Management and Conservation Article

Woodland Caribou Extirpation and Anthropogenic Landscape Disturbance in Ontario

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ABSTRACT The decline of woodland caribou (*Rangifer tarandus caribou*) has been attributed to anthropogenic landscape disturbances, but critical distance thresholds and time lags between disturbance and extirpation are unknown. Using a database of caribou presence and extirpation for northern Ontario, Canada, geo-coded to 10×10-km cells, we constructed logistic regression models to predict caribou extirpation based on distance to the nearest of each of 9 disturbance types: forest cutovers, fires, roads, utility corridors, mines, pits and quarries, lakes, trails, and rail lines. We used Akaike's Information Criterion to select parsimonious models and Receiver-Operating Characteristic curves to derive optimal thresholds. To deal with the effects of spatial autocorrelation on estimates of model significance, we used subsampling and restricted randomizations. Forest cutovers were the best predictor of caribou occupancy, with a tolerance threshold of 13 km to nearest cutover and a time lag of 2 decades between disturbance by cutting and caribou extirpation. Management of woodland caribou should incorporate buffers around habitat and requires long-term monitoring of range occupancy. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1249–1256; 2007)

KEY WORDS extirpation risk, landscape disturbance, Ontario, *Rangifer tarandus caribou*, spatial modeling, thresholds, woodland caribou.

Woodland caribou (*Rangifer tarandus caribou*) once occupied much of North America's boreal forest but have declined significantly since European settlement (de Vos and Peterson 1951, Bergerud 1974). In Ontario, Canada, for example, caribou range has receded approximately 34 km per decade (Schaefer 2003), the manifestation of widespread range collapse (Laliberte and Ripple 2004) and population decline (Mallory and Hillis 1998). In 2000, the Committee on the Status of Endangered Wildlife in Canada (2000) listed forest-dwelling caribou in Canada as threatened (likely to become endangered if limiting factors are not reversed).

The demise of woodland caribou has frequently been attributed to human landscape disruption. For example, the conversion of forests by logging may result in greater abundance of other ungulates, like moose (*Alces alces*), and increased predation by gray wolves (*Canis lupus*; Bergerud 1974, Bergerud and Elliot 1986, Seip and Cichowski 1996). Roads and trails may facilitate travel by predators (James and Stuart-Smith 2000) and hinder caribou movements (Dyer et al. 2002). The influences of natural and anthropogenic landscape features on caribou distribution are well-documented, including range shifts following fire (Schaefer and Pruitt 1991), attraction to lakes (Ferguson and Elkie 2005), and avoidance of industrial developments (Smith et al. 2000, Dyer et al. 2001, Nellemann et al. 2003, Cameron et al. 2005, Schaefer and Mahoney 2007). Their effects on population persistence, however, are virtually unknown. Such knowledge is important to identify thresholds and potential time lags between anthropogenic disturbance and caribou extirpation and to detect populations at risk.

We used a database of historical woodland caribou occupancy in Ontario (Fig. 1) to build models of caribou presence and extirpation and assess the importance of 9 anthropogenic disturbance types in defining the southern limit of caribou range. From these models, we derived critical distance thresholds and time lags after disturbance to predict caribou occurrence.
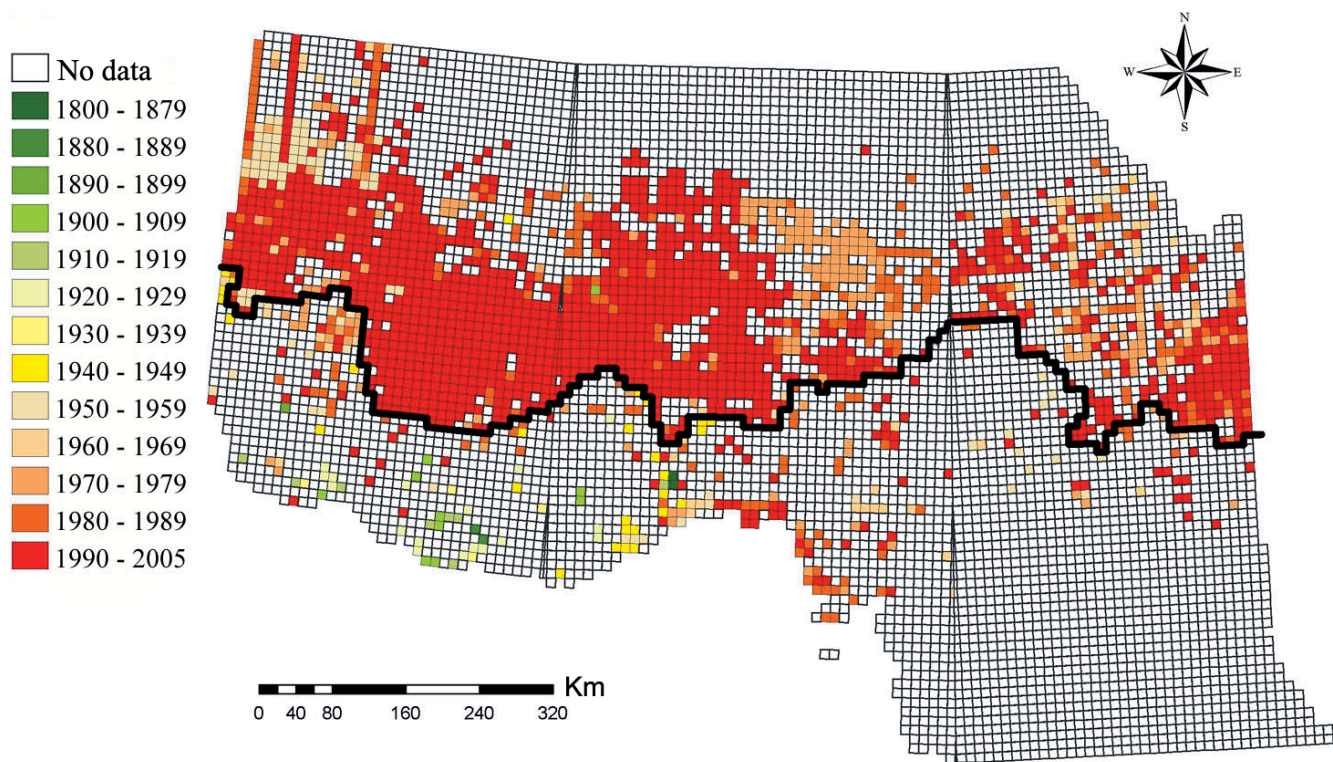
STUDY AREA

This study encompassed Ontario north of 48° N (Fig. 1), all of which was historically (since 1900) or recently (since 1990) occupied by woodland caribou. The area was characterized by closed stands of spruce (*Picea* spp.), balsam fir (*Abies balsamea*), and tamarack (*Larix laricina*), with more frequent occurrence in the south of white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), and white pine (*Pinus strobus*). Lichens, shrubs and forbs dominated the groundcover of this mosaic of soils and rock. Characteristic large mammals included moose, wolf, and black bear (*Ursus americanus*).

METHODS

Data Preparation

We focused on relationships between disturbance and the limits of continuous caribou range. To delineate this

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Figure 1. Study area in northern Ontario, Canada. Squares are coded to the most recent decade of caribou observation. The line represents the southern boundary of continuous caribou range, 1990–2005.

boundary, we used a database of woodland caribou occupancy in Ontario, consisting of 10 × 10-km Universal Transverse Mercator (UTM) cells (Fig. 1), coded for the decade of most recent observation of caribou, 1800–1999. Racey and Armstrong (2000) compiled these data from structured studies (e.g., aerial surveys, radiotelemetry) and incidental observations from forest workers, trappers, hunters, fur trade diaries, railway and land survey records, and Ontario Ministry of Natural Resources (MNR) records. We augmented this dataset with observations from recent (1990–2005) studies in northern Ontario (Brown 2005; A. Magoun and J. Ray, Wildlife Conservation Society of Canada, unpublished data; E. Armstrong, W. Beckett, M. Gauthier, R. Leith, G. Racey, and J. Sadowsky, MNR, unpublished data). We regarded cells with records of caribou occupancy from 1990 to 2005 as presences and all other cells as absences.

From these data, we established a coarse-resolution southern range boundary using the edges of cells. The line followed the southern limit of contiguous presence (occupied by caribou) cells (Fig. 1). We crossed gaps ≤3 cells (i.e., 30 km) to join groups of ≥2 occupied cells. We treated cells north of this boundary ($n = 3,670$) as presences and cells south of the line ($n = 3,057$) as absences. The northern limit of caribou range followed Schaefer (2003). We considered single occupied cells south of the continuous distribution to be beyond the generalized limit of distribution (Gaston 2003). Clusters (>2 cells) of caribou occupancy have persisted on the north shore of Lake Superior and are now separated from continuous caribou

range by >100 km (Bergerud 1974, Racey and Armstrong 2000). Our focus was continuous range; thus, we excluded these clusters from analysis.

We included 10 landscape disturbances and features: provincial roads (primary, secondary, and tertiary roads), unimproved roads (all classes plus unimproved, seasonal and logging roads shown on 1:20,000 Ontario Base Maps, obtained from the MNR Natural Resource Values Information System [NRVIS]), fires, cutovers, pits and quarries, utility corridors, rail lines, multipurpose trails, mines, and lakes (>12 km^2). We obtained coverage for unimproved roads, utility line corridors, trails, pits and quarries, railways, and lakes from the MNR NRVIS database in ArcMap. We used forest harvest and fire Geographic Information System data from the MNR Forest Landscape Ecology Program, and mine locations from the Ontario Ministry of Northern Development and Mines. To explore time lags between disturbance by cutting and extirpation, we combined cutover maps cumulatively by decade from 1941 onward. Forest harvesting in Ontario has proceeded progressively northward; there is no evidence of caribou, once extirpated, becoming reestablished in these areas.

An obvious implication of delineating a range boundary based on 10 × 10-km cells is that the spatial resolution of the caribou range map is coarser than that of the independent disturbance variables. To make the resolution of these maps comparable, we computed an average distance to nearest feature from each cell to each predictor feature. We divided each 10 × 10-km cell into 100 × 100-m subcells

and calculated the distance to the nearest disturbance feature for each subcell. We used the Zonal Statistics tool of the Spatial Analysis extension in ArcMap to calculate the mean of the subcell distances to disturbance for each cell. These distance-based measures indicated the degree of disturbance both within and beyond the cell boundaries. We transformed these data by the base 10 logarithm.

Data Analyses

To achieve our primary goal (assessment of disturbance effects on caribou occupancy and estimation of distance thresholds) we developed logistic regression models to predict continuous contemporary (1990–2005) caribou range using distances to nearest disturbance as independent variables. Using the full dataset of 6,727 cells, we estimated model coefficients and measures of fit and identified the most parsimonious models with Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We based the first set of models on contemporary disturbances; we based a second set on historical (1950–1995) cutovers. In this analysis, 3 issues demanded particular attention: multi-collinearity, spatial autocorrelation, and estimation of thresholds.

Multicollinearity.—Correlations between all independent variables were high ($0.614 < r < 0.860$), potentially compromising the reliability of parameter estimation and model selection. To address this multicollinearity, we adopted a "residual and sequential regression" approach (Graham 2003:2812). We used logistic regression based on sets of 2 collinear disturbance variables with distance to cutovers as the primary explanatory variable. We based this choice on our expectation (Graham 2003) of the impacts of forest harvesting on caribou extirpation (Schaefer 2003), confirmed by simple logistic regression. To remove the correlations with cutovers in the remaining independent variables, we calculated residuals of each of those variables regressed on distance to cutovers before entering them into the models.

Spatial autocorrelation.—The spatial dependence among observations could lead to overestimation of degrees of freedom. To deal with this spatial autocorrelation, we used 2 strategies proposed by Dale and Fortin (2002): subsampling and Monte Carlo restricted randomizations.

First, we estimated the subsample size required to achieve independence of observations by calculating Moran's I for caribou observations for random samples of cells. We used the Spatial Statistics extension in S-Plus (Insightful Corporation, Seattle, WA). We drew 10 random samples of size 50, 60, 70, . . . , 100, 500, 1,000, 2,000, and 3,000 cells, calculated Moran's I for each trial, then the mean I for each sample size. At a subsample size of 60 cells, spatial autocorrelation dropped below significance ($P = 0.05$) and captured variation representative of the full dataset (Vors 2006). Accordingly, we randomly subsampled the entire dataset 1,000 times with a sample of 60 cells and estimated all logistic regression models. We ranked the models based on mean AIC for all subsamples.

Second, we used Monte Carlo restricted randomizations to assess model significance by generating distributions of a fit statistic under the null hypothesis (Noreen 1989). We considered this approach a justified and valuable complement. The Akaike's Information Criterion is also susceptible to spatial autocorrelation, and the strict emphasis in wildlife science on the information theoretic approach has also recently been questioned (Guthery et al. 2005). Complete randomization of the dependent variable was not appropriate because its spatial structure would be lost (Fortin and Payette 2002), so we used restricted randomizations (Dale and Fortin 2002). We repeatedly and randomly shifted the relative locations of the disturbances and caribou range, and estimated the model coefficients and fit to generate a distribution of values based on no relationship between the 2 data sets. The approach conserves the spatial structure of the data. We randomly rotated a polygon of caribou range and placed it randomly over the maps of disturbances, designating cells within the polygon as presences and cells outside the polygon as absences. We repeated this process 1,000 times for each disturbance type, each time reestimating the logistic regression model to compile the null distributions.

We used a fit-ratio, analogous to the coefficient of determination (R^2), as a measure of model fit. We computed the fit-ratio as Slope Coefficient $\times$ [1 − (Residual Deviance/Null Deviance)], where we calculated deviances (Venables and Ripley 2002) in S-Plus. We assessed model significance by computing the proportion of times the value from the actual data was exceeded by values generated under the null hypothesis. For example, for a given disturbance, if the fit-ratio values from restricted randomizations were greater than those from the true dataset in 38 of 1,000 instances, we deemed the model significant at $P = 0.038$.

Critical thresholds.—We derived distance thresholds for each model using maximum-accuracy thresholds obtained from Receiver-Operating Characteristic (ROC) curves (Zweig and Campbell 1993, Guénette and Villard 2005). The area-under-the-curve (AUC) of the ROC curve provides an estimate of the accuracy of the logistic regression model to classify cells. We obtained observed and predicted values for each model in S-Plus. For multivariate models we calculated 3 thresholds with the independent residual variable set at zero, plus one standard deviation, and minus one standard deviation. We imported observed and predicted values into ROC Plotting and AUC Calculation Transferability Test (Schröder 2004). This program calculated the maximum-accuracy threshold based on the number of prediction errors in each model and an assumption of equal cost for false-positive and false-negative errors. We back-transformed the maximum accuracy predicted P-value through the logit function and anti-$\log_{10}$ to produce thresholds for each model.

To visualize the results, we graphed critical thresholds and mapped the probability of caribou occurrence as predicted for each decade of cumulative cutovers.

RESULTS

We found a strong relationship between woodland caribou extirpation and distance to all anthropogenic landscape

Table 1. Parameter estimates and fit measures for models of woodland caribou range in Ontario, Canada, 1990–2005, predicted by distance to disturbance.

Model	Full dataset					Subsampling		Randomization
	Intercept	Slope	Fit-ratio	AIC[a]	w_i[a]	$\bar{x}$ AIC	w_i	P of fit-ratio
Cutovers	−7.869	2.100	0.441	5,193.1	>0.999	34.69	>0.999	0.049
+ rails residual		1.453						
Cutovers	−7.906	2.100	0.438	5,217.7	<0.001	35.03	0.843	0.043
+ mines residual		1.324						
Cutovers	−7.906	2.100	0.438	5,217.7	<0.001	35.14	0.796	0.043
+ utility lines residual		1.324						
Cutovers	−7.874	2.097	0.435	5,244.5	<0.001	35.29	0.741	0.040
+ provincial roads residual		1.319						
Cutovers	−7.823	2.079	0.427	5,320.1	<0.001	36.14	0.483	0.056
+ unimproved roads residual		1.134						
Cutovers	−7.891	2.116	0.426	5,328.6	<0.001	36.20	0.470	0.049
+ trails residual		0.915						
Cutovers	−7.826	2.082	0.419	5,394.7	<0.001	36.68	0.369	0.045
+ pits and quarries residual		0.969						
Cutovers	−7.917	2.080	0.408	5,490.9	<0.001	40.52	0.054	0.042
Unimproved roads	−8.590	2.455	0.387	5,685.6	<0.001	42.45	0.021	0.033
Provincial roads	−12.439	2.890	0.332	6,198.9	<0.001	46.65	0.003	0.047
Rails	−14.087	3.119	0.328	6,235.7	<0.001	46.76	0.002	0.055
Pits and quarries	−12.301	2.882	0.305	6,445.9	<0.001	49.16	<0.001	0.046
Trails	−8.758	2.202	0.290	6,590.4	<0.001	50.55	<0.001	0.064
Utility lines	−11.991	2.748	0.266	6,811.8	<0.001	52.32	<0.001	0.031
Mines	−12.654	2.881	0.263	6,838.3	<0.001	52.78	<0.001	0.084
Lakes	−2.341	0.638	0.034	8,957.8	<0.001	71.94	<0.001	0.318
Fires	0.571	−0.108	−0.001	9,263.9	<0.001	74.55	<0.001	0.543

[a] AIC = Akaike's Information Criterion; w_i = AIC wt.

disturbances, especially cutovers (Table 1). Among the simple logistic models, distance to cutovers was the best predictor of continuous caribou range. Adding the residuals from all other disturbances marginally improved models over the simple cutovers model, as evidenced by the fit-ratio and subsample AIC weights. For the entire dataset, AIC weights indicated strong support for one multivariate model—distance to cutovers and residuals from distance to rails. Support for this model must be viewed cautiously, however, because of spatial autocorrelation in the dependent variable.

When we eliminated spatial autocorrelation with subsampling, the same multivariate model, distance to cutovers and residuals from distance to rails, was most parsimonious (Table 1). In this case, however, AIC weights indicated weaker support for the cutovers-and-rails model as best model. The differences in AIC among all multivariate models was <2.0, indicating that no multivariate model was clearly superior (Burnham and Anderson 2002).

The restricted randomization tests of the fit-ratios identified 11 models as significant ($P < 0.05$) and 3 others as marginally significant ($0.05 < P < 0.10$; Table 1). As in all analyses, lakes and fires offered no explanatory power.

Historical analyses identified a 2-decade lag between disturbance by cutovers and caribou extirpation. Cumulative cutovers to 1970 were the best predictor of contemporary caribou presence (1990–2005) based on AIC weights, fit-ratios and fit-ratio significance (Table 2). Cutovers occurring up to 1995 ranked second. Caribou presence predicted by cutovers to 1970 matched the current caribou distribution most closely, whereas later decades predicted large areas north of the continuous caribou distribution line with a low probability of occupancy (Fig. 2).

Critical distance thresholds ranged from 4 km to 82 km (Table 3; Fig. 3). The threshold for cutovers of all ages was approximately 13 km and, when additional disturbances were included, was 8–22 km. The relationships based on fire, lakes, or cutovers prior to 1950 were too weak to derive meaningful thresholds.

Table 2. Parameter estimates and fit measures for models of woodland caribou range in Ontario, Canada, 1990–2005, predicted by distance to historical cutover disturbances.

Model	Full dataset					Subsampling		Randomization
	Intercept	Slope	Fit-ratio	AIC[a]	w_i[a]	$\bar{x}$ AIC	w_i	P of fit-ratio
Cutovers 1941–1970	−14.940	3.327	0.428	5,309.2	>0.999	38.99	0.613	0.041
Cutovers 1941–1995	−7.917	2.080	0.408	5,492.9	<0.001	41.29	0.194	0.041
Cutovers 1941–1990	−8.851	2.231	0.394	5,624.8	<0.001	42.51	0.105	0.053
Cutovers 1941–1980	−10.712	2.502	0.385	5,703.8	<0.001	42.89	0.087	0.055
Cutovers 1941–1960	−15.891	3.306	0.270	6,749.7	<0.001	52.32	0.001	0.064
Cutovers 1941–1950	−9.317	1.809	0.091	8,430.9	<0.001	67.57	<0.001	0.336

[a] AIC = Akaike's Information Criterion; w_i = AIC wt.
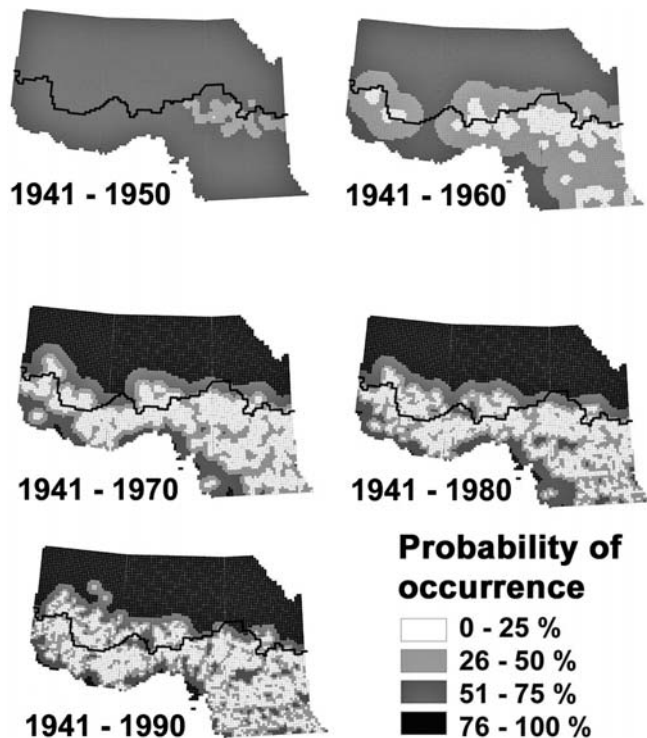
Figure 2. Probability of woodland caribou occurrence in Ontario, Canada, predicted by the mean distance to cumulative historical cutovers: 1) 1941–1950, 2) 1941–1960, 3) 1941–1970, 4) cutovers 1941–1980, and 5) 1941–1990. The line represents the southern boundary of continuous caribou range, 1990–2005.

DISCUSSION

The relationship between anthropogenic landscape disturbance and woodland caribou persistence is clearly strong and negative. Human encroachment has many potential consequences for caribou, including direct mortality from poaching and vehicle collisions, changes in predator–prey relationships, energetic costs associated with disturbance, barrier effects, displacement, and avoidance (Dyer et al. 2001). Virtually all industrial developments such as hydroelectric dams, oil-drilling and tourism infrastructure, and linear corridors, have been shown to affect caribou and reindeer negatively; caribou occupancy is often reduced within 1–10 km from such disturbances (Edmonds 1987, Duchesne et al. 2000, Nellemann et al. 2003, Cameron et al. 2005, Schaefer and Mahoney 2007). The proposition that woodland caribou can deal with industrial development and exhibit "a high degree of resilience to human disturbance" (Bergerud et al. 1984:7) is questionable. Whether caribou are able to persist may depend on the cumulative effects of wolf–prey interactions, productivity of the ecosystem, and impact of industry (Johnson et al. 2004, Weclaw and Hudson 2004). The loss of suitable areas may be particularly serious for sedentary caribou (Bergerud 1996) whose spacing out (dispersing from conspecifics to secluded refugia) strategy at calving may be impaired.

Our study identified cutovers from forest harvesting as the strongest predictor of caribou extirpation. This was not surprising; the northern front of forest harvesting in Ontario closely matches the southern boundary of continuous caribou occupancy (Schaefer 2003) and timber harvesting may lead to reduced occurrence of woodland caribou (Chubbs et al. 1993, Smith et al. 2000, Schaefer and Mahoney 2007). The predictive power of our models substantiated this pattern; recent (<10-yr-old) cutovers appeared in all top-ranked models (Tables 1, 2). Caribou home ranges comprise very small proportions of immature forest (Mosnier et al. 2003). In addition, caribou may avoid

Table 3. Area under the curve (AUC) and critical threshold distances for predictions of caribou range in Ontario, Canada, 1990–2005, based on distance to disturbance.

Model	AUC	Critical threshold distance (km) at:		
		Residual variable = 0	Residual = +1 SD	Residual = −1 SD
Cutovers + rails residual[a]	0.898	11	6	22
Cutovers + mines residual[a]	0.889	11	6	21
Cutovers + utility lines residual[a]	0.900	8	4	15
Cutovers + provincial roads residual[a]	0.898	9	5	17
Cutovers + unimproved roads residual[a]	0.896	8	5	14
Cutovers + trails residual[a]	0.890	8	5	13
Cutovers + pits and quarries residual[a]	0.890	11	8	17
Cutovers	0.891	13		
Unimproved roads	0.883	4		
Provincial roads	0.866	30		
Rails	0.870	53		
Pits and quarries	0.848	27		
Trails	0.831	22		
Utility lines	0.841	38		
Mines	0.832	31		
Cutovers 1941–1970	0.915	52		
Cutovers 1941–1995	0.891	13		
Cutovers 1941–1990	0.890	18		
Cutovers 1941–1980	0.896	40		
Cutovers 1941–1960	0.850	82		

[a] We calculated threshold distances for optimal P-values based on Receiver-Operating Characteristic curves and equal costs for false-positive and false-negative errors; for multivariate models 3 distance thresholds were calculated: model residual variables set at zero, +1 SD and −1 SD.
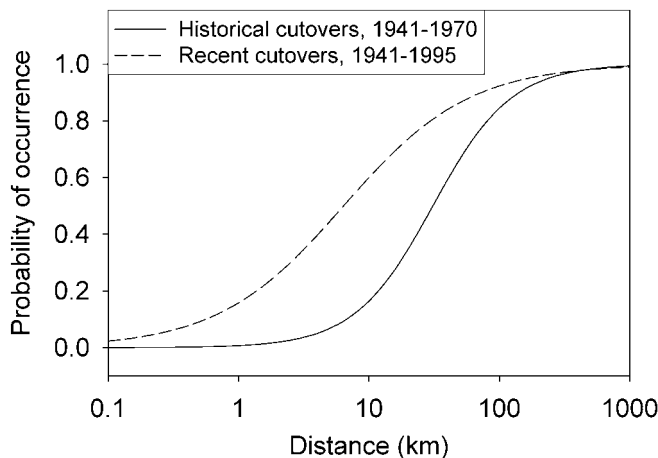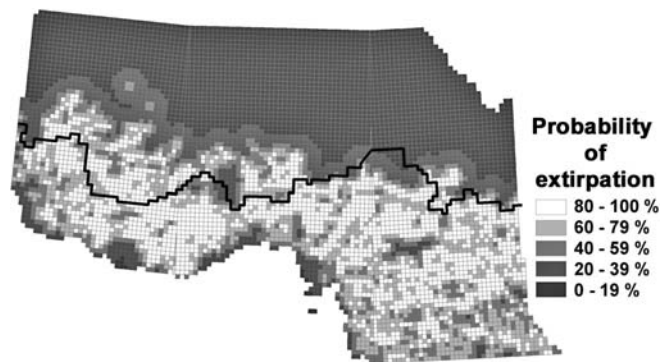
Figure 3. Predictive logistic regression functions and critical distance thresholds for the effect of historical cutovers on woodland caribou extirpation in Ontario, Canada, 1990–2005.

Figure 4. Areas at risk of woodland caribou extirpation in Ontario, Canada to 2015, as predicted by the model based on cumulative cutovers to 1970 applied to cumulative cutovers to 1995.

ongoing cutting operations in response to human activity (e.g., vehicular traffic, noise) and unsuitability of this habitat when occupied by humans (Chubbs et al. 1993). Hence, forest harvesting may have immediate (behavioral) and long-term (demographic) effects on woodland caribou. Nevertheless, the strong correlations among landscape disturbances imply that no single variable in our study can be unequivocally regarded as key to caribou range recession.

Climate change has been implicated in poleward range shifts of many other species (Parmesan and Yohe 2003). Although we cannot wholly dismiss a contribution from global warming, the distributional change by caribou in Ontario has been much faster (34 km/decade; Schaefer 2003) than global range shifts of other organisms ($\bar{x} = 6.1$ km/decade; 95% CI = 1.26–10.87; Parmesan and Yohe 2003). Many of these other species, furthermore, were birds and butterflies whose responses to climate warming are likely to be more rapid than caribou. We surmise that climate change is unlikely to account for the pattern of range collapse in our study.

The extinction debt, the delay between habitat loss and species disappearance (Janzen 1988), has serious ramifications for habitat management. Our study points to approximately a 2-decade lag between forest harvesting and caribou disappearance. This may represent the time during which moose increase to a density sufficient to support a large wolf population that may reduce caribou numbers below a minimum viable population. Indeed, moose populations increase 2–15 years after logging, but tend to peak 15–40 years after disturbance (Eason 1985, Payne et al. 1985, Crête 1988, Timmerman and McNichol 1988, Maier et al. 2005). Wolves may become noticeable within 7 years after moose become locally abundant (Bergerud and Elliott 1986). Rettie and Messier (1998) suggested caribou may avoid habitats with abundant moose; caribou whose ranges overlap with moose may face predation mortality that threatens them with extirpation in the absence of positive net migration. Bergerud and Elliot (1986) proposed that moose–wolf interactions are funda-

mental in shaping caribou populations, and other studies have inferred the moose–caribou–wolf interactions that occur following anthropogenic landscape disturbance (Seip 1992, Seip and Cichowski 1996).

When the results of the logistic regressions were mapped, we found reasonable correspondence between areas of caribou persistence along the north shore of Lake Superior (Fig. 1) and the model predictions (Fig. 4). Caribou may be able to persist south of the line of continuous occupancy because thresholds have not been breached. In these refugia in Ontario, the distance to forest cutovers of all ages is ≥10 km and the distance to cumulative cutovers up to 1970 is ≥40 km.

Caribou range recession in Ontario is an extirpation front that mirrors the geography of human activity (Schaefer 2003), a pattern reiterated in other species that have experienced range collapse (Channell and Lomolino 2000, Laliberte and Ripple 2004). In our study, woodland caribou were predictably absent from an area surrounding cutovers, regardless of age, by ≥13 km, and were absent from the vicinity of cutovers ≥20 years old by a threshold of approximately 50 km (Table 3). The range occupancy predicted by cutovers to 1995 is cause for concern. Assuming a 2-decade time lag between disturbance by forestry and caribou extirpation, there are large areas north of the line of continuous range occupancy that appear to be at risk (Fig. 4). The extinction debt implies that further range retraction of woodland caribou is likely.

MANAGEMENT IMPLICATIONS

Our study emphasizes the need for refugia for woodland caribou situated at large distances from human landscape disturbances. The median area of sedentary caribou population ranges in North America is 9,000 km^2 (Schaefer and Mahoney 2003) to which, according to our study, a surrounding zone of intact forest, >13 km wide, would be needed. This critical distance contrasts starkly with current prescriptions for forest harvesting, such as a 1,000-m buffer around calving lakes in Ontario (Ontario Woodland Caribou Recovery Team 2005). These figures also imply that even the largest protected areas, such as Woodland Caribou Provincial Park (4,500 km^2) and Wabakimi

Provincial Park (8,920 km^2), may be insufficient in themselves for maintaining woodland caribou in northern Ontario. Our work also highlights the likelihood of long delays between management actions and caribou disappearance. Such delays pose challenges to adaptive management, where success or failure of habitat interventions may not be evident for decades. For woodland caribou, long-term monitoring is needed to detect further range recession and assess the efficacy of buffers and other management interventions.

ACKNOWLEDGMENTS

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