
and 2013 for three boreal caribou	Nottaway	2003	Inventory	62 ^a	18
populations of Normerin Quebee	Nottaway	2007	Composition	30	8
	Nottaway	2009	Composition	16	2
	Nottaway	2011	Composition	7	2
	Assinica	2003	Inventory	124 ^a	47
	Assinica	2007	Composition	48	15
	Assinica	2009	Composition	47	13
	Assinica	2010	Composition	97	17
	Assinica	2011	Composition	100	19
Survey types are described in	Assinica	2012	Composition	46	11
methodology and data treatment'	Assinica	2013	Inventory	268	77
^a To correct for a large number	Témiscamie	2002	Inventory	37	19
of unclassified animals (i.e. male	Témiscamie	2007	Composition	37	12
vs. female; $n = 55$), these	Témiscamie	2009	Composition	20	5
adjusted assuming bull cow	Témiscamie	2010	Composition	12	3
ratios observed during the	Témiscamie	2011	Composition	54	11
exhaustive 2013 inventory of the Assinica population	Témiscamie	2012	Composition	17	0

than one local caribou population (Schaefer and Wilson 2002). Assuming no inherent structure, we determined the optimal number of local populations by maximizing Dunn's (normalized) coefficient. Individuals were assigned so as to maximize individual membership coefficients.

Due to temporal variation in range occupancy, accurate representations of population distributions likely require \geq 7 years of high quality monitoring data (Environment Canada 2011; Rasiulis et al. 2012). Using GPS telemetry data collected between 2004 and 2011, we defined population ranges by estimating non-parametric kernel density probability distributions. The plug-in method of bandwidth selection was used since it tends to outperform the reference and LSCV methods and produces relatively smooth outer contours useful for range delineation (Gitzen et al. 2006). Because sensitivity analyses demonstrated little relative difference in estimates of range disturbance as a function of varying confidence intervals, polygons delineating local population ranges were derived from the 100% probability contours of the kernel surface. All analyses were conducted using R version 2.15.2 (R Core Team 2012) and GRASS version 6.4.2 (GRASS Development Team 2012).

Spatiotemporal range disturbance mapping

We used 1:20,000 digital forest inventory maps produced by the MFFP to classify polygons into categories based on land cover type, stand age and origin. We updated these maps annually to include habitat modifications resulting from anthropogenic (i.e. cutblocks, roads, mining developments) and natural disturbances (i.e. fires, insect outbreaks, windthrow). Minimum mapping unit size was 4 ha for forested polygons and 2 ha for nonforested areas (e.g. water bodies). Polygons representing historic fires (≥ 0.1 ha) occurring north of the current limit of commercial forestry were obtained from the Canadian National Fire Database. A semi-exhaustive verification of polygon data was conducted in order to ensure that year of disturbance corroborated with evidence provided by satellite images. Attribute data was corrected and polygons and road segments were digitized or removed as appropriate to ensure consistency with satellite imagery from one year to the next.

In order to assess cumulative disturbance levels from 2002 to 2013, we created 11 binary raster surfaces (100-m resolution) representing the year-specific total combined footprint of both natural (\leq 40 years) and anthropogenic disturbances (\leq 50 years). In accordance with Environment Canada (2011), we added a 500-m buffer to all anthropogenic disturbances (i.e. cutovers, roads, mining) and report estimates of cumulative disturbance calculated from within the 100% probability contours of the weighted population kernels. Disturbed proportions were estimated using binary raster surfaces to avoid the confounding effect of overlapping polygons.

Demographic parameter estimation

Recruitment rate was calculated for each calendar year and population as the total number of calves per 100 adult females observed (Table 1). We retroactively adjusted 2003 estimates by assuming 62.7% of unclassified adults (n = 81) were females, a ratio obtained during a comprehensive aerial census of the Assinica population in 2013. All animals classified as adult females (>1.5 years old) were considered to be sexually mature. After Hatter and Bergerud (1991), we assumed an equal sex ratio in calves. Annual population recruitment (R) was calculated as:

$$\mathbf{R} = \mathbf{C}\mathbf{C}/(100 + \mathbf{B}\mathbf{C} + \mathbf{C}\mathbf{C})$$

where CC is the number of calves per 100 adult females and BC is the number of adult males per 100 females (Hatter and Bergerud 1991).

Using the known life histories of 61 collared caribou, adult female survival rate (ASR) was defined as the probability that an animal alive in year *t* would still be alive in year t + 1 (Heisey and Fuller 1985). Preliminary Mantel–Haenszel tests of Kaplan–Meier survival estimates revealed no significant differences between populations ($\chi^2_{(2, n=61)} = 2.4$, P = 0.296) or years ($\chi^2_{(7, n=61)} = 11.5$, P = 0.119). Adult survival was therefore estimated via random sampling with replacement (10,000 iterations) of pooled data (complete study period, populations combined):

$$ASR = ((no. animal days - no. deaths)/no. animal days)^{365.25}$$

The 95% confidence intervals were derived from the bootstrap sample population to obtain coefficients of variation for truncated data as per Environment Canada (2011). To examine the effect of subsistence hunting on adult survival, we estimated ASR under a hypothetical scenario in which no harvest occurred. We did so by right-censoring harvested individuals (n = 8) from the mortality count. Resulting bootstrap estimates informed the development of demographic scenarios used to determine range conditions theoretically able to support stable populations (see "Demographic modeling" section). The annual finite rate of change (λ) was calculated using the recruitment-mortality equation defined by Hatter and Bergerud (1991):

$$\lambda = (1 - \mathbf{M})/(1 - \mathbf{R})$$

where M is adult female mortality (or 1 - ASR) and R is population recruitment.

Demographic modeling

Testing the intra-population disturbance-recruitment model

The sampling design behind Environment Canada's disturbance-recruitment model can be viewed as a form of chronosequence (Foster and Tilman 2000), a spatial snapshot of complementary populations situated at different stages along a range disturbance gradient. We reasoned that the relationship of this 'inter-population' chronosequence model should be discernible within a single population given adequate variation in range conditions over time. Using a repeated measures design, we tested this hypothesis by evaluating the cumulative impact of additive forest management practices on our three regional caribou populations over a decade in terms of disturbance footprint and corresponding annual calf recruitment rates. This 'intra-population' disturbance-recruitment model assessed withinpopulation demographic responses to fluctuations in range quality over time via pairwise binomial logistic regression with mixed effects. Since sample size influences estimate precision, observations were weighted by the number of females contributing to individual estimates of annual recruitment rate (i.e. number of calves per 100 adult females). Furthermore, Poole et al. (2013) demonstrate that cow:calf and bull:cow ratios may be biased when heterogeneously distributed populations are incompletely surveyed. This weighting scheme had the additional benefit of according greater confidence to estimates derived from aerial censuses, which are comparatively more accurate.

The dataset used to produce Environment Canada's disturbance–recruitment model considered caribou of the James Bay region (Jamésie in their model) as a single population, whereas recent findings suggest it is more accurately considered a metapopulation constituting at least three distinct local populations (Rudolph et al. 2012). To better reflect this knowledge and thereby obtain improved parameters for predictive purposes, we replaced the Jamésie datum used by Environment Canada (2011, p. 250) with three new records corresponding to the Nottaway, Assinica and Témiscamie populations surveyed over a 10-year time period. We calculated mean recruitment rates for each population weighted by the number of adult females contributing to each annual estimate, and entered cumulative range disturbances as of 2013. Recruitment estimates were derived from the most recent years of data, spanning a maximum sampling interval of 5 years, as per Environment Canada (2008). With this newly modified dataset, we re-estimated the disturbance– recruitment model via simple linear regression. Adjusted model parameters served to identify range conditions predicting recruitment rates expected to maintain each population given vital rates observed.

Exploring range-specific disturbance tolerance thresholds

To remain stable, a population requires sufficient recruitment to compensate for mortalities over a given time period. A population exhibiting relatively high adult survival can tolerate relatively low recruitment levels until senescence of ageing cohorts sufficiently diminishes its reproductive capacity. On the contrary, one exhibiting relatively low adult survival requires comparatively greater recruitment in order to sustain itself. Similarly, birth rates depend on the relative abundance of sexually mature females in the population. When birth rate declines, juvenile survival must increase in order for a population to remain stable. On the contrary, high birth rates may compensate to some degree for lower recruitment.

The 65% minimum undisturbed habitat threshold adopted by Environment Canada correlates with a recruitment rate of approximately 29 calves/100 adult female caribou, which reportedly generates a 60% probability of a self-sustaining population when adult survival rate, sex ratio and variances are as expected based on values reported in the literature. Given these assumptions are not always met in real populations, we asked how the amount of undisturbed habitat required to sustain a population is influenced by changes in these underlying determinants of growth rate. To accomplish this we used Monte Carlo simulations to estimate the probability of a self-sustaining population [Pr($\lambda \ge 0.99$)] when adult survival (S), adult sex ratio (BC) and calf recruitment (CC) vary. For a given scenario, or set of demographic parameters, we iteratively resampled 10,000 times from separate normal distributions expressing variation around mean estimates referenced from empirical data. Finite annual rate of change (λ) was estimated for each unique combination of sampled parameters. Reported estimates (and associated SE) were equivalent to the mean (and SD) of each bootstrap sample population or demographic scenario.

To evaluate the sensitivity of disturbance tolerance thresholds to variation in vital rates, we combined simulation results with predictions generated by the updated disturbance–recruitment model to derive scenario-specific disturbance thresholds affording an equivalent 60% probability of population quasi-stability consistent with Environment Canada (2011). To accomplish this we modeled the relationship between $Pr(\lambda \ge 0.99)$ and a range

of recruitment rates associated with differing amounts of undisturbed habitat, keeping all other parameters equal for a given scenario. Our first set of scenarios examined the assumptions underlying the 65% undisturbed habitat threshold identified by Environment Canada. Relative to the baseline scenario, we independently varied adult survival rates and sex ratios according to 25th and 75th sample quantiles drawn from the literature (Environment Canada 2008, 2011). Our second set of scenarios leveraged empirical data from our study area to estimate $Pr(\lambda \ge 0.99)$ and disturbance tolerance thresholds for the Nottaway, Assinica and Témiscamie populations. Since recent estimates of adult sex ratio were unavailable for the Nottaway and Témiscamie populations, we substituted the national average (i.e. 64 adult males per 100 adult females). We then estimated the influence of subsistence hunting on these parameters by right-censoring harvested individuals from the adult survival rate.

Results

Range delineation and cumulative disturbance trajectories

C-means fuzzy clustering provided statistical evidence for the three distinct local populations depicted in Fig. 1 (Dunn's normalized coefficient = 0.4). The number of unique individuals per population was 11 (21.6%), 27 (52.9%) and 13 (25.5%) for the Nottaway, Assinica and Témiscamie populations, respectively. Kernel utilization distributions rendered local population ranges of 36,400 km² (Nottaway), 27,900 km² (Assinica) and 47,500 km² (Témiscamie) in size, with a 6200 km² area of overlap between the Nottaway and Assinica ranges.

Annual maps portraying the evolution of cumulative disturbances from 2002 to 2013 permitted us to quantify the deleterious impact of the adapted forestry regime, in addition to natural disturbances, on range conditions over time (Fig. 2). Despite the buffering effect of some post-fire habitat renewal in certain years, disturbance levels increased in a quasi-linear fashion over time (Fig. 2a). Annual rates of increase were substantially higher on average for the Assinica (+1.2%)/year) and Témiscamie (+1.3%)/year) ranges than for the Nottaway range (+0.3%)/year). The physical footprint produced by road network expansion and associated 500-m buffer was the main driver of range deterioration, accounting for 57.9% (Nottaway), 69.3% (Assinica) and 78.8% (Témiscamie) of total range disturbance (Fig. 2b). As of 2013, total disturbance levels within the 100% probability contours of local subpopulation ranges were 33.0% (Nottaway), 51.5% (Assinica) and 47.0% (Témiscamie) (Fig. 2a).

Demographic modeling

Despite considerable annual variation in our dependent variable, the intra-population disturbance-recruitment model produced evidence of a strong pairwise relationship between annual calf recruitment estimates and range condition over time (P < 0.01; $R^2 = 0.77$) (Fig. 3). This model fit our data better than the original and updated ('chronosequence') disturbance-recruitment models, both in terms of predictive power and residual variance (Table 2). However, given the specificity of the model and the limited range of predictor values observed within each population range, predictions obtained from the intra-population disturbance-recruitment model were overly optimistic at low



Fig. 2 Evolution of cumulative disturbances within the 100% kernel probability contours of the Nottaway, Assinica and Témiscamie populations over approximately a decade. **a** Total cumulative range disturbance (anthropogenic and natural) over time as per Environment Canada (2011). **b** Range disturbance levels strictly attributable to linear features (with 500-m buffer)

disturbance levels and overly pessimistic at high disturbance levels (Table 2). Differences between Environment Canada's original model parameters (df = 22) and those obtained from the updated version (df = 24) were minor, the updated model converging on a slightly lower intercept and slope.

Assuming mean vital rates (S, BC), 28.7 calves/100 females and 65% undisturbed habitat, our simulations generated a 52.8% probability of a self-sustaining population (Table 3). For comparison purposes, we subsequently considered 52.8% to be functionally equivalent to 60% sensu Environment Canada (2011). Adult female survival had the greatest impact on corresponding disturbance tolerance thresholds. When survival was high (S₇₅ = 0.92), considerably less habitat was theoretically required to maintain population quasi-stability (25.9%). In contrast, no amount of undisturbed habitat was sufficient to compensate for mortality when survival was low (S₂₅ = 0.78). Adult sex ratio had a similar effect, although to a lesser degree, generating disturbance tolerance thresholds



Fig. 3 Fitted curves of the intra-population disturbance–recruitment model as applied to recruitment rates and associated range disturbance levels observed over a decade among the three principal boreal caribou populations of the James Bay region of Northern Quebec. The model was derived using pairwise binomial logistic regression with random variation about the intercept for individual populations. Recruitment rates were weighted by the total number of females contributing to individual estimates

ranging from 28% (BC₂₅ = 81.4 males/100 females) to 40.3% (BC₇₅ = 49.8 males/100 females).

Empirical estimates of calf recruitment, adult survival and sex ratio from the James Bay region indicated that all three populations are declining (Table 3), with $Pr(\lambda \ge 0.99)$ ranging from 37% (Témiscamie) to 47% (Assinica). Differences in estimated population trend were largely attributed to variation in mean calf recruitment and associated sample deviations.

The amount of undisturbed habitat required to achieve $Pr(\lambda \ge 0.99) = 0.528$ was 61.5% (Assinica), 65.3% (Nottaway) and 66.8% (Témiscamie), centering closely upon the 65% federal benchmark (64.5% ± 2.7 (SD)). The primary difference in this case was the greater proportion of adult females observed in the Assinica population, whereas differences in threshold rates (e.g. minimum CC, % undisturbed habitat) between the Nottaway and Témiscamie populations were primarily attributed to different sample deviances.

Adult female survival for the James Bay Region (three local populations confounded) was 0.854 ± 0.11 (CV), slightly higher than the reported national average (0.852 ± 0.12 ; Environment Canada 2011) despite Aboriginal subsistence harvesting. Among confirmed causes of mortality (n = 23), predation accounted for 54.3% of adult deaths and subsistence hunting 22.9%.

Excluding hunting-related deaths increased adult survival rate to 0.885 ± 0.10 (Table 3), in which case $Pr(\lambda \ge 0.99)$ for the Assinica and Nottaway populations exceeded 52.8% and minimum undisturbed habitat requirements dropped to between 45.5% (Assinica) and 48.9% (Témiscamie). Mortality rates derived exclusively from the known fates of collared animals may underestimate the influence of subsistence harvesting given that collared individuals represent a relatively small portion of the population and in practice multiple animals are frequently harvested at one time.

Table 2 Comparison of three models lin	ıking disturbance	to demography as a	applied to three w	oodland caribou po	pulations of the James	Bay region	
Model	Population	Observed range disturbance (%)	Intercept $(y_0 \pm SE)$	Slope (1 \pm SE)	Predicted recruitment (calves/ 100♀)	Observed recruitment (calves/ 100♀)	Residual
(A) Inter-population chronosequence	Nottaway	33.07	44.27 ± 2.94	-0.43 ± 0.06	30.06	22.64	-7.42
model (Environment Canada 2011)	Assinica	51.46	44.27 ± 2.94	-0.43 ± 0.06	22.17	24.27	2.1
	Témiscamie	46.97	44.27 ± 2.94	-0.43 ± 0.06	24.09	18.45	-5.65
(B) Updated inter-population	Nottaway	33.07	43.50 ± 2.86	-0.42 ± 0.059	29.51	22.64	-6.87
chronosequence model	Assinica	51.46	43.50 ± 2.86	-0.42 ± 0.059	21.73	24.27	2.53
	Témiscamie	46.97	43.50 ± 2.86	-0.42 ± 0.059	23.63	18.45	-5.19
(C) Intra-population time-series model	Nottaway	33.07	$0.766 \pm 0.73^{\rm a}$	-0.06 ± 0.017^{a}	24.83	22.64	-2.24
	Assinica	51.46	$1.719 \pm 0.73^{\rm a}$	-0.06 ± 0.017^{a}	24.81	24.27	-0.54
	Témiscamie	46.97	$1.352 \pm 0.73^{\rm a}$	$-0.06\pm0.017^{\mathrm{a}}$	23.88	18.45	-5.45
(A) Environment Canada's disturbance population disturbance-recruitment model inhabiting Northern Québec. Shown are - predicted and observed mean recruitment ^a Parameters of model (C) are interpretec	eccruitment mode 1 with a random i observed range o : rates (expressed d on the logarith	el (2011), (B) an ur intercept for each po fisturbance levels (9 l as the number of c mic scale	pulation of pulation (Nottawa %) as of 2013 aloo alves per 100 adu	model (A) integra y, Assinica and Té ng with the interce It females) and ass	ting new data from ou miscamie) comprising i pts and slopes of each ociated residual varian	r study region, and (C the boreal caribou meta i fitted relationship as v ces) an intra- population well as the

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Table 3 Influ (S \pm coefficie. of a self-sustai	tence of variation nt of variation, here ining population [P	in demographic part eafter CV), and sex ra $r(\lambda \ge 0.99)$], minimu	ameters [recruiti tio (BC), express am recruitment r	nent ratu sed as the ates (in e	e (CC \pm CV), e number of adul calves per 100 a	expressed as the numbe the males per 100 adult fen dult females) and minim	rr of calves per 100 nales] on finite annua num undisturbed hab	0 adult females, al rate of change itat requirements	adult survival (λ), probability (in %)
Population	Scenario	Recruitment rate (CC \pm CV) (calves/100 $^{\circ}$)	Adult survival $(S \pm CV)$	Sex- ratio (BC)	Finite rate of change $(\lambda \pm SE)$	Probability of self- sustaining population $Pr(\lambda \ge 0.99)$	Minimum recruitment rate (calves/100?)	Minimum undisturbed habitat (%)	Disturbance tolerance threshold (%)
Hypothetical	High adult survival (75th percentile)	28.7 ± 0.25	0.921 ± 0.12	0.64	1.061 ± 0.11	0.745	12.2	25.9	74.1
Hypothetical	High % adult females (75th percentile)	28.7 ± 0.25	0.852 ± 0.12	0.50	1.009 ± 0.12	0.567	26.4	59.7	40.3
Multiple boreal	Average baseline conditions	28.7 ± 0.25	0.852 ± 0.12	0.64	0.997 ± 0.12	0.528	28.7	65.0	35.0
Hypothetical	Low % adult females (25th percentile)	28.7 ± 0.25	0.852 ± 0.12	0.81	0.984 ± 0.11	0.484	31.7	72.0	28.0
Hypothetical	Low adult survival (25th percentile)	28.7 ± 0.25	0.783 ± 0.12	0.64	0.920 ± 0.12	0.283	49.4	>100	0
Assinica		24.3 ± 0.21	0.854 ± 0.11	0.59	0.980 ± 0.11	0.474	27.2	61.5	38.5
Nottaway	Best empirical estimates	22.6 ± 0.39	0.854 ± 0.11	0.64	0.968 ± 0.11	0.426	28.8	65.3	34.7
Temiscamie		18.4 ± 0.65	0.854 ± 0.11	0.64	0.949 ± 0.12	0.369	29.4	66.8	33.2
Assinica		24.3 ± 0.21	0.885 ± 0.10	0.59	1.015 ± 0.10	0.599	20.4	45.5	54.5

Table 3 cont	inued								
Population	Scenario	Recruitment rate (CC \pm CV) (calves/100 \bigcirc)	Adult survival $(S \pm CV)$	Sex- ratio (BC)	Finite rate of change $(\lambda \pm SE)$	Probability of self- sustaining population $Pr(\lambda \ge 0.99)$	Minimum recruitment rate (calves/100 ²)	Minimum undisturbed habitat (%)	Disturbance tolerance threshold (%)
Nottaway	Hunting mortalities excluded	22.6 ± 0.39	0.885 ± 0.10	0.64	1.003 ± 0.10	0.551	21.3	47.4	52.6
Témiscamie		18.4 ± 0.65	0.885 ± 0.10	0.64	0.982 ± 0.11	0.480	21.9	48.9	51.1
The latter two baseline cond: vary proportio	o estimates were d itions, S is the most mally to S and BC	lerived by solving for I st influential determinan . Empirical estimates fr	$Pr(\lambda \ge 0.99) = ($ int of $Pr(\lambda \ge 0.99$ from the James Ba).528. As () follow ty region	s evidenced by h ed by BC. CC als indicate populat	ypothetical scenarios in so strongly influences esti tions are declining and ge	which determinant p mates of lambda (λ) , nerate minimum und	arameters deviat and minimum re listurbed habitat	e from average scruitment rates requirements of

vary proportionally to S and BC. Empirical estimates from the James Bay region indicate populations are declining and generate minimum undisturbed habitat requirements of $\sim 65\%$. These requirements theoretically decrease to $\sim 47\%$ in the absence of subsistence harvesting. Differences in threshold rates (minimum CC, % undisturbed habitat requirements of disturbance tolerance) between the Notaway and Témiscamie populations are primarily attributed to ΔCV_{CC}

Discussion

Disturbance-demography relationships and population dynamics modeling

By associating empirical estimates of calf recruitment, adult survival and sex ratio with changing range conditions over time, our modeling exercise provides a refined perspective on the disturbance–demography relationship. First, we demonstrate that declines in recruitment, despite stochastic variation, can be detected within a single population as a function of cumulative range disturbances over time. Indeed, our results indicate that the disturbance–recruitment relationship may be characterized both spatially (i.e. intra-population chronosequence model as per Environment Canada) and temporally (i.e. intrapopulation time-series model). Second, we demonstrate that populations may respond to different degrees to equivalent levels of range disturbance for reasons we will explore. Lastly, we evaluated the sensitivity of disturbance tolerance thresholds to range-scale determinants of growth rate (i.e. adult survival, sex ratio).

Considering recruitment rates may vary over time as succession and disturbance modulate the availability of undisturbed habitat, the adjustment and predictive performance of Environment Canada's inter-population disturbance-recruitment model may be compromised by temporal mismatching of sample observations. Indeed, whereas range conditions were estimated from 2008 to 2010 satellite images, recruitment estimates most commonly centered around 2003, an average time lag of 5–7 years. As our results suggest, refinement of the model may produce smaller confidence intervals. We therefore recommend a concerted effort be made to update and re-evaluate the disturbance-recruitment model using the most accurate and temporally concordant model inputs. To better account for potential sampling bias and/or imprecision, recruitment estimates may be differentially weighted as a function of datum quality (e.g. with respect to sample size, % range area surveyed, etc.).

To our knowledge, there has been no comprehensive evaluation or critique to date of the body of work produced by Environment Canada (2011). Sleep and Loehle (2010) scrutinized the predictive accuracy of a related model produced by Sorensen et al. (2008). However, unlike Environment Canada (2011), their model was not built on data spanning the full array of predictor values present in boreal caribou ranges across Canada. Furthermore, their choice of growth rate as the dependent variable incurs assumptions about additional parameters (e.g. adult sex ratios, parturition and survival rates) that are difficult to estimate with certainty and may vary from one population to another. Indeed, while we were able to control for potential biases in the field, estimates derived from incompletely surveyed populations tend to be imprecise and therefore potentially inaccurate (Poole et al. 2013). This is problematic considering the cost effectiveness of composition surveys and the consequent frequency with which they are employed to produce demographic estimates. Poole et al. (2013) evaluated the effect of survey coverage on estimates of bull:cow and cow:calf ratios in Greenland. While generally speaking they observed higher calf ratios in lower density strata, results depended on the area sampled since populations were heterogeneously structured. It is therefore challenging to conclude and account for potential directional bias in estimates derived from incomplete surveys. The inter-population 'chronosequence' approach accounts for sample imprecision by preferentially employing multiple-year mean estimates of calf recruitment. In evaluating within-population responses to range disturbance over time, we did so by weighting annual recruitment estimates by the number of adult females observed. Demographic simulations were Populations may respond differently to habitat loss in part due to variation in local habitat composition as a determinant of predation risk. For example, calving on refuge islands may favour neonate survival even on relatively disturbed ranges (Bergerud et al. 1990). Similarly, availability of protective cover may influence detectability by predators and therefore calving success. Results of the intra-population disturbance-recruitment model indicate the Nottaway may respond more severely to habitat loss than the Assinica and Témiscamie populations (Fig. 3). We suggest this may be attributed to its significantly greater use of peatland environments and substantially lower use of closed canopy forest types during calving and post-calving, periods during which neonates are most vulnerable (Leclerc et al. 2014), although this merits further investigation. Indeed, forest productivity is generally lower on the Nottaway range than elsewhere in our study area (Gauthier et al. 2015), which suggests a lower resilience to disturbances (Imbeau et al. 2015).

Evidently, range disturbance alone cannot account for all the biotic and abiotic determinants of caribou calf survival. For example, variation in snow depth and hardness strongly influence both mobility and access to winter food (Tyler 2010), thereby influencing the survival and body condition of parturient caribou with direct consequences for the survival of their offspring. Maternal experience can also influence phenology and success of calving, with similar consequences for recruitment (Adams 2005). Such climatic and maternal effects are likely to explain some portion of the residual variance in annual recruitment. Interactions are also plausible; for example, habitat depletion may reduce winter forage quality and availability, and thus fitness. Furthermore, depleting range conditions augment predation risk and favour behavioural decisions by females that could have detrimental fitness consequences (Leclerc et al. 2014; Losier et al. 2015; Leblond et al. 2016).

Disturbance tolerance thresholds and risk management

In order to make informed choices about complex problems, land use managers require information on the nature, direction and magnitude of inherent risks. Such information may serve to establish threshold conditions that are pragmatically unwise to exceed. In conservation biology, extinction thresholds can be defined as the *minimum proportion of suitable habitat... that is necessary for population persistence* (Lande 1987). In certain cases, these may represent a point-of-no-return beyond which an ecological state shift is set in motion that cannot be readily reversed (Johnson 2013). Accordingly, precaution must be exercised in setting habitat-based conservation targets, particularly in the case of non-linear relationships (e.g. Drapeau et al. 2009; Villard and Jonsson 2009). In reality, however, decisions governing the fate of species at risk are influenced in large part by socio-economic considerations. Consequently trade-offs are made between conservation and development (Levin et al. 2015), although resulting protection measures are often insufficient to ensure population recovery.

Our results demonstrate that the minimum amount of undisturbed habitat necessary to afford a 60% probability of a self-sustaining caribou population (as per Environment Canada 2012) varies markedly as a function of adult survival, sex ratio and variance estimates (Table 3). Only while these parameters remain equal or superior to average expected values is 65% undisturbed habitat theoretically sufficient to sustain viable populations. For this reason, permitting 35% of boreal caribou ranges to erode by design, or ceasing restoration efforts upon obtaining 65% undisturbed habitat, will in many cases fail to maintain viable populations. Moreover, whereas it is inherently assumed that adult

survival varies around a stable mean, studies demonstrate that adult mortality may in fact be significantly higher in disturbed areas (e.g. Courtois et al. 2007; Wittmer et al. 2007). Evidence is therefore sufficient to suggest that management strategies treating the 65% undisturbed habitat benchmark as a maximum rather than a minimum are unlikely to succeed in maintaining viable woodland caribou populations.

The techniques we employ in this study can be applied to any species for which a habitat–demography relationship is known or can be derived and for which growth rate (λ) can be estimated. In order to bolster the likelihood of success, we recommend that decision-makers adopt precautionary quantitative habitat targets that incorporate the best available knowledge about the populations they stand to affect and afford substantial leeway for stochastic variation and other potential risk factors. Furthermore, since many First Nations (e.g. the Cree people of Eeyou Istchee, Northern Quebec) depend on wildlife populations for cultural and subsistence purposes, the rigorous and transparent approach we advocate is likely to benefit governments and businesses in their efforts to obtain the free prior informed consent of local indigenous people before engaging in activities that may impact their traditional way of life (UN General Assembly 2008).

Management implications

Our study documents the cumulative effects of 10 years of extensive forest harvesting on woodland caribou range conditions in the boreal forest of Northern Québec. In striving to maintain equitable forest cover within comparatively small trap lines across a vast land base, the staggered cutting system (dispersed clearcuts) of the Paix des Braves agreement produced an extensive and continuously expanding road network and thereby inadvertently compromised the viability of three local caribou populations (Rudolph et al. 2012). Indeed, the net negative effect of linear features (roads, hydroelectric corridors, seismic lines) on caribou calf survival far exceeds that of any other form of landscape disturbance (Environment Canada 2011). We therefore conclude that existing forest harvesting modalities entrenched in the Paix des Braves agreement are ineffective in achieving caribou conservation. Alternative forest management practices must be considered that concentrate activities within already disturbed areas and away from intact forests (Lesmerises et al. 2013), and a suite of mitigation and restoration efforts must be deployed in order to facilitate near-term habitat renewal (Rudolph et al. 2012; Environment Canada 2012). Whether or not boreal caribou persist into the future depends on political commitments to securing habitat protection, significant investments in restoration efforts, and the framing of industrial development within management guidelines compatible with woodland caribou recovery.

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