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DECLINES IN POPULATIONS OF WOODLAND CARIBOU

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Abstract: We summarize the demography of woodland caribou (*Rangifer tarandus caribou*) inhabiting 6 ranges in northeast Alberta, Canada, from 1993 to 2002. Among ranges, mean annual survival of radiomarked adult females averaged 0.88 (range: 0.86–0.93). Predation by wolves (*Canis lupus*) and other predators was implicated as the most common cause of death for adult caribou in northeast Alberta. Pregnancy rates (90–100%) and calf production (75–95%) were relatively high in all caribou ranges; however, mean annual recruitment was near or below 20 calves per 100 cows in most ranges ($\bar{x}$ = 17.1, range = 11.4–22.7). Caribou populations in 3 ranges have declined at average rates exceeding those that would lead to a 50% decline from initial population size over 3 generations; another population is declining at half this rate. Populations of caribou in 2 ranges appear to be stable, declining marginally since inception of our study. The current distribution, intensity, amount, and type of human activity in and near caribou ranges is likely compromising the integrity of caribou habitat. Treatment of declines will require new land-use guidelines that promote caribou conservation.

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Woodland caribou are thought to be declining throughout most of their range in North America (Gray 1999), and the species currently is listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002). The combination of habitat destruction, hunting, disturbance by humans (e.g., construction of roads, seismic lines, and pipelines), and predation (e.g., wolf and black bear [*Ursus americanus*]) all are factors implicated in the decline of woodland caribou (Ferguson and Gauthier 1992, Mallory and Hillis 1998, Gray 1999, Dzus 2001). In many parts of woodland caribou range, forest management practices and the spread of agriculture, oil and gas exploration, and mining have resulted in the loss, alteration, and fragmentation of important caribou habitat and introduction of novel caribou predators (e.g., coyotes [*Canis latrans*]; Crête and Desrosiers 1995) and diseases (meningeal brainworm [*Parelaphostrongylus tenuis*]; Bergerud and Mercer 1989, Pitt and Jordan 1994). Woodland caribou have been extir-

pated from vast areas in the southern part of their range (Fig. 1), the area where most human intrusion and development has occurred (Gray 1999).

In Alberta, the government supports exploration and resource extraction in woodland caribou range “provided the integrity of the habitat is maintained to support its use by caribou” (Alberta Energy 1991). Agencies such as World Wildlife Fund Canada, COSEWIC, the Canadian Wildlife Federation, and the Alberta Conservation Association have all recognized the need for a conservation strategy to protect woodland caribou in the province. In addition, several companies in the forestry, oil, and gas industries have committed themselves to the concept of sustainable development, thus supporting steps to mitigate negative effects of resource exploration and extraction on caribou.

Although most agree that woodland caribou in Alberta must be protected, knowledge of the ecology of caribou in the region has been limited, impairing the development of management strategies that would achieve this goal (Stuart-Smith et al. 1997). For example, only circumstantial evidence suggests that caribou have declined throughout most of their range in the province (Edmonds and Bloomfield 1984, Brown and Hobson 1998), making it difficult to support or refute the general perception of population declines (e.g., Bradshaw and Hebert 1996). Here,

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Fig. 1. Our study area encompassed 6 woodland caribou ranges in northeast Alberta, Canada (stars with range names): the West Side of the Athabasca River (WSAR), East Side of the Athabasca River (ESAR), Alberta and Saskatchewan sections of the Royal Canadian Air Force's Cold Lake Air Weapons Range (CLAWR-AB and CLAWR-SK), in the Caribou Mountains (CM), and near the community of Red Earth (RE). Shaded regions indicate areas of current woodland caribou distribution. The hatched line approximates the historic southern limit of woodland caribou range (adapted from Dzus 2001).

we quantified declines in populations of the boreal forest ecotype of woodland caribou (boreal caribou) in northeast Alberta from 1993 to 2002. Our work was part of a multifaceted research program (Boreal Caribou Research Program [BCRP]) initiated by government, industry, and academic partners (Boreal Caribou Committee [BCC]) to address concerns about the potential effects of human developments on caribou in Alberta.

METHODS AND STUDY AREA

Study Area

Our study area encompassed 6 boreal caribou ranges in northeast Alberta: the West Side of the Athabasca River (WSAR), East Side of the Athabasca River (ESAR), Alberta and Saskatchewan sections of the Royal Canadian Air Force's Cold

Lake Air Weapons Range (CLAWR-AB and CLAWR-SK), in the Caribou Mountains (CM), and near the community of Red Earth (RE; Fig. 1). Elevations range between 500 and 700 m, with little topographic variation except in the Caribou Mountains (elevation 1,000 m). Black spruce (*Picea mariana*) and tamarack (*Larix laricina*) dominated fens and bogs in lowlands. Uplands were dominated by white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), and trembling aspen (*Populus tremuloides*). Bradshaw et al. (1995) provides a detailed description of the landscape typical of boreal caribou range in northeast Alberta.

Animals and Telemetry

Between 1991 and 2002, the BCRP physically immobilized 332 female caribou using nets projected from a net gun and fired from a helicopter. All animals were equipped with very high-frequency (VHF) radiocollars (Lotek Engineering Inc., Newmarket, Ontario, Canada; Telonics Inc., Mesa, Arizona, USA). We monitored survival of caribou by aerial location of radiomarked caribou on a monthly or biweekly basis during 1993–2002 for ESAR and WSAR, 1995–2002 for RE and CM, and 1998–2002 for CLAWR-AB and CLAWR-SK. Our objective was to maintain a sample size of at least 20 female caribou per range each year ($\bar{x} = 27.1$, $SD = 7.9$, $n = 40$ range-years) by redeploying radiocollars in ranges where mortalities or battery failures occurred. When possible, we determined cause of death by recovering radiocollars as soon as mercury switches indicated prolonged (>8 hr) lack of animal motion.

Adult Survival Rates

We used Pollock et al.'s (1989) staggered-entry modification of Kaplan and Meier's (1958) survivorship model to estimate adult annual survival (S). We calculated survival for each range and each year (May–Apr). Data were processed using a computer program coded from Krebs (1989). We based means on the geometric average across all years (Steele and Torrie 1980). We bootstrapped our data (1,000 replicates) to obtain 95% confidence intervals for average survival rates (Manly 1997).

Calf Production and Recruitment Rates

Calf production was assessed by determining pregnancy rates based on analyses of serum collected during captures in January–February of each year of study (Stuart-Smith et al. 1997), and by counting the number of cows observed with calves at their side during the calving season

Table 1. Geometric means and 95% confidence intervals (CI) of adult annual female survival (*S*) and yearly ratio of calves per 100 cows (*R*) for woodland caribou in Alberta, Canada, 1993–2002.

Range ^a	Years monitored	<i>S</i>	95% CI	<i>R</i>	95% CI
WSAR	9	0.891	0.865 to 0.915	0.227	0.194 to 0.270
ESAR	9	0.861	0.838 to 0.888	0.183	0.134 to 0.248
RE	7	0.866	0.790 to 0.945	0.160	0.114 to 0.232
CM	7	0.889	0.830 to 0.952	0.121	0.087 to 0.166
CLAB	4	0.929	0.909 to 0.950	0.114	0.078 to 0.162
CLSK	4	0.863	0.825 to 0.891	0.220	0.160 to 0.303
Total ($\bar{x}$)	40	0.883		0.171	

^a The caribou ranges encompassed by our study area: West Side of the Athabasca River (WSAR), East Side of the Athabasca River (ESAR), near the community of Red Earth (RE), in the Caribou Mountains (CM), and Alberta and Saskatchewan sections of the Royal Canadian Air Force's Cold Lake Air Weapons Range (CLAWR-AB and CLAWR-SK).

(Apr–Jun). We determined calf recruitment (*R*) from aerial surveys in March of the following year by counting the number of calves and adults in each range associated with radiomarked caribou. Once located, groups of caribou were counted and animals classified as adult female, mature male, and calf. We identified females by the presence of a black vulva patch and males by lack thereof. Recruitment was expressed as a ratio of calves per 100 adult females (Hatter and Bergerud 1991). We averaged each annual ratio of calves per 100 cows over years to obtain a geometric mean (Steele and Torrie 1980) and obtained the 95% confidence interval by bootstrapping our data with 1,000 replicates (Manly 1997; Hayes et al. 2003).

Rates of Increase

For each range and year, we estimated the finite rate of population increase (λ) from annual recruitment of females (assuming a 50:50 sex ratio in calf production and equal survival of sexes to time of census) and annual adult female mortality (*M*; calculated as $1 - S$) obtained from both natural and known human-caused sources. We used the formula outlined by Hatter and Bergerud (1991):

$$\lambda = (1 - M) / (1 - R).$$

This method lends itself well to estimating population growth rates when measuring adult survival and recruitment from calf surveys (review in Hatter and Bergerud 1991). For each range, we determined λ for the entire period of study as the geometric mean of annual estimates of λ (Caughley 1977). We bootstrapped 95% confidence intervals for estimates of λ for the period of study from annual estimates (Manly 1997).

RESULTS

Survival and Recruitment

Average annual adult survival of female caribou varied from 0.86 to 0.93 for monitored ranges during our study (Table 1). The frequency of mortality events showed strong seasonal bias, with 78.8% of mortalities occurring within the snow-free period (Apr–Oct; Fig. 2). Predation (suspected wolves and other predators) was implicated as the most common cause of death for adult caribou in northeast Alberta (52% of 112 mortalities). Five mortalities (4%) were assigned to natural causes other than predation (e.g., carcass without signs of predation). We could not ascertain cause of death for 32 mortalities (29%), largely due to delays between the occurrence of mortalities and site investigations. Hunting and/or poaching was the cause of 9 deaths of adult caribou (8%). Eight additional radiocollar disappearances (7%) were classified as suspicious (suspected human-caused as radio-

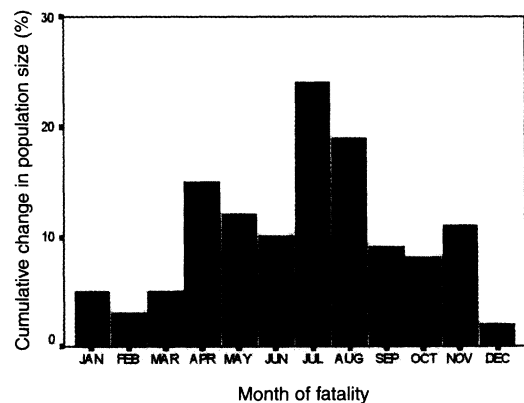


Fig. 2. Frequency distribution of mortalities by month ($n = 112$) for caribou in northern Alberta, Canada, 1993–2002.

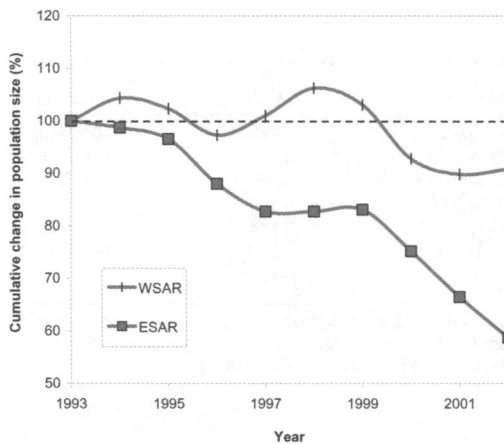


Fig. 3. Cumulative change in population size (%) for woodland caribou in on the East (ESAR) and west (WSAR) side of the Athabasca River, Alberta, Canada, 1993–2002.

collars disappeared with no apparent weakening of battery signal during previous relocations). Suspicious disappearances were censored from Kaplan-Meier estimates of survival.

Pregnancy rates and calf production in north-east Alberta was high in all ranges. Stuart-Smith *et al.* (1997) reported an 86% pregnancy rate based on analysis of progesterone in blood serum for caribou in WSAR and ESAR. From 1998 to 2000, our collection of serum samples from females captured in CLAWR-AB, CLAWR-SK, CM, RE, and WSAR ($n = 93$) indicated that 90–100% of adult females were pregnant. Pregnancy rates for females field-aged as young adults (likely 1.5 yr old) were lower (3 of 11 in 1998, but 3 of 3 in 2000). Observations of cows with calves in spring support the results of blood analyses with 70–95% of females producing calves. Because some calves die very soon after parturition, our estimates for calf production from aerial surveys should be considered minimal.

In most ranges, calf recruitment averaged near or below 20 calves per 100 cows (Table 1). Red Earth had the highest single-year calf recruitment, with 45 calves per 100 cows in 1997–1998. Caribou Mountains and CLAWR-AB herds had the lowest single-year calf recruitment, with only 6 calves per 100 cows in 2000–2001. Recruitment observed in March 2001 was the lowest since inception of study for WSAR (17 calves per 100 cows), ESAR (10 calves per 100 cows), and CLAWR-SK (13 calves per 100 cows). Red Earth experienced its lowest recruitment in 2002 (8 calves per 100 cows).

Rates of Increase

Caribou populations in 4 ranges exhibited substantial declines during our study: ESAR ($\lambda = 0.963$, 95% CI: 0.914 to 1.015), RE ($\lambda = 0.963$, 95% CI: 0.864 to 1.091), CM ($\lambda = 0.955$, 95% CI: 0.875 to 1.045), and CLAWR-SK ($\lambda = 0.976$, 95% CI: 0.918 to 1.038). Populations of caribou in WSAR ($\lambda = 1.010$, 95% CI: 0.970 to 1.057) and CLAWR-AB ($\lambda = 0.991$, 95% CI: 0.947 to 1.036) appeared to be stable. Trends in population growth, expressed as a percentage of unknown population size at commencement of our study, illustrate inter-annual variation captured in confidence intervals of λ (Figs. 3, 4).

DISCUSSION

Survival rates of adult female caribou in our study (Table 1) compare favorably to populations that are thought to be stable or declining in adjacent provinces (e.g., 0.71–0.92 in southeast British Columbia, Seip 1992; 0.84 in central Saskatchewan, Rettie and Messier 1998). Our results also agree with prior assessments of adult female survival for caribou in Alberta (0.85, Fuller and Keith 1981; 0.75, Edmonds 1988; 0.88, Stuart-Smith *et al.* 1997). Recruitment (Table 1), however, appears to be lower than for populations with adult survival rates similar to our study (e.g., 37 calves per 100 cows in Wells Gray Provincial Park, British Columbia, Seip 1992; 32 calves per 100 cows in Muskwa, British Columbia, Bergerud and Elliot 1998; 28 calves per 100 cows in Saskatchewan, Rettie and Messier 1998). Al-

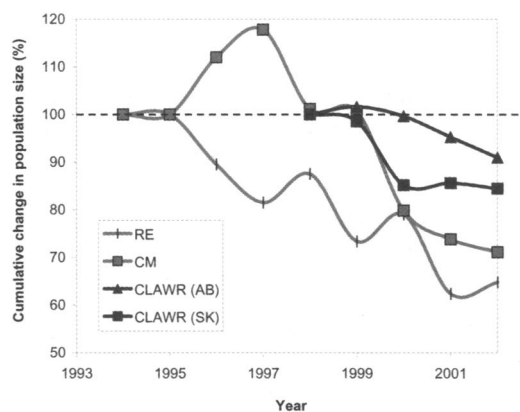


Fig. 4. Cumulative change in population size (%) for woodland caribou in Alberta, Canada, near the community of Red Earth (RE) and in the Caribou Mountains (CM), 1994–2002; and in the Alberta and Saskatchewan sections of the Royal Canadian Air Force's Cold Lake Air Weapons Range (CLAWR [AB] and CLAWR [SK]), 1998–2002.

though survival rates in our study were consistent with those of stable populations, recruitment rates appear too low to prevent population declines.

Analyses of population viability (Boyce 1992) have yet to be conducted for caribou in northeast Alberta, largely because accurate estimates of current population sizes do not exist (the provincial metapopulation is estimated at between 3,600 and 6,700 animals; Dzus 2001). Nonetheless, we can roughly anticipate conservation prospects for boreal caribou in the province. Based on our data, the outlook is not promising. Consider a population with 400 animals that is declining according to a finite rate of increase of 0.965, which is the average for caribou in ESAR, RE, CM, and CLAWR-SK (400 animals would be an optimistic population size for all of these ranges). Within 60 years, such a population would be reduced to only 50 animals and subject to potentially severe effects of demographic stochasticity and inbreeding (Caughley and Gunn 1996) and would exhibit a high probability of immediate extinction (White 2000). Further, a high likelihood exists of catastrophic fire events in the boreal forest of Alberta that would undoubtedly affect persistence probabilities for caribou (e.g., an average of 41% of the area of caribou home ranges in CM have burned in the past 20 yr, primarily due to 2 large fires in 1982 and 1995; J. Dunford, University of Alberta, unpublished data). We strongly feel that unless rates of decline are reduced or reversed for declining populations, caribou likely will be extirpated from large areas of northern Alberta in the near future.

Reversing population trends of caribou will not be easy, likely requiring a number of steps and considerable political will. Caughley and Gunn (1996) provide a sound framework for diagnosing causes of and treating population declines. Having detected trends and determined rates of decline in our study, we should now focus our energy into researching causes of declines of boreal caribou populations in Alberta. Caughley and Gunn's (1996) strategy is to develop associations between potential agents of decline and populations in time and/or space.

Because caribou historically have coexisted with predators in the boreal forest for thousands of years and are only now facing extirpation from large parts of Alberta, the recent (<60 yr) addition of large-scale anthropogenic disturbances in the system likely has played a role in generating population declines. Some progress has already been made on identifying potential relationships

between human activity and observed declines in woodland caribou populations (e.g., James and Stuart-Smith 2000, Dyer et al. 2001). For example, human disturbance in the boreal forest has been linked to enhancing the functional response (i.e., search time) of predators such as wolves to woodland caribou (James and Stuart-Smith 2000).

Although wolves often are reported to be less abundant in areas with high road density (e.g., Thiel 1985, Jensen et al. 1986, Mech et al. 1988), roads and other linear corridors that receive little human use may be attractive to wolves as easy travel routes (Thurber et al. 1994). Seismic lines, cut as part of geophysical research programs, and roads that cut through caribou habitat may provide wolves with increased access to caribou herds and allow wolves to travel more rapidly through the environment, increasing hunting efficiency. In north-central Alberta, James and Stuart-Smith (2000) reported that locations of wolves equipped with Global Positioning System (GPS) radiocollars were closer to linear corridors than expected from random, and that caribou mortalities attributed to wolf predation were closer to linear corridors than were locations from live caribou, implying that caribou that lived closer to linear corridors were at higher risk of being killed by wolves. In addition, travel rates of GPS radiomarked wolves on linear corridors were almost 3 times faster than the average speed of travel in the surrounding forest (James 1999).

High wolf use, and thus high predation risk, may explain why boreal caribou in Alberta tend to avoid seismic lines and roads (Dyer et al. 2001). Predation therefore probably should be viewed as only a proximate limiting factor for boreal caribou in northern Alberta. Disturbances resulting in large-scale changes in habitat structure that affect habitat use and movements of predators and alternate prey may be ultimately responsible for declines of caribou populations in the province. Further research into causes of observed caribou population declines will help focus treatments to conserve boreal caribou in Alberta. Unfortunately, testing hypotheses by experiment to confirm that putative agents are causally linked to population declines (Caughley and Gunn 1996) will not be easy due to the rarity of boreal caribou, lack of suitable treatment sites (e.g., control areas without extensive industrial footprints already in place), and the high expense of conducting research on caribou.

Treatment of caribou population declines should not, however, go without for lack of defin-

itive causal links between putative agents and population declines. Where strong inference suggests a cause, treatments applied as experiments may have the dual power of confirming diagnoses and evaluating success, which would be measured by an increase in populations (reverse in trends) and not by treatment level (Caughley and Gunn 1996). In Alberta, agencies such as the BCC have enabled us to work with industry and government to take steps toward applying several treatments as experiments. For example, the BCC currently is working to initiate a project to recover linear features on the landscape and measure effects on caribou populations. However, reclamation activities likely will take several years to affect habitat effectiveness, unless reducing access is part of the treatment. The BCC is also researching the efficacy of "best practices" such as cutting low-impact (≤ 3 m wide) seismic lines, as opposed to traditional (≥ 5 m wide) seismic lines, on improving caribou habitat effectiveness.

Treatment of declines may also include a review of government and industry policies and practices that restrict caribou conservation. Current land-use guidelines must be reviewed, improved, implemented, and adhered to. For example, improved coordination among stakeholders conducting activities simultaneously in the same area (e.g., sharing transportation corridors) may minimize potential negative effects on caribou populations. Caribou conservation may benefit from identification of a cumulative effects threshold that can be incorporated into the management of caribou ranges as part of a comprehensive strategy to integrate caribou conservation and human activity on a common land base. Regardless of treatment, caribou population declines should be reassessed after treatments are likely to have taken effect to gauge the success of population recovery strategies.

MANAGEMENT IMPLICATIONS

Our study presents the first concrete assessment of long-term population declines for woodland caribou in North America. The International Union for the Conservation of Nature (IUCN) considers negative growth rates leading to a 50% decline over 3 generations as the primary criterion for designating a species as "endangered" (IUCN 1994). For ESAR, RE, and CM, populations of caribou are declining at rates exceeding this threshold, if we assume 3 generations for caribou span 20 years (average age of females is 6.9 yr; Fuller and Keith 1981). "Threatened" status would apply to caribou of CLAWR-SK, which are declining at a

rate that would result in $>20\%$, but $<50\%$, decline in population size over 3 generations (IUCN 1994). Populations of caribou in WSAR and CLAWR-AB appear to be stable. Future research into the causes of observed declines in boreal caribou range is critical to the proper treatment of declines. However, we must recognize that research alone will not ensure the persistence of Alberta's caribou populations. Land-use guidelines must be reviewed, improved, and implemented to promote caribou conservation in the region. Adherence to a conservation strategy that requires application of mitigative measures using an experimental design will serve to better identify putative agents of caribou population declines in northeast Alberta. This will benefit caribou conservation not only in Alberta, but also in other North American populations of woodland caribou that—although less well-studied—are also thought to be declining.

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