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LONG-TERM CHANGES IN DEMOGRAPHY AND MIGRATION OF NEWFOUNDLAND CARIBOU

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Long-term studies of demography and movements are rare but critical to understanding long-lived mobile mammals like caribou (*Rangifer tarandus*). We studied changes in the abundance, vital rates, body size, and timing of migration of the Buchans Plateau caribou herd in Newfoundland, Canada. From the early 1960s to 2000, the population grew at 6.5%/year, although survival and recruitment indicated a declining growth rate (1.4%) by the late 1990s. The numerical increase was negatively associated with other population attributes. Rates of parturition, survival to 6 months of age, and recruitment diminished significantly. Adults exhibited substantial decreases in body size. Spring migration was significantly later and autumn migration significantly earlier. We surmise that these responses may reflect heightened density-dependent competition for summer forage.

Key words: body size, density dependence, migration, population growth, *Rangifer tarandus*, recruitment, regulation

The regulation of abundance remains a central question in mammalian population ecology. For highly migratory herbivores, such as caribou (*Rangifer tarandus*) and wildebeest (*Connochaetes taurinus*), evidence is mounting that competition for high-quality forage is regulatory (Dublin et al. 1990; Mduma et al. 1999; Messier et al. 1988; Skogland 1985). For these species, migration appears to represent an effective strategy to escape predation. Mobile ungulates and their precocial young may be able to space themselves from their less mobile predators (Bergerud 1988; Fryxell and Sinclair 1988; Fryxell et al. 1988).

Further associations between the spatial dynamics and demography of large herbivores might be anticipated. For example, because migratory species may experience seasonal limitations in food, the timing of migration might be sensitive to heightened intraspecific competition for resources (Fryxell and Sinclair 1988). This hypothesis has not been tested. For long-lived mobile mammals, however, understanding such relationships often requires extensive observations in space and time (Mduma et al. 1999; Stirling et al. 1999). Despite recent advances (Bergerud 1996), the dynamics of migratory caribou remain incompletely understood. Long-term studies may help to resolve that shortcoming.

The Buchans Plateau caribou (*R. t. caribou*) herd (Fig. 1) affords an opportunity for long-term investigation. Migration of the Buchans herd represents a traditional movement of caribou on the island of Newfoundland; since the late 1950s it has been intensively studied (Bergerud 1974), along with herd size, population structure, and body size. By augmenting long-term data with more recent observations from radio telemetry and age and sex classifications, we assembled a data set of >40 years on

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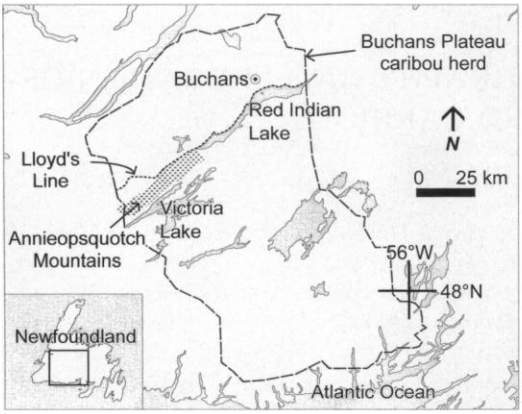

FIG. 1.—Range of the Buchans Plateau caribou (*Rangifer tarandus*) herd, Newfoundland, Canada, 1994–2000.

the movements and demography of caribou. We report on long-term trends in population ecology of the herd. We anticipated, coincident with a 20-fold numerical increase, that the Buchans herd would exhibit signs of density-dependent feedback in growth, vital rates, body condition, and timing of migration, consistent with migratory caribou elsewhere (Bergerud 1996; Couturier et al. 1990; Messier et al. 1988; Skogland 1985).

MATERIALS AND METHODS

Study area.—The Buchans herd occupied 12,000 km^2 in west-central Newfoundland (Fig. 1). Migratory animals used a narrow corridor to move between calving and summer ranges in the north and winter range in the south. Winter range was composed primarily of expansive dwarf shrub heaths, fens, and bogs, dominated by shrubs such as willow (*Salix*) and alder (*Alnus*) and characterized by low snow depths and frequent thaws that provide caribou with accessible forage (Daaman 1983). Calving and summer ranges on the Buchans Plateau were also primarily open land, a broad expanse of shallow patterned peatland, which offered excellent visibility and terrain for predator avoidance. Scattered forests were composed primarily of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and tamarack (*Larix laricina*). These seasonal ranges were geographically separated by the Red Indian Lake watershed (Fig. 1), which was perpendicular to the migration route. Annual snow accumulation averaged approximately 280 cm and persisted until late May. Mean daily temperatures at Buchans (Fig. 1) during 1965–1990 were −8.1°C in January and 16.2°C in July.

The population was hunted annually after 1965; from 1966 to 1997, approximately 5,834 animals were harvested. Wolves (*Canis lupus*) have been absent from Newfoundland since about 1922, but lynx (*Lynx canadensis*) and black bear (*Ursus americanus*) occurred throughout the study area and preyed regularly on young caribou (Mahoney et al. 1990). Coyotes (*Canis latrans*), which reached the island of Newfoundland in 1985, occurred in the study area and were known to kill both young and adults. Moose (*Alces alces*) were widespread in forested areas. Human access to the study area was confined largely to a few scattered logging roads. A hydroelectric development was constructed in the midst of the migratory pathway of the herd during 1997–1998 (Mahoney and Schaefer 2002).

Data collection.—Aerial censuses were conducted intermittently, from 1960 to 2000, in spring or autumn with systematic strip, random block, or stratified–random block procedures (S. P. Mahoney, in litt.). Population structure was estimated in most years, 1966–2000, from ground surveys, with the aid of a spotting scope, or from a helicopter. At calving time (3–16 June), adult (≥2-year-old) females were deemed parous if accompanied by young, if carrying antlers, or if possessing an extended udder (Whitten 1995). In autumn (19 September–3 November), the sex ratio of adults and proportion of young in the herd were determined. In addition, the percentage of young was determined in late spring (14–23 May) during 1997–2000. Each season, ≥220 animals were categorized into age and sex classes.

Information on body size was gathered during live-captures in 1963 and 1994–1996: total length (tip of the nose to end of the last tail vertebra), hind foot length (tuber calcis to distal tip of hoof), shoulder height (tip of spinous process to distal tip of hoof), and chest circumference (girth of the thorax directly behind the scapula) were measured to the nearest 1 cm. Animals were captured and handled according to the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Radio tracking was initiated in 1994 (Mahoney and Schaefer 2002). Adult caribou were immobilized with xylazine hydrochloride during October 1993 ($n = 14$), September 1994 ($n = 37$), and October 1996 ($n = 27$) and were fitted with mortality-sensing VHF radio transmitters (Lotek Engineering, Newmarket, Ontario, Canada) with a battery life expectancy of 48 months. Radio telemetry reconnaissance was conducted from 23 September 1994 to 14 June 2000. Each year, 34–51 radiocollared caribou were monitored with a STOHL-equipped Cessna 185 aircraft with an onboard global positioning system. The median interval between consecutive relocations of individuals was 6 days. Radiolocations had an accuracy of ≤ 500 m based upon repeated blind positioning of test transmitters.

Data from radio telemetry were supplemented by intermittent, direct observations of migration, from 1957 to 1963 (Bergerud 1974) and from 1979 to 1982 (Newfoundland and Labrador Wildlife Science Division, in litt.). In those studies, daily observations of caribou and their tracks were made along logging roads for >10 days each year. Studies during 1957–1963 were conducted in the vicinity of Victoria Lake; those during 1979–1982 were southeast of Red Indian Lake, along Lloyd's Line (Fig. 1).

Data analyses.—To compute a population growth rate, we regressed the natural logarithm ($\log_e$) of estimated population size from aerial surveys against time (Messier et al. 1988). For 1996–1999, we also calculated finite rates-of-increase (λ) from survival–recruitment schedules (Bergerud and Elliot 1986) based on $\lambda = (1 - M)/(1 - R)$, where M is mortality rate and R is recruitment rate for the entire herd. We estimated M using Heisey–Fuller procedure (Heisey and Fuller 1985) on data collected from 1 May to 30 April, and R as the percentage of young in late May.

We analyzed changes in the rates of parturition (percentage of females parous) and recruitment (young as percentage of the total population and young per 100 females in autumn) by dividing the study into 2 periods (1966–1982 and 1991–2000) and applying t-tests to examine differences. We tested for changes in survival of young as the difference between parturition rate in spring and recruitment rate (young per 100 females) in autumn, with an F-test, as the interaction between period and rate. Morphological differences in animals ≥ 4 years old were examined with sex and period (1963 or 1994–1996) as factors. Because all 4 linear measurements of body size were interrelated ($r > 0.46$), we employed 2-way multivariate analysis of variance (MANOVA).

For analysis of migration, we used 54 individuals (14 males, 40 females) tracked for ≥ 360 days and ≥ 30 locations each. Because males and females did not differ in timing of migration (Mahoney and Schaefer 2002), we pooled data across sexes. To document timing of migration, we drew a line near Lloyd's River (Lloyd's Line) along the north shore of Red Indian Lake and the woods road extending to the southeast and northwest (Fig. 1). For each animal and year, we estimated dates of migration as the midpoint between 2 successive radiolocations when the line was crossed. To maintain precision, we used only observations ≤ 14 days apart. Although arbitrary, we considered this approach preferable to inclusion of observations from highly infrequent relocations.

To assess long-term variation, we determined the modal date of each migration. Although our long-term analysis of migration may suffer from bias by the more southerly observations at Victoria Lake (Bergerud 1974) compared with those from southeast of Red Indian Lake (Fig. 1), average speed of caribou during migration (>11 km/4 days—J. A. Schaefer and S. P. Mahoney, in litt.) relative to distance between those 2 observation sites (<15 km) indicates that such bias was minimal. In addition, we analyzed timing of migration in relation to snowfall in April, May, October, and November, recorded at the meteorological station at Buchans (Fig. 1; Environment Canada, in litt.).

Nonparametric tests (Fisher's exact test, Spearman rank correlation, Mann–Whitney tests) were used for dates. Analyses were conducted using Statistica '99 Edition (Statsoft Inc., Tulsa, Oklahoma). Data are presented as mean ± *SE*.

RESULTS

Aerial estimates indicated that the Buchans herd grew from 450 animals in 1960 to 6,102 animals in 2000 (Fig. 2). The exponential rate of increase (r), indicated by the slope of natural log of the population esti-

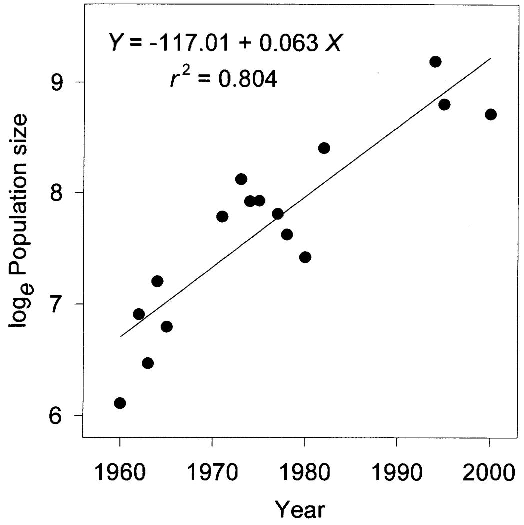

FIG. 2.—Growth of the Buchans Plateau caribou (*Rangifer tarandus*) herd, Newfoundland, Canada, 1960–2000, as determined by aerial census estimates.

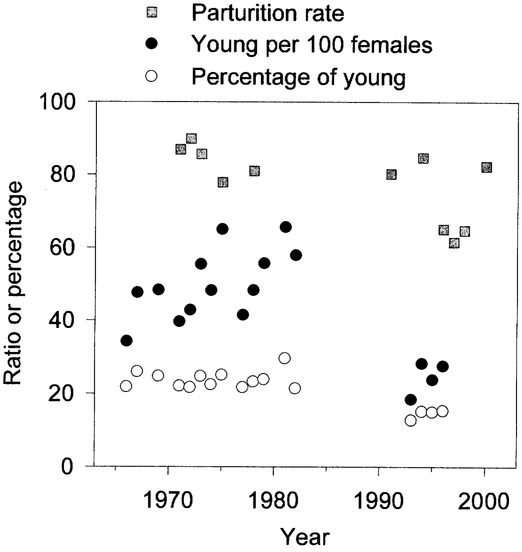

FIG. 3.—Dynamics of the Buchans Plateau caribou (*Rangifer tarandus*) herd, Newfoundland, Canada, 1966–2000, displayed as the parturition rate (percentage), ratio of young per 100 adult females in autumn, and young as percentage of the total population in autumn.

mates over the entire period, was 0.063, but there was some indication of slower growth after an estimated peak of 9,834 caribou in 1994 (Fig. 2). Indeed, during 1996–1999, annual rates of survival (0.898 ± 0.0073) and recruitment (0.134 ± 0.0011) revealed progressively lower growth: r = 0.0511 in 1996–1997, 0.0425 in 1997–1998, and 0.0135 in 1998–1999. During 1996–1999, mean annual survival was not substantially higher for adult females (0.876) than for males (0.773; $t = 1.618$, *d.f.* = 8, $P = 0.144$), although the sex ratio in autumn for >1-year-olds was skewed toward females (25.3 ± 1.7% males, 1966–1996). Mortalities of radiocollared animals were caused by legal harvest ($n = 6$; all males) or bear predation ($n = 4$; all females); causes of other mortalities ($n = 14$) were undetermined.

Rates of parturition and recruitment declined over the course of the study (Fig. 3). During 1966–1982 and 1991–2000, respectively, there were significant declines in percentage of females that were parous in spring (84.2 ± 2.1 versus 73.0 ± 4.2; $t = 2.20$, *d.f.* = 9, $P = 0.055$), number of young per 100 adult females in autumn (50.1 ± 2.6 versus 24.6 ± 2.3; $t = 5.12$, *d.f.* = 15, $P = 0.0001$), and young as percentage of the total population in autumn (23.7 ± 0.6 versus 14.6 ± 0.6; $t = 7.42$, *d.f.* = 15, $P < 0.0001$). There was no significant change in adult sex ratio, expressed as the percentage of males in the adult population (26.2 ± 2.0 versus 24.9 ± 3.0; $t = 0.337$, *d.f.* = 15, $P = 0.741$). The recruitment rate (young per 100 females in autumn) declined more precipitously than the parturition rate, a result that was marginally significant (Fig. 3; $F = 4.02$, *d.f.* = 1, 24, $P = 0.056$), indicating reduced survival of young to 6 months of age.

The change in growth for the Buchans herd was further reflected in a decline in body size of adults. Males and females were dimorphic (MANOVA; Rao's $R = 6.90$, *d.f.* = 4, 35, $P < 0.001$), and both sexes exhibited decreases in all linear measures of approximately 6%, from 1963 to the 1990s (Table 1; Rao's $R = 10.22$, *d.f.* = 4, 35, $P < 0.001$). The decline was equitable for

TABLE 1.—Morphological measurements of male and female Buchans caribou (*Rangifer tarandus*; ≥4 years old), 1963–1996, in Newfoundland, Canada.

		Shoulder height (cm)		Hind foot length (cm)		Total length (cm)		Chest circumference (cm)	
Period	*n*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*
Males									
1963	5	127.4	2.0	59.2	0.6	204.0	2.2	128.4	5.7
1994–1996	4	119.0	3.6	54.5	0.9	190.0	4.3	124.0	4.3
Females									
1963	19	118.8	1.3	56.5	0.6	192.1	1.6	121.6	1.1
1994–1996	14	115.1	1.2	54.1	0.4	180.5	1.4	110.6	0.9

males and females; there was no interaction between sex and time (Rao's $R = 1.86$, *d.f.* = 4, 35, $P = 0.139$).

Migratory behavior of radiocollared animals did not appear to differ between the sexes. Twelve (5 males, 7 females) of 54 animals were nonmigratory in ≥1 year; 3 animals (1 males, 2 females), resident in the northern portion of the range, did not migrate in any year. Although slightly biased toward males, the propensity to be nonmigratory was not associated with sex (Fisher's exact test; $P = 0.150$).

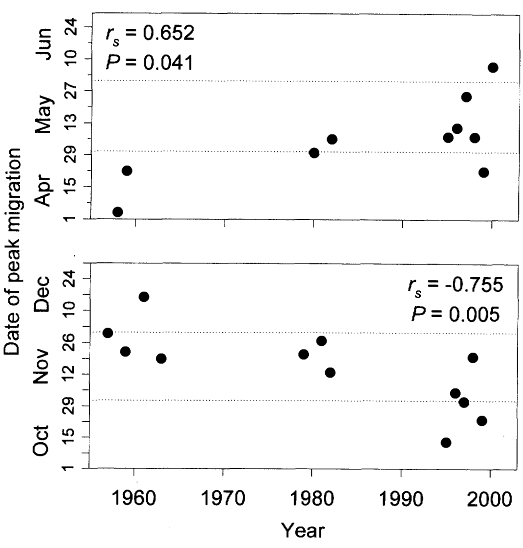

FIG. 4.—Variation in the timing of peak migration in spring and autumn by the Buchans Plateau caribou (*Rangifer tarandus*) herd, Newfoundland, Canada, 1957–2000. Observations during 1957–1963 were derived from Bergerud (1974). Months are delimited by dashed lines.

There were significant, long-term shifts in timing of both spring and autumn migrations (Fig. 4). Peak of spring migration occurred during 4–22 April in 1958–1959, 30 April–6 May in 1980–1982, and 22 April–7 June in 1995–2000. Peak in autumn migration occurred during 19 November–16 December 1957–1963, 13–27 November 1979–1982, and 13 October–20 November 1995–1999. These shifts indicated that, over 42 years, the herd spent approximately 60 days less per year on their calving and summer ranges. There was no relationship between autumn migration and snowfall in October ($r_s = -0.029$, $P = 0.929$) or November ($r_s = -0.147$, $P = 0.648$), or between spring migration and snowfall in April ($r_s = 0.402$, $P = 0.249$) or May ($r_s = 0.462$, $P = 0.179$).

DISCUSSION

The migration of caribou has been interpreted as a strategy to reduce the risk of mortality, because caribou space themselves away from wolves (Bergerud 1988, 1996), their principal predator (Hearn et al. 1990). Newfoundland caribou, including the Buchans herd, have continued to migrate and aggregate on traditional calving grounds, even though wolves have been extinct for decades. The proximate influences on autumn migration may be snowfall (Bergerud 1974). We failed to document snowfall as a predictor of the timing of migration in spring or autumn, although our analysis was hindered by the coarse temporal scale of weather data.

During the growth phase of the Buchans herd, vital rates were comparable to those of other expanding populations of migratory caribou. For example, when the Porcupine herd of Alaska–Yukon (Fancy et al. 1994) was increasing at a rate, r, of 0.0467, those caribou exhibited a similar parturition rate (80%), annual survival rate of adult males (0.826) and females (0.842), and adult sex ratio (62 males : 100 females). The George River herd of Québec–Labrador during its increasing phase (r = 0.110—Messier et al. 1988) had similar schedules of recruitment (about 52 young per 100 females; Couturier et al. 1990; Messier et al. 1988) and adult female survival (0.865—Hearn et al. 1990). Bergerud (1992) concluded that, when hunting mortality is <5%, young (6–10 months of age) representing >15% of the population are indicative of growth. Indeed, the Buchans herd maintained an average of 23.7% young in autumn during 1966–1982 but only 14.6% during 1993–1996 (Fig. 3). This pattern supports our contention that the herd had slowed, or perhaps halted, its growth by the late 1990s.

Population regulation remains a dominant theme in mammalian ecology. For the Buchans herd, the apparent decline in population growth was mirrored in other facets of its demography, including changes in parturition, survival of young, recruitment (Fig. 3), and body size (Table 1). Similarly, for Norwegian reindeer living in the absence of wolves, diminished fecundity, juvenile survival, and body size were the manifestation of density-dependent winter food limitation (Skogland 1985).

Perhaps the best test case of population regulation of migratory *Rangifer* has been the George River herd. Coincident with its numerical increase have been degradation of its calving and summer habitat (Manseau et al. 1996), diminished body size, and reduced rates of pregnancy, recruitment (Couturier et al. 1990), and adult survival (Crête et al. 1996). Heightened competition for high-quality summer food has been implicated as a regulatory mechanism (Crête and Huot 1993; Messier et al. 1988). These findings stimulated a profound shift in ecological understanding of migratory caribou. The hypothesis of regulation by wolf predation (Bergerud 1967) was not supported. Especially in the absence of wolves, similar mechanisms of regulation of the Buchans herd might be anticipated. Our results are consistent with this conclusion. At the same time, the decreases in body size (Table 1) and in time spent on the calving and summer grounds (Fig. 4) by Buchans caribou appear to discount regulation by other predators.

Fryxell and Sinclair (1988) hypothesized that migratory ungulates, experiencing seasonal forage competition at high densities, might adjust the timing of migration to optimize the use of resources. Indeed, the progressively earlier autumn migration of the Buchans herd, coupled with its tardier spring migration (Fig. 4), may be related to its burgeoning numbers and a depletion of summer forage. Compared with the late 1950s, Buchans caribou in the late 1990s spent approximately 2 months less per year on their calving and summer ranges. An analogous response was exhibited by the George River herd. After that population peaked in 1989 (Crête et al. 1996), autumn migration was postponed; the mean date of crossing tree line shifted by approximately 3 weeks between 1987 and 1992, presumably a response to relaxed competition for summer food (A. T. Bergerud, in litt.). Conversely, before 1987, the date of calving by George River caribou became progressively delayed (Couturier et al. 1990). Such responses underscore that, for *Rangifer*, abundance and distribution are intimately linked (Bergerud 1996). We believe that further, important insights into ungulate demography are likely to be gleaned from sustained research efforts.

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