Research Note

Long-Term Range Recession and the Persistence of Caribou in the Taiga

JAMES A. SCHAEFER

Biology Department, Trent University, 1600 West Bank Drive, Peterborough, Ontario, K9J 7B8, Canada, email jschaefer@trentu.ca

Abstract: *Spatial patterns can help in understanding the decline and future prospects of threatened species, but the dynamics of range retraction have not been applied to these fundamental questions. I analyzed long-term changes in occupancy by taiga-dwelling caribou (*Rangifer tarandus caribou*) to estimate their rate of disappearance and time to extirpation in Ontario, Canada. Patterns of range recession, 1880–1990, indicated that half of historic woodland caribou range has been lost, a rate of disappearance of 34,800 km^2 per decade, and a northward range recession of 34 km per decade. The mean metapopulation density, the abundance of discrete winter groups, was one group per 1,900 km^2, suggesting an average loss of 18 caribou wintering areas per decade during this period. There was a strong coincidence between the recent southern limits of caribou occupancy and the northern front of forest harvesting, implying an anthropogenic agent of decline. The estimated time to extirpation of forest-dwelling caribou in Ontario, inferred from the sustained rate of disappearance, was 91 years (95% confidence interval: 57–149 years). The persistence of woodland caribou may depend on spatial separation from human incursion.*

Recesión de Rangos a Largo Plazo y la Persistencia de Caribú en la Taiga

Resumen: *Los patrones espaciales pueden ayudar a comprender la declinación y esperanzas futuras de especies amenazadas, pero no se ha aplicado la dinámica de la retracción de límites a estas preguntas fundamentales. Analicé cambios a largo plazo en la ocupación de taiga por caribúes (*Rangifer tarandus caribou*) para estimar su tasa de desaparición y tiempo hasta la extirpación en Ontario, Canadá. Los patrones de recesión de rangos, 1880-1990, indicaron que se ha perdido la mitad del área histórica de bosques utilizados por caribúes, una tasa de desaparición de 34,800 km^2 por década y una recesión de rango hacia el norte de 34 km por década. La densidad media de la metapoblación, la abundancia de grupos invernales discretos, fue de un grupo por 1,900 km^2, lo que sugiere una pérdida promedio de 18 áreas invernales para caribúes por década durante ese período. Hubo gran coincidencia entre los límites sureños recientes de ocupación por caribúes y el frente norte de la explotación forestal, lo que implica un agente de declinación antropogénica. El tiempo estimado hasta la extirpación de caribúes de los bosques de Ontario, inferida de la tasa sostenida de desaparición, fue de 91 años (95% CI: 57–149 años). La persistencia de caribúes puede depender de su separación espacial de la incursión humana.*

Introduction

Two of the central research goals in conservation biology are to detect declines of species and populations and to estimate their likelihood of persistence. The approaches are varied (Caughley & Gunn 1996; Beissinger & Westphal 1998). Spatial patterns, although less frequently examined, can be a valuable complement to standard demographic analyses. For example, species declines are typically accompanied by range collapse (Channell & Lomolino 2000; Lobo 2001; Rodríguez 2002), and species with limited distributions experience a higher risk of extinction (Johnson 1998; Purvis et al. 2000).

The geographic patterns of occupancy may aid in understanding the rate of decline and future prospects of

Paper submitted July 1, 2002; revised manuscript accepted February 5, 2003.

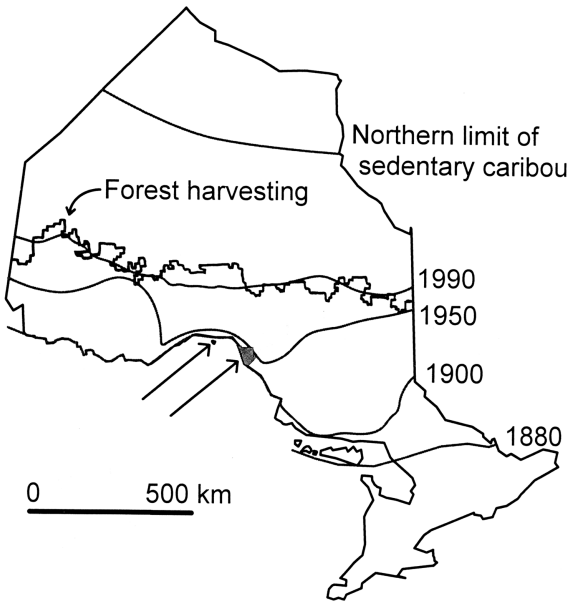

Figure 1. Range recession of sedentary woodland caribou and recent northern limit of forest harvesting in Ontario, Canada (adapted from Cumming & Beange 1993; Perera & Baldwin 2000). Arrows indicate remnant caribou populations on the Slate Islands and Pukaskwa National Park.

threatened species such as woodland caribou (*Rangifer tarandus caribou*). Forest-dwelling caribou are regarded as the sedentary ecotype. They are distinguished from the migratory ecotype by their more limited movements and the dispersion, rather than aggregation, by adult females at parturition (Bergerud 1988, 1996). The two ecotypes differ in habitat occupancy. Migratory caribou typically give birth and spend the summer on the tundra and overwinter in coniferous forests; sedentary caribou live year-round in mature coniferous forests and peatlands. The two ecotypes also tend to differ numerically. Migratory caribou often attain high abundance; sedentary populations tend to exist at low densities (Bergerud 1996). For instance, in Ontario, Canada, approximately three-quarters of *Rangifer* are migratory and most belong to just one herd (Cumming 1998), even though the majority of caribou range is occupied by sedentary populations (Fig. 1).

Across the circumpolar taiga, sedentary caribou are in trouble (Mallory & Hillis 1998). For example, from 1880 to 1990, forest-dwelling caribou in Ontario experienced progressive and dramatic erosion of the southern limit of their distribution (Fig. 1). The decline appears to stem from anthropogenic landscape disturbances. Logging, for instance, converts forests to early successional stages that invite the higher abundance of other ungulates, such as moose (*Alces alces*; Rempel et al. 1997), and wolves (*Canis lupus*; Ballard et al. 2000), leading to increased predation on caribou (Bergerud 1974; Bergerud & Elliot 1986; Seip & Cichowski 1996). Roads and trails may facilitate travel by predators (James & Stuart-Smith 2000) and hunters (Bergerud 1974). An alternative hypothesis, decline due to poorer range and nutrition, has frequently been discounted. Rates of pregnancy and parturition of woodland caribou are often high (Seip & Cichowski 1996; Rettie & Messier 1998), even in decreasing populations (Schaefer et al. 1999).

I analyzed the recent and historical range occupancy of taiga-inhabiting caribou in Ontario. My aim was to estimate the rate of decline and population loss, the relationship to human encroachment, and the projected time to extirpation for this threatened (Committee on the Status of Endangered Wildlife in Canada 2002), sedentary ecotype. To my knowledge, the dynamics of range retraction have not previously been used to estimate persistence time for any species or population.

Methods

My analysis was based on geographic patterns of woodland caribou occupancy in Ontario and adjacent regions. I prepared historic maps of range recession based on the work of Kelsall (1984) for North America and that of Cumming and Beange (1993) for Ontario. The latter series of maps (Fig. 1) were generated from numerous wildlife surveys conducted by the Ontario Ministry of Natural Resources (OMNR), incidental sightings and reports to OMNR staff, questionnaires, fur-trade diaries, land survey records, and railway construction archives (de Vos & Peterson 1951; Cumming & Beange 1993; Racey & Armstrong 2000). I interpolated the northern limits of sedentary caribou (cf. Harris 1999) from the neighbouring regions of Manitoba (Edmonds 1991) and Québec-Labrador (Bergerud 1994). The northern limit of forest harvesting in Ontario to 1995 (Perera & Baldwin 2000) was used as an indicator of the extent of human activity.

I conducted spatial analyses with MapInfo (version 5.0, MapInfo, Troy, New York). Because of the unidirectional, northward range recession (Fig. 1), I used the latitudinal extent of caribou occupancy to quantify the rate of range collapse and time to extirpation. The north-south breadth of sedentary caribou range was measured at systematic 40-km intervals for each of the four periods, 1880–1990. To gauge the effect of errors in occupancy on estimated persistence time, I carried out sensitivity analysis by varying the historical range limits. Each of the southern limits of caribou occupancy was varied north and south, up to 80 km, a value that approximates the extent of one population unit (Rettie & Messier 2001).

Population units of sedentary caribou are difficult to discern (Schaefer et al. 2001), and the logistics and cost

of estimating population densities are often prohibitive. As a surrogate of population density to express the rate of decline, I computed a "metapopulation density," the abundance of discrete wintering areas of woodland caribou, from existing maps of caribou occupancy. These maps were based on winter aerial surveys conducted in single winters in northwestern Ontario (Ontario Ministry of Natural Resources 1986; Racey & Armstrong 2000) and two winters in eastern Manitoba (Stardom 1977). During winter, groups of woodland caribou are conspicuous, comparatively large, and consistent in their use of space from year to year (Darby & Pruitt 1984). Stardom (1977) reported no noticeable interannual change in winter caribou distribution from an extensive regional survey in eastern Manitoba; Cumming et al. (1996) found high concordance in winter range use during four winters in northwestern Ontario, and Rettie and Messier (2001) noted that the seasonal ranges of individual females tended to overlap in consecutive years. The density of wintering areas could therefore provide a reasonable and measurable index of abundance for this gregarious ungulate.

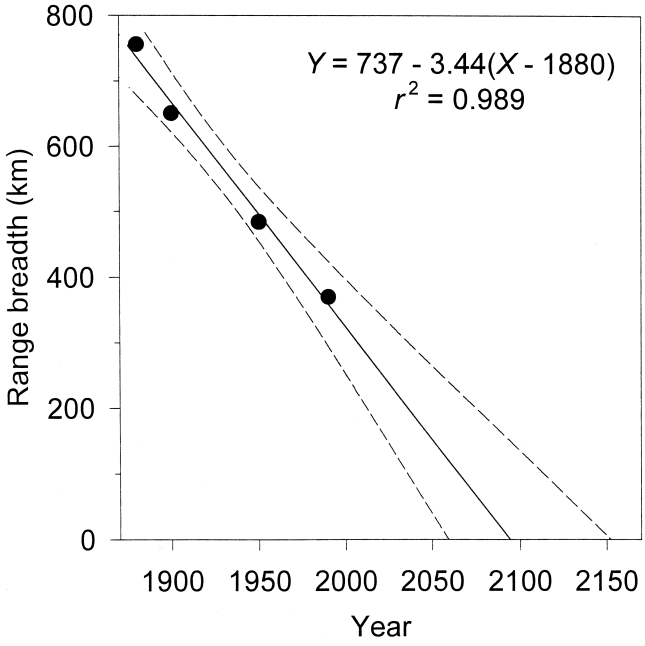

Figure 2. Past and projected latitudinal breadth of woodland caribou range in Ontario, Canada. Dashed lines represent 95% confidence limits for the regression.

Results

The historic range of taiga-dwelling caribou in Ontario, approximately 762,000 km^2 in 1880, was halved to 379,000 km^2 by 1990 (Fig. 1). The rate of disappearance was apparently consistent during this 110-year period ($r = -0.998$), an estimated 34,800 km^2 per decade. This corresponded to a northward range retraction of 34 km per decade (Fig. 2). The degree of range collapse was comparable at the continental scale: I computed that 51% of the historic range of the sedentary ecotype in North America (Edmonds 1991; Bergerud 1994) remained in the early 1980s (Kelsall 1984).

The metapopulation density, the number of discrete areas of caribou occupancy during winter, was comparable among studies (i.e., six areas in 14,000 km^2 [Stardom 1977], three areas in 5,000 km^2 [Ontario Ministry of Natural Resources 1986], and 38 areas in 65,000 km^2 [Racey & Armstrong 2000]). The average range loss of 34,800 km^2 per decade and a mean metapopulation density of one caribou area per 1,900 km^2 (SE = 215 km^2) imply a rate of disappearance of 18.3 caribou wintering areas per decade during the 110-year decline in Ontario. These estimates were comparable to the patterns from northwestern Ontario. Racey and Armstrong (2000) compiled a detailed record of caribou occupancy in 10 × 10 km cells from a 170,000-km^2 region, per decade from 1900 to 1990. From their map, I enumerated the loss of 84 discrete caribou areas. This corresponded to a metapopulation density of one caribou area per 2,024 km^2 and a loss of 9.3 caribou areas per decade.

Projecting forward, under the assumption of a sustained pace of disappearance, sedentary caribou will be virtually extirpated in Ontario in 2094; the 95% confidence limits for the year of extirpation were 2060 and 2152 (Fig. 2). This projection was most sensitive to error

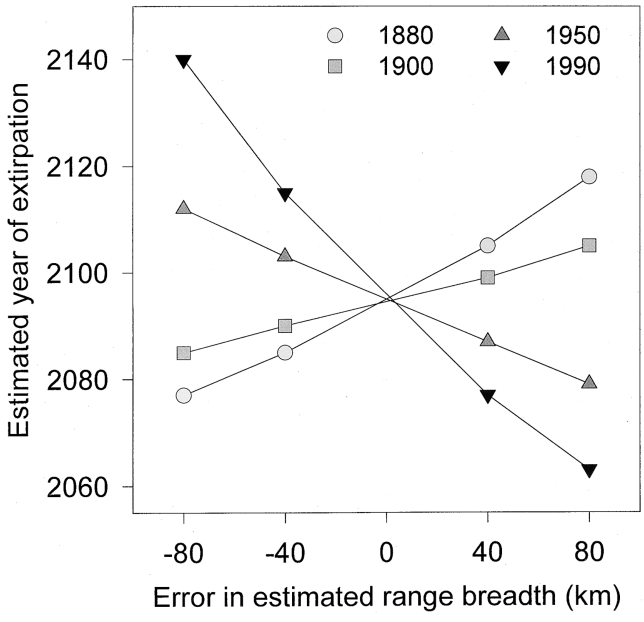

Figure 3. Sensitivity of estimated persistence time of woodland caribou in Ontario, Canada, to errors in range delineations, 1880–1990.

variation in the earliest and latest observations, especially those from 1990. Errors in the 1990 southern range limits (i.e., 80 km north or south) modified the expected time to extirpation by 76 years (Fig. 3).

Discussion

Woodland caribou epitomize biological conservation as "a hard-to-perceive, slow-motion crisis" (Ehrlich 2002:33). In Ontario, taiga-dwelling caribou have been slowly and systematically swept away for more than a century on an erosion of range that has been apparent for more than 50 years (de Vos & Peterson 1951). This trend is continuing (Thompson 2000). During 1998–2001, for example, woodland caribou at the southeastern range limits in Ontario declined at a population rate of growth, r, of -0.15 (W. J. Rettie, unpublished data). Approximately half of the historic range of woodland caribou in the province remains. Similarly, for 18 other species of medium to large mammals in North America, Ceballos and Ehrlich (2002) reported an average loss of 44% of their historic ranges.

The decline of a species entails the progressive loss of populations (Hughes et al. 1997; Hobbs & Mooney 1998; Schaefer et al. 2001; Ceballos & Ehrlich 2002). Although range recession might be tolerably estimated, transcribing this spatial pattern into a decrease in animal numbers or extinction of populations is more problematic (Ceballos & Ehrlich 2002). Indeed, population estimates of woodland caribou in Ontario have varied widely (de Vos & and Peterson 1951; Cumming & Beange 1993; Cumming 1998), owing to the imprecision of assessing low animal densities over a vast area. The metapopulation density, the number of discrete winter groups per unit area, may provide a useful alternative. I found comparable regional metapopulation densities among studies of taiga-inhabiting caribou, although this pattern remains to be examined in other landscape structures, such as peatlands (Stuart-Smith et al. 1997). Coupled with the sustained tempo of range retraction, this indicates the disappearance of approximately 18 caribou wintering areas per decade during the decline in Ontario, 1880–1990.

The recession of woodland caribou in a consistent, northerly direction—in contrast to retraction toward the center of the range—implies an anthropogenic agent of decline (Channell & Lomolino 2000; Rodríguez 2002). Indeed, the southern limits of caribou distribution corresponded remarkably well to the northern front of human encroachment, as indicated by the extent of timber harvesting (Fig. 1). Similarly, Voigt et al. (2000) ascribed woodland caribou disappearance in Ontario from 1950 to 1995 to landscape disturbance, although they did not differentiate wildfire from logging. Timber removal, however, may represent only a surrogate for other effects of human incursion, such as roads and faunal change. The decline of woodland caribou has increasingly been attributed to overharvesting or elevated predation, resulting from facilitated human access or from habitat alterations leading to increases in wolves and other prey (Bergerud 1974; Bergerud & Elliot 1986; Seip & Cichowski 1996).

Refugia from human encroachment may be vital. Indeed, remnant "island" populations of woodland caribou (e.g., Pukaskwa National Park and the Slate Islands along the north shore of Lake Superior [Fig. 1; Bergerud 1996]) are consistent with patterns of other endangered species. Where detrimental human effects spread like contagion, species' persistence becomes more likely at the periphery, rather than the core, of their range (McShea et al. 1999; Channell & Lomolino 2000).

Assessing the likelihood of population persistence is an important task of conservation biology (Beissinger & Westphal 1998). The consistent, long-term range recession of woodland caribou (Fig. 2) provides a novel, geographic approach to this question, indicating that the ecotype is liable to be extirpated from Ontario within a century. As with all long-term population viability analyses (Boyce 1992), however, some caution is warranted. Errors in the historical range delineations affected the projected time to extirpation (Fig. 3). A constant rate of range recession (Fig. 2), moreover, is implied by this analysis. The present data are inadequate to evaluate this assumption. Nevertheless, a slight curvilinear trend (Fig. 2) could dramatically increase the persistence time for woodland caribou.

On the other hand, the projected scenario may be optimistic. First, the rate at which forests are being converted by clearcutting is accelerating in the province (Perera & Baldwin 2000), and recently the Ontario government proposed the Northern Boreal Initiative, land-use planning north of the current limits of forest harvesting (Fig. 1) that would extend forestry and other resource activities northward (Ontario Ministry of Natural Resources 2001). Second, theory suggests that it is not essential to destroy all habitat patches to eradicate a whole metapopulation (Caughley & Gunn 1996). Third, the potential time-lag between habitat change and local disappearance—the "extinction debt" (Tilman et al. 1994)—suggests that a decline may continue even after the deleterious agent has been removed.

The twentieth century has marked a period of unabated decline for caribou in the taiga. Documenting a decline, however, represents only the first step to species recovery (Caughley & Gunn 1996). The challenge, which is considerable for an animal operating on such large spatial and temporal scales (Bergerud 1988; Racey & Armstrong 2000), will be to stem the demise of woodland caribou during the twenty-first century.

Acknowledgments

I am grateful for the efforts of personnel from the Ontario Ministry of Natural Resources to collect and collate

the large-scale, long-term data on which these analyses were based. B. R. Patterson and two anonymous reviewers provided useful comments that substantially improved the manuscript.

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