

Losing the predator–prey space race leads to extirpation of woodland caribou from Pukaskwa National Park ¹

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Abstract: Persistence for woodland caribou (*Rangifer tarandus*) in Pukaskwa National Park (PNP, Ontario, Canada; 1878 km²) was tied to females finding safe calving areas on offshore islands with a water barrier created by Lake Superior. During 1975–1988, PNP caribou fluctuated around a carrying capacity of 24, but after 1988 the population declined, falling to 5 individuals by 2009. Caribou are now likely extirpated from PNP, even in the absence of any local or increased anthropogenic disturbance since the protected area was created in 1978. As moose (*Alces alces*) in the region declined concurrently, their relative density remained higher along the Lake Superior coastal strip than further inland, the reverse of the situation during 1975–1988; moose especially held to the coast during heavy snow years. Wolves (*Canis lupus*) accordingly shifted more of their hunting effort to the coast, likely encountering both moose and caribou with increasing search efficiency. These behaviours are described as a predator–prey “space race” that wolves eventually won.

Keywords: *Canis lupus*, *Rangifer tarandus*, predation, Pukaskwa National Park, woodland caribou, wolves.

Résumé: La persistance du caribou des bois (*Rangifer tarandus*) dans le parc national Pukaskwa (PNP, Ontario, Canada; 1878 km²) était liée au succès des femelles à trouver des aires de mise bas sécuritaires sur des îles avec la barrière d'eau que constitue le lac Supérieur. Durant la période 1975-1988, la population de caribous du PNP a fluctué autour d'une capacité de support de 24 individus, mais après 1988 la population s'est mise à décliner atteignant 5 individus en 2009. Le caribou est maintenant probablement disparu du PNP, même en l'absence de perturbations locales ou d'une augmentation des perturbations anthropiques depuis la création de l'aire protégée en 1978. La population d'orignaux (*Alces alces*) a aussi diminué dans la région au cours de la même période, leur densité relative est demeurée plus élevée en bordure du lac Supérieur qu'à l'intérieur des terres, ce qui est l'inverse de la situation qui a prévalu en 1975-1988; les orignaux sont demeurés près des rives du lac en particulier durant les années de forte accumulation de neige. Les loups (*Canis lupus*) ont conséquemment augmenté leurs efforts de chasse près des rives du lac, rencontrant probablement autant des orignaux que des caribous avec de plus en plus de succès. Ces comportements sont décrits comme une « course à l'espace » entre un prédateur et une proie, course que les loups ont finalement remportée.

Mots-clés: *Canis lupus*, caribou des bois, loups, parc national Pukaskwa, prédation, *Rangifer tarandus*.

Nomenclature: Flora of North America Editorial Committee, 1993; Wilson & Reeder, 2005.

Introduction

Woodland caribou (*Rangifer tarandus caribou*) are declining throughout Canada's boreal forest (Thomas & Gray, 2002). Decline in caribou since European settlement has been most directly due to increased predation, primarily by wolves (*Canis lupus*), and also to overhunting (Bergerud, 1974). With hunting woodland caribou in North America now largely outlawed, wolf predation should more often be the ultimate factor associated with their decline, while anthropogenic effects on the forest, such as logging or oil and gas exploration, persist as stressors on the animals and their habitat that initiate the decline (Schaefer, 2003; Vors *et al.*, 2007; Semeniuk *et al.*, 2012). We illustrate the

role of wolf predation in caribou decline and extirpation from Pukaskwa National Park (PNP) in Ontario, Canada by reporting how predator and prey interact on a landscape where early 20th-century industrial activity isolated a prey population and set up a “space race” for survival in a narrow strip of habitat along Lake Superior. We track caribou, moose (*Alces alces*), and wolves to show how an increased influence of wolves, likely on both prey, co-occurs with range restriction for caribou and a shift of moose toward the coastal habitat. The “space race” between predators and prey, as described by Sih (2005), is such that the side that has a stronger spatial constraint loses the race. Where individuals in a prey population reduce their activity in response to predators, predators will win the race (Sih & McCarthy, 2002). Our illustration with PNP caribou parallels the cases where other isolated caribou populations in

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Canadian national parks, including Revelstoke, Glacier, and Banff, were extirpated and predation was a strong factor in their demise (Hebblewhite, White & Musiani, 2010; Serrouya & Wittmer, 2010).

Woodland caribou were described in 1910 as “very abundant on the north shore of Lake Superior where they replace the Deer [*Odocoileus virginianus*] and Moose of the Canadian [southern] Zones” (de Vos & Peterson, 1951). A collection of small populations near the current southern margin of their range, woodland caribou on the north shore of Lake Superior historically included a stable population in PNP; the park was established in 1978 as a protected area in part to allow persistence of the caribou. The PNP population is isolated from areas of continuous woodland caribou distribution to the north by a mountainous, deep-snow area and from other Lake Superior coastal populations by railway construction and mine development at the turn of the 20th century in areas just outside PNP. Inside PNP, logging and other anthropogenic disturbances have been virtually absent due to the remoteness of the area. With the lack of immigration of caribou from elsewhere in the region a chronic factor affecting the stability of the PNP population, an extirpation trajectory launched by early industrial activity began in earnest in 1989, and the last caribou was photographed there in December 2011. Illustrating the effect of wolf predation in initiating the recent decline of the PNP caribou population is the purpose of this paper. Why would a population persistent for most of a century, if not longer, now fail within the protection of a national park?

We will answer this question by describing the PNP system as a loss of what we document as density-dependent (DD, 1975–1988) regulation at a carrying capacity defined by a narrow coastal range for caribou. When anchored to offshore islands as a relative safety refuge along the Lake Superior coast, caribou adopted a new set of behaviours associated with the “landscape of fear” created by predators (Brown, Laundré & Gurung, 1999; Laundré, Hernández & Alterndorf, 2001). Wolves forced inverse density dependence (IDD, 1989–2009) and population decline in caribou when land-fast ice enabled them to cross Lake Superior to the islands. Our description is an example of the potential anti-regulatory effect of wolves on caribou, in which predation rate increases with declines in prey

density, ultimately caused by the predictability of caribou behaviour on a landscape (Wittmer, Sinclair & McLellan, 2005; McLellan *et al.*, 2010).

Methods

STUDY AREA

Pukaskwa National Park (PNP) is located along 83 km of the northeastern Lake Superior coast and encompasses an area of 1878 km². The coastal zone accounts for 22% of this area and is dominated by 2 forest types, black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) coniferous forest and balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) mixedwood forest (Vance *et al.*, 2008). Lightning-caused fires in 1936 burned about 466 km² in the northwestern part of PNP, constituting the largest area of disturbance during the mid-20th century.

The centre of caribou distribution in PNP, Otter Island, is 83 km at its closest point from the Trans-Canada Highway, which is separated from the Lake Superior shoreline by a mountainous area in the interior of PNP that rises 641 m above sea level, 458 m above the mean level of Lake Superior. There is only 1 road accessing the shoreline, near the north end of the protected area. Four packs of wolves have territories that include the coastal distribution of caribou at PNP; these packs are named for the rivers that most often form their travel routes to the shoreline from inland (Forshner *et al.*, 2003; Table I; Figure 1). In total there are 48 islands and islets along the Lake Superior shoreline, some of which are large enough and far enough away from the mainland that they are available as winter refuges for caribou in the absence of land-fast ice. Caribou are relatively safe from wolves when they move to such offshore islands; black bears (*Ursus americanus*) sometimes reach the islands, as do moose. The only cases of predation on caribou on offshore islands we observed occurred when land-fast ice connected the islands to the mainland in winter and wolf tracks were observed crossing the ice. Some islands, especially those protected from wind, are rarely free of ice in winter and are therefore not frequented by caribou. Moose are managed in the surrounding provincial Wildlife Management Unit 33, which encompasses a somewhat more accessible area of about 65 000 km² surrounding PNP,

TABLE I. Aggregations, based on annual winter surveys of moose, caribou, and wolves within 5 km of the Pukaskwa National Park shoreline, corresponding to 4 coastal areas occupied by wolf packs from 1974 to 1988.

Wolf pack and area hunted	Aggregations			Ratios ^a	
	Moose·km ⁻²	Caribou·km ⁻²	Wolves·km ⁻²	Caribou–wolf	Moose–wolf
Willow River Pack					
Willow River and Oiseau Bay, 65 km ²	86 (1.32)	67 (1.03)	43 (0.67)	1.6	2.0
Swallow River Pack					
Nicols Cove to Cascade River, 125 km ²	141 (1.13)	84 (0.67)	38 (0.27)	2.2	3.7
Cascade River Pack					
Cascade River, Otter Island, and Otter Head, 35 km ²	22 (0.62)	60 ^b (1.71)	12 (0.34)	5.0	1.8
Pukaskwa River Pack ^c					
Tagouche Creek to Otter River, 40 km ²	54 (1.35)	14 (0.26)	17 (0.42)	0.8	3.2

^a Correlation coefficients: caribou and wolves, $R = 0.01$, $P = 0.89$; moose and wolves, $R = 0.50$, $P = 0.02$.

^b Twenty-four (40%) on Otter Island.

^c The boundary along the shoreline between the Pukaskwa River and the Cascade River packs is not clear, as the Pukaskwa River wolves were never radio-collared. The Pukaskwa River Pack travels far up the river and ranges east outside the park.

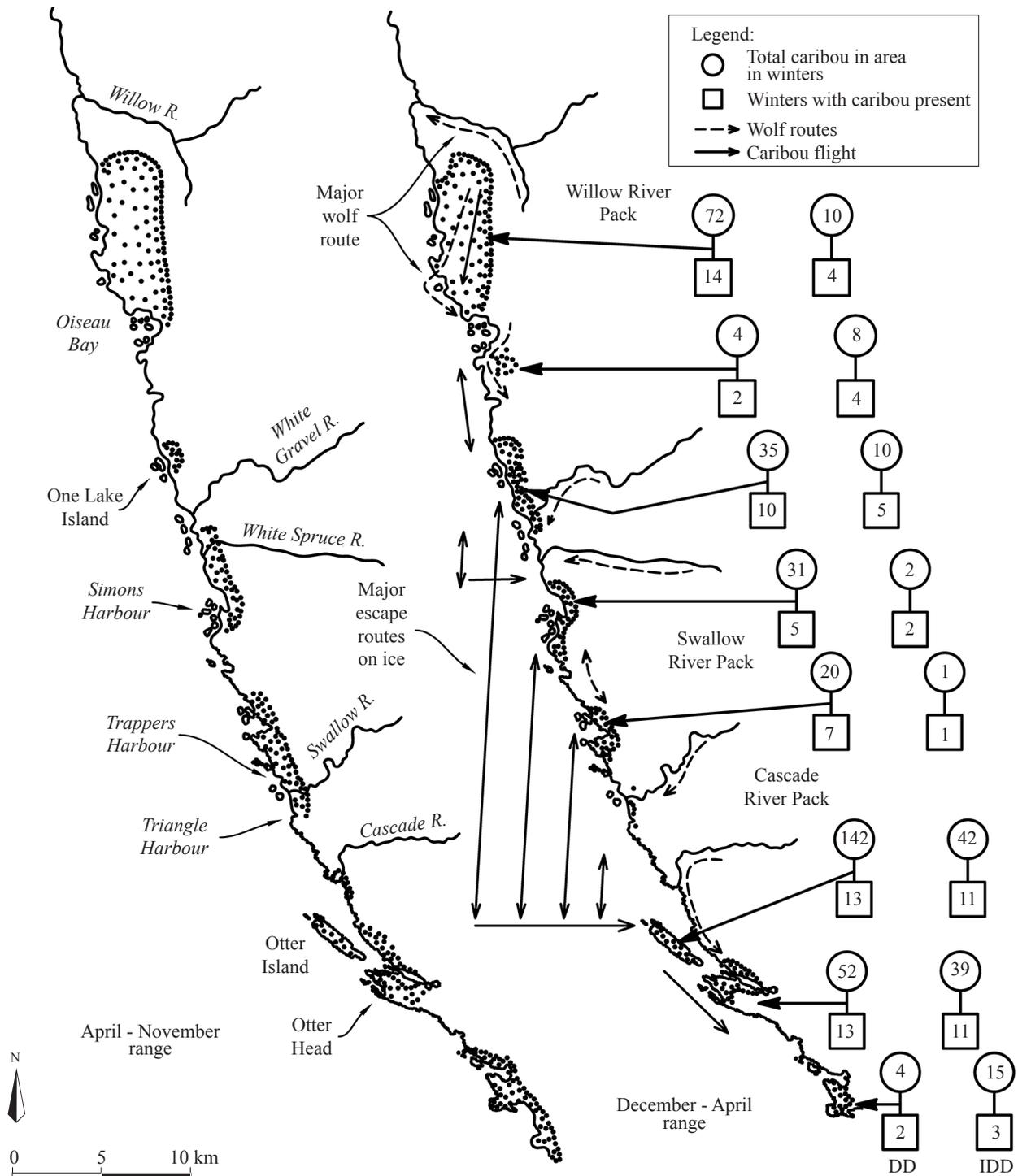


FIGURE 1. Distribution of caribou (dotted areas) along the shoreline of Pukaskwa National Park, Ontario (Canada) in summer (left) and winter (right), from 1974 to 1988. Typical routes of wolves approaching and traveling along the coast (dashed arrows) and flight paths of caribou leaving Otter Island (solid arrows) are also shown for winter, when wolves occasionally reach the island on land-fast ice. Note the lack of caribou at the mouths of rivers where wolves reach the coast. On the right margin, total numbers of caribou observed (in circles) over a stated number of winters (in squares) in different aggregations are listed separately for 1974–1988, when the population appears density dependent (DD) and for 1989–2009, when the population declines in an inverse density-dependent (IDD) fashion.

about 25% with road access and about 75% inaccessible except by foot.

Three features of the physical environment at PNP direct wolves, moose, and caribou toward a variable and

rugged coastal habitat distinct from the upland interior of the protected area. First, land-fast ice generally occurs when the December through March mean temperature falls below $-3.5\text{ }^{\circ}\text{C}$, creating a bridge linking offshore islands to the

PNP shoreline (Findlay, 1973). The January mean temperature at Wawa, Ontario, a weather station south of PNP and on the shoreline, was used as our index of winter severity in determining the effect of winter severity on caribou calf recruitment. Second, “balds”, rounded, alpine hilltops, occur at elevations above the river valleys traversed by wolves, extending along the Lake Superior shoreline, and are commonly occupied by caribou for their good sight and scent lines (Bergerud, 1985). Third, PNP receives more snowfall and experiences greater snow depths than any other point in Ontario, with average totals from December to April ranging from 330 cm near the coast to 455 cm in the interior (Findlay, 1973). During winters with deeper snow, moose move toward the coast, where both caribou and moose have better flight opportunity from predators than in the interior, due to shallower snow accumulation and windswept snow packs (Bergerud *et al.*, 2007). Snow depth at the end of February recorded at Wawa is used in our annual estimates of the effect of midwinter snow on predator and prey spatial distribution and our estimates of the effect of winter severity on caribou calf recruitment.

WINTER SEVERITY INDICES AND OTHER STATISTICS

We compared January mean temperature and midwinter snow depth between the 2 periods we identified in examining the trends, DD (1974–1988), the density-dependent period, and IDD (1989–2009), the decline period, by *t* test, following Shapiro–Wilk and Bartlett’s tests for normality and equality of variances; we also tested for correlations between the 2 indices of winter severity using Pearson’s product-moment. Our tests for normality and homogeneity of variances were standard for all series compared (as described below), and all correlations, linear regressions, and curve-fitting were done in BASIC microcomputer models (Spain, 1982).

CARIBOU COUNTS AND TELEMETRY

Caribou or their tracks were counted after fresh snowfalls in annual aerial surveys during February or March 1972–2009. Surveys were completed in as few consecutive days as possible (4.3 ± 0.3 d; mean \pm SE, $n = 20$) and were attempts to determine an annual minimum number of caribou. Before 1984, surveys were flown mostly parallel to the Lake Superior shoreline at 2-km intervals extending 5 km inland; survey crews also flew to known wintering areas and crisscrossed local ranges with circling patterns (Bergerud, 1985). After 1984, flight lines extended 3–5 km inland and perpendicular to the Lake Superior shoreline, separated into 500- to 1000-m intervals. Despite variation in methodology over the years, the population trend is reliable (Patterson *et al.*, 2014). Caribou were radio-tracked with very high frequency (VHF) collars in 1976 ($n = 4$), during 1983–1986 ($n = 8$), in 1992 ($n = 3$), and in 1996 ($n = 5$). Those tracked during 1983–1986 were monitored from the ground or a boat, by visual observation, or by radio-location and triangulation; they were not monitored routinely during winter or from the air, and replication was insufficient to use them to track survival systematically.

The difference in the number of adult caribou seen from survey year to survey year, minus the calves from the previous year recruited into the adult population, served as an index of adult mortality. In most winter surveys, there were caribou for which sex was not determined. Hence, the best index of calf recruitment was the percentage of calves observed in winter surveys rather than the number of calves per 100 adult females. Numbers of adults over time were modeled with the best-fit linear or polynomial regressions separately for the DD (1974–1988, $n = 11$) and IDD (1989–2009, $n = 9$) periods. Residuals were compared to a normal distribution by reviewing a normal probability plot. We compared our indices of calf recruitment and adult mortality to the number of adults in the same survey using a similar approach to regression modeling, but just for the DD period, because winter survey frequency switched from annual to biannual in 1988, so the 2 indices of population change were unavailable for the decline period. Calf recruitment and adult mortality were compared by *t* test between 2 series within the DD period: 6 years when land-fast ice connecting all offshore islands occurred and 5 years without land-fast ice. Calf recruitment was also compared to midwinter snow depth and January mean temperature in the same year as the winter survey.

MOOSE COUNTS AND TELEMETRY

Moose were counted in mid- to late winter, only after fresh snowfalls and by helicopter. In 5 annual counts during 1975–1979, transects were flown in fixed-wing aircraft to locate low- and high-density strata; the high-density stratum was surveyed by quadrat counts, with the helicopter circling towards the centre (Bergerud, Wyatt & Snyder, 1983). After 1979, surveys followed the methods outlined by Gasaway *et al.* (1986) that have been standardized across Ontario. The accuracy of the moose counts was improved when 35 moose were captured, fitted with VHF radio collars, and tracked in 1995 and 1996. Corrected moose density estimates were plotted for 1975–2008 ($n = 12$) and separately for 1986–2008 ($n = 7$) along the coastal strip <10 km from the Lake Superior shoreline to estimate linear trends as linear regressions through time. From aerial surveys during 1975–2008 ($n = 10$) in Wildlife Management Unit (WMU) 33 just outside of PNP, a third linear regression was estimated as a moose population trend for the region.

WOLF COUNTS AND TELEMETRY

Wolves were counted throughout PNP each year in January and/or February, depending on the presence of new snow, from 1975–1979 (Bergerud, Wyatt & Snider, 1983) and also during all moose surveys (Bergerud *et al.*, 2007). Counting wolves involved flying transects in helicopters north and south across PNP and generally perpendicular to rivers. The length of 29 wolf trails was 6.7 ± 0.9 km, long enough to be easily intercepted by flights with transects at 2–5 km intervals. Whenever tracks were found, the immediate area was circled to evaluate their uniqueness from other track aggregations. Population estimates of wolves during 1994–1998 were based on VHF tracking by Forshner *et al.* (2003) of 26 wolves across at least 7 packs, at a frequency of 4 times monthly in April through October

and 6 to 8 times monthly in November through March. Wolf track aggregations were compared by *t* test for years with and without land-fast ice.

FOOT RECONNAISSANCE

We walked the coastal hiking trail (58.7 km) from Pic River to the North Swallow River in May and September 1984, 1985, and 1986. During the walks, we counted tracks and scats of moose, caribou, and wolves, recording the location along each kilometre of trail, resulting in a fine-grained understanding of the distribution of the 2 ungulates and their predator in the northern portion of PNP. For the key island refuge for caribou, Otter Island, as well as the entirety of the coastal portion of PNP, we conducted additional foot reconnaissance during 1983–1986 by landing at regular intervals from a boat. Using both 4-km and 2-km Universal Transverse Mercator (UTM) grid cells on topographic maps, we plotted this foot tracking data and compared abundance of sign of moose, caribou, and wolves by calculating Pearson’s correlation coefficients separately for the May (winter sign) and September (summer sign) periods at the 2 UTM grid scales.

MAP ANALYSIS

Spatial analysis is germane to our study of the predator–prey “space race”. We plotted the winter survey observations of moose, caribou, and wolves on topographical maps separately for the DD and the IDD periods. We then divided the PNP shoreline area into 4 regions to quantify distribution and movement of caribou relative to the 4 wolf packs that frequent the area. On the basis of the distribution of wolf tracks along the coast in the 4 areas, we estimated whether 0, 1, 2, 3, or 4 packs had hunted the shoreline. We also segregated tracks as old or recent, and estimated the distance of all wolves and moose from the shoreline during the winter surveys. From this information, the routes of wolves approaching and traversing the coast were plotted. We used estimates of the mean distances of wolves and moose from the shoreline each year during the DD period to calculate linear regressions between these estimates, as well as with each against midwinter snow depth. We used the collared caribou locations to calculate annual ranges as minimum convex polygons encompassing all telemetry locations except for excursions during the breeding period for males during both DD and IDD periods. We also used them to estimate mean distances of caribou to the shoreline each year during both periods. We compared the DD and IDD periods in terms of caribou range size, predator and prey distance from the shoreline, caribou travel distances during breeding and post-calving, and predation rates on caribou using *t* test and Fisher’s exact χ^2 tests. We also compared for each period the co-occurrence of caribou and wolf aggregations spotted on “balds” during winter surveys with χ^2 tests of homogeneity.

Results

THE CARIBOU DEMOGRAPHIC SHIFT

During the DD period (density-dependent, through 1988), the PNP caribou population fluctuated with no significant long-term trend around a carrying

capacity of 24 individuals (number against years from 1974, $y = -600 + 0.314x$, $t_{14} = 1.19$, $P = 0.25$, $R^2 = 0.03$; Figure 2). An asymptotic, upward-trending curve of the observed number of calf recruits each winter was fit to population size ($y = 64x^{-0.107} + 100$, $t_{15} = 1.95$, $P = 0.04$, $R^2 = 0.35$); this curve intersected an exponential, upward-trending curve of our index of adult mortality fit to population size ($y = 20 / [1 + 1230e^{-0.25x}]$, $t_{11} = 5.14$, $P < 0.01$, $R^2 = 0.58$) at a theoretical point of stability of 24 caribou in the population. During the DD period, an increased number of caribou were observed in many surveys immediately following a year of decrease. The number of winter calf recruits was unrelated to midwinter snow depth ($R = -0.318$, $P = 0.35$, $n = 12$); calf recruitment did not, in fact, vary much ($16.8 \pm 1.8\%$ SE, $n = 16$). However, in 6 winters with some land-fast ice, calves were $13.3 \pm 1.6\%$ of caribou counted in surveys and the number of missing adults was 6.8 ± 1.7 , whereas in 5 winters with very little land-fast ice, the number of calf recruits was higher ($22.6 \pm 3.6\%$; $t_5 = 2.45$, $P = 0.05$) and missing caribou adults were fewer (1.2 ± 2.2 ; $t_8 = 2.32$, $P = 0.05$).

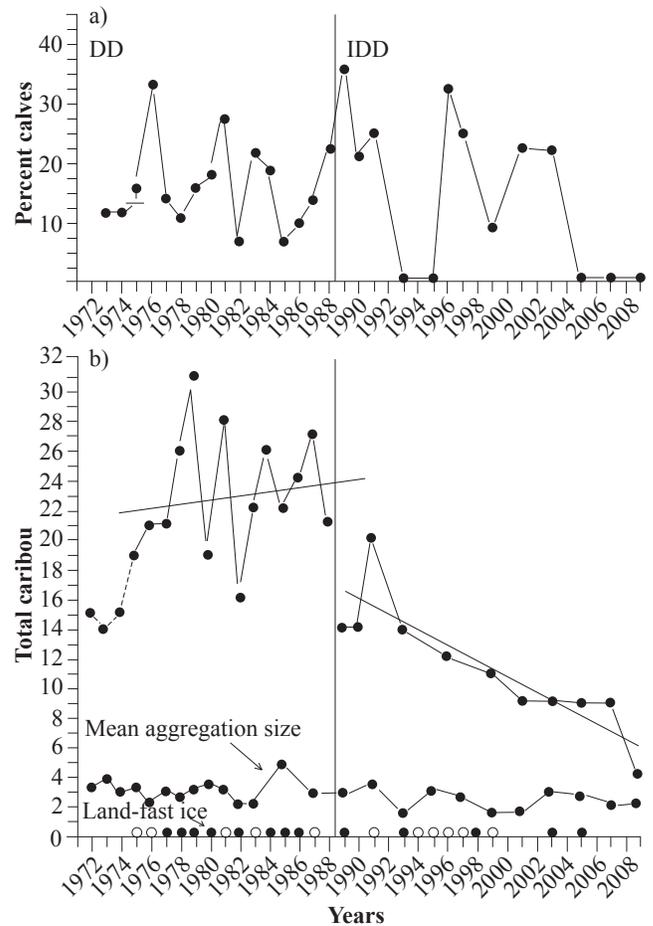


FIGURE 2. Percent calves (a) among the total number of woodland caribou counted annually in February or March 1972–2009 in Pukaskwa National Park (b, top series), mean caribou aggregation size (b, middle series), and presence (closed circles) or absence (open circles) of land-fast ice on Lake Superior (b, bottom series). The straight line regressions shown for total numbers by year can also be fit to exponential curves (see text). The series are divided into DD and IDD years, as defined in Figure 1.

During the subsequent IDD period (inversely density-dependent, from 1989), the caribou population declined ($y = 987 - 0.488x$, $t_{10} = -5.34$, $P < 0.001$, $R^2 = 0.73$; Figure 2). Calf recruitment was much lower than during the DD period ($10.8 \pm 3.2\%$; $t_{10} = -4.41$, $P = 0.001$). Moose, which increased in WMU 33 through the entire study period to at least 2005 (density [$\text{moose} \cdot \text{km}^{-2}$]), from 1974 over a period of 10 surveys: $y = 0.104 + 0.007x$, $t_9 = 4.43$, $P < 0.01$, $R^2 = 0.67$), declined within PNP during the same period but over 6 surveys: $y = 0.296 - 0.006x$, $t_5 = -4.74$, $P < 0.01$, $R^2 = 0.68$. Review of the 7 WMU 33 surveys that occurred after 1985 indicates that higher moose density occurred near the PNP shoreline relative to points inland, although density also declined near the shoreline (density [$\text{moose} \cdot \text{km}^{-2}$]), <10 km from the shoreline, from 1985, $y = 0.415 - 0.007x$, $t_6 = -2.83$, $P = 0.01$, $R^2 = 0.50$). Moose density within PNP declined from 0.18–0.20 $\text{moose} \cdot \text{km}^{-2}$ during 4 surveys in 1986–1990 to about 0.10 $\text{moose} \cdot \text{km}^{-2}$ in a 2008 survey. Number of calves per 100 female moose declined from 1985 ($y = 19.52 - 0.33x$, $t_{11} = -1.74$, $P = 0.05$, $R^2 = 0.32$).

CARIBOU, MOOSE, AND WOLF INTERACTIONS IN THE EARLY YEARS

During the DD period, we recorded 226 observations of caribou; all but 6 of these were <2 km from the Lake Superior shoreline, and 16% were on the shoreline. A regression with x in units of 0.1 km captured all caribou distances from the shoreline as $y = -192x^{0.506x} + 200$, $t_{225} = 10.4$, $P < 0.001$, $R^2 = 0.76$. The shoreline and larger offshore islands, including Refuge Island (about 5 ha), Otter Island (about 200 ha), and One Lake Island (actually a group of 3 islands totaling about 23 ha), served caribou throughout the study as areas to occupy during calving

and post-calving. Strong site fidelity to these refuges was observed among radio-collared females, and calves born on Otter Island were suspected to return over many later years to produce their own calves there (Table II, Figure 3). Adults captured for radio collaring had flight distances on release of only 414 ± 46 m ($n = 53$) and did not leave the islands where they were caught. In contrast, when tracks observed during winter surveys showed that wolves had reached an offshore island, caribou tracks were also observed leaving the island on land-fast ice (Figure 1). One such flight included 12 individuals that ran about 15 km before halting on the ice at Simons Harbour. Two collared females (Eunice and Velvet), both pregnant, left Otter Island in March 1984 when a wolf killed another caribou crossing on land-fast ice (Table II). Caribou flights such as these, observed from winter tracks, generally ended in an adjacent wolf territory.

In contrast to caribou (Figures 4a, 4b), wolves (Figure 4c), and especially moose (Figure 4d), were observed further inland from the shoreline. From tracks observed during winter surveys and from the radio-tracking by Forshner *et al.* (2003), we know that wolves approached the Lake Superior shoreline along major rivers, including the Cascade, Swallow, and White Gravel (Figure 1). Their paths bypassed more rugged coastal topography and suggested direct orientation to the shoreline. Wolves were often spotted along the shoreline, especially in winters when land-fast ice was present and they were able to search offshore islands for caribou. In 1977, 1980, and 1985 ice extended >0.5 km offshore, providing wolves easy access to Otter Island. In these winters, the number of wolf track aggregations counted was 10.2 ± 1.4 ($n = 3$), while in the 9 y without heavy ice during this first part of the study, significantly fewer were

TABLE II. Dates and locations for caribou captured^a and monitored in Pukaskwa National Park during 1983–1986.

Caribou and year	May-June	July-August	September-October	Dates (and locations) seen on mainland
Eunice				
1983	Otter Island (young female)	Otter Island	Otter Island	na
1984	Otter Island (18 June) ^b	Otter Island	Otter Island ^c	3 May (Trapper Harbour) ^b
1985	Otter Island (8 May) ^c	na	Otter Island (10 April)	18 April, 13 December
1986	Otter Island ^c	Otter Island	Otter Is./Mainland	25 April
Velvet				
1983	Otter Island (collared as calf)	Otter Is./Mainland	Mainland	10, 16 September
1984	Otter Island (18 June) ^b	Otter Island	Mainland	3 May (Refuge Island) ^b
1985	Otter Island ^c	Otter Is./Mainland	Mainland	See Figure 3c
1986	Otter Island ^c	Otter Is./Mainland	Mainland	16 May
Megan				
1984	Otter Island	Otter Island	Mainland	7, 8, 16, 18, 22 October
1985	Pointe La Canadienne	Otter Island	Otter Island	18 April
1986	Otter Island (20 June) ^c	Otter Island	Otter Island	13 September
Carla				
1984	Otter Island	Otter Island	Otter Island	12, 13, 14 August
1985	Mainland ^d	Otter Is./Mainland	Mainland	18 May, 12 June ^e
1986	Otter Island ^c	Otter Island (24 August)	Otter Is./Mainland	8 October

^a Captures (and recaptures) were all on Otter Island on the following dates: Eunice: 24 April 1983 (likely 1 y of age), 1 July 1983, 10 April 1985; Velvet: 18 June 1983 (at the time a calf), 22 June 1983, 17 June 1984, 13 June 1985, 2 October 1985; Megan: 29 June 1984; Carla: 30 June 1984.

^b A wolf reaches Otter Island in March and kills a male; Eunice and Velvet return to the mainland. By 18 June both are back on Otter Island without calves at heel.

^c Calf at heel.

^d At Otter Head (mainland) then moves 9 km to Pointe La Canadienne; may have lost a calf.

^e Moves 16 km (5 km inland) on 18 May 1985; may have lost a calf; returned to Otter Island with Megan for calving in 1986.

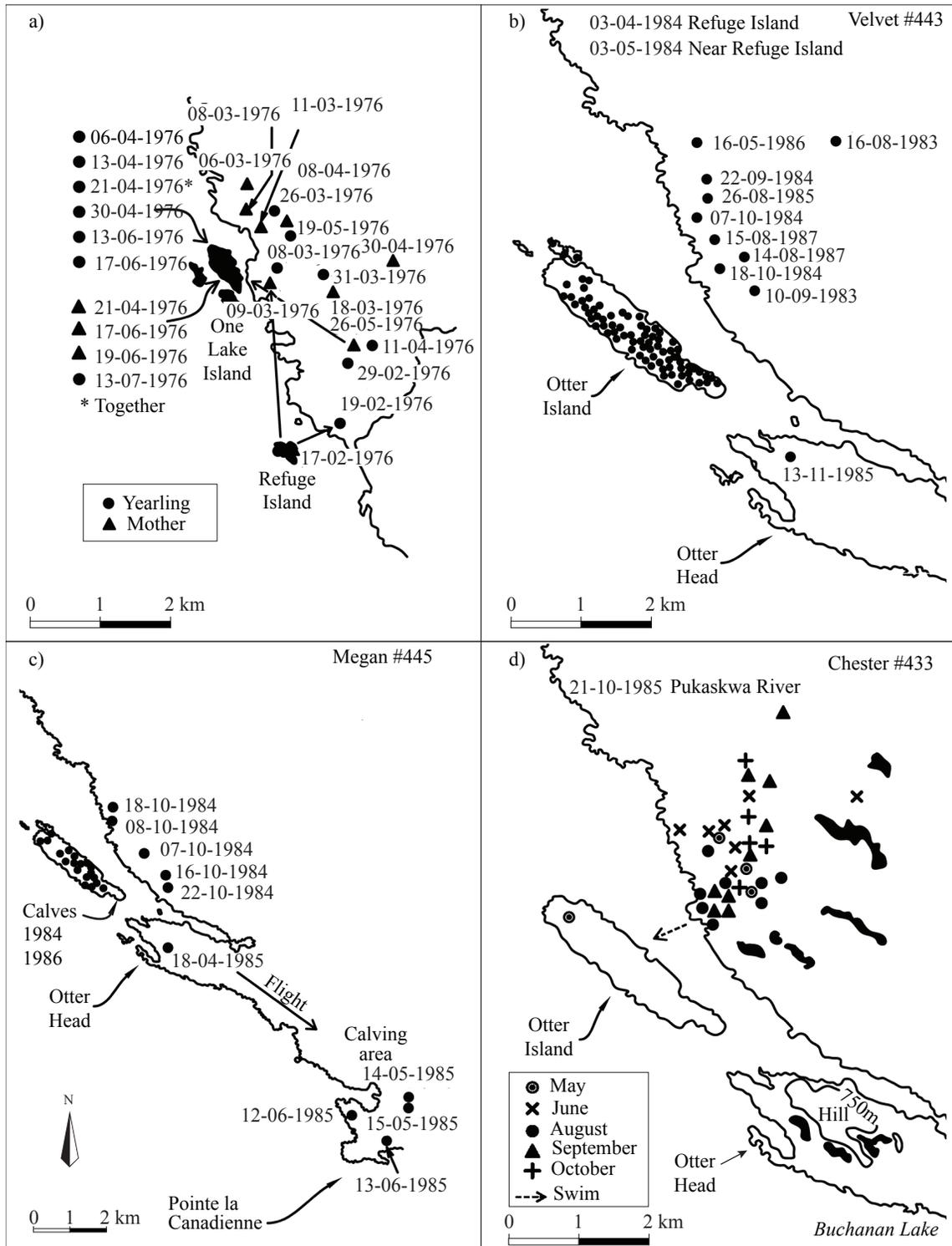


FIGURE 3. Four examples of movement and distribution of individual caribou tracked by radio telemetry in Pukaskwa National Park during the DD period: a) 1 female in 1976, b) 1 female in 1983–1987, c) 1 female in 1984–1985, and d) 1 male in 1985. The female collared on Refuge Island on 17 February 1976 in a) moved to One Lake Island and reunited with her calf, also collared. The calf imprinted to the new range and was there as a yearling together with the adult female the next year; the pair appeared exactly 10 y later with 5 other females north of Oiseau Bay, >10 km up the shoreline. Shoesmith (1978) documented a similar sequence of progeny imprinting to a safe area adjacent to a birth site in the first collaring work with caribou.

counted (Table III; $t_2 = 5.33$, $P = 0.03$); in 3 of the years without land-fast ice (1976, 1981, and 1983), no wolf tracks were seen along the entire coast.

During 1976–1987, midwinter snow depth was positively correlated with mean winter temperature ($R = 0.902$, $P < 0.01$, $n = 12$). With warmer winters and more snow,

more moose were spotted <10 km from the shoreline and the mean distance of moose from the shoreline was negatively correlated with midwinter snow ($R = -0.567$, $P < 0.01$, $n = 12$). Over the same period, mean distance of wolves from the shoreline was positively correlated with mean distance of moose from the shoreline ($R = 0.758$, $P < 0.01$, $n = 12$). Caribou ranged along the coast about 35 km, most of which was also occupied by wolves (Figure 4). The moose population was higher in winter and summer between White Gravel and North Swallow rivers, but lower opposite Otter Island and on Otter Point (Table I,

Figure 4d). The area of shoreline with fewest wolf sightings during winter aerial surveys during 1972–1987 was Otter Head, where the fewest moose occurred and caribou observations were most frequent. Of the very few wolf aggregations not observed on “balds”, 10 were travelling on rivers and 5 were travelling on ice on inland lakes.

Wolves occurred in 0.91 aggregations (packs)·km⁻¹ ($n = 11$), an occupancy rate similar to that seen in the interspersed spans of shoreline less frequented by caribou, where wolves were observed in 0.88 aggregations·km⁻¹. At the north and south ends of their PNP distribution, caribou

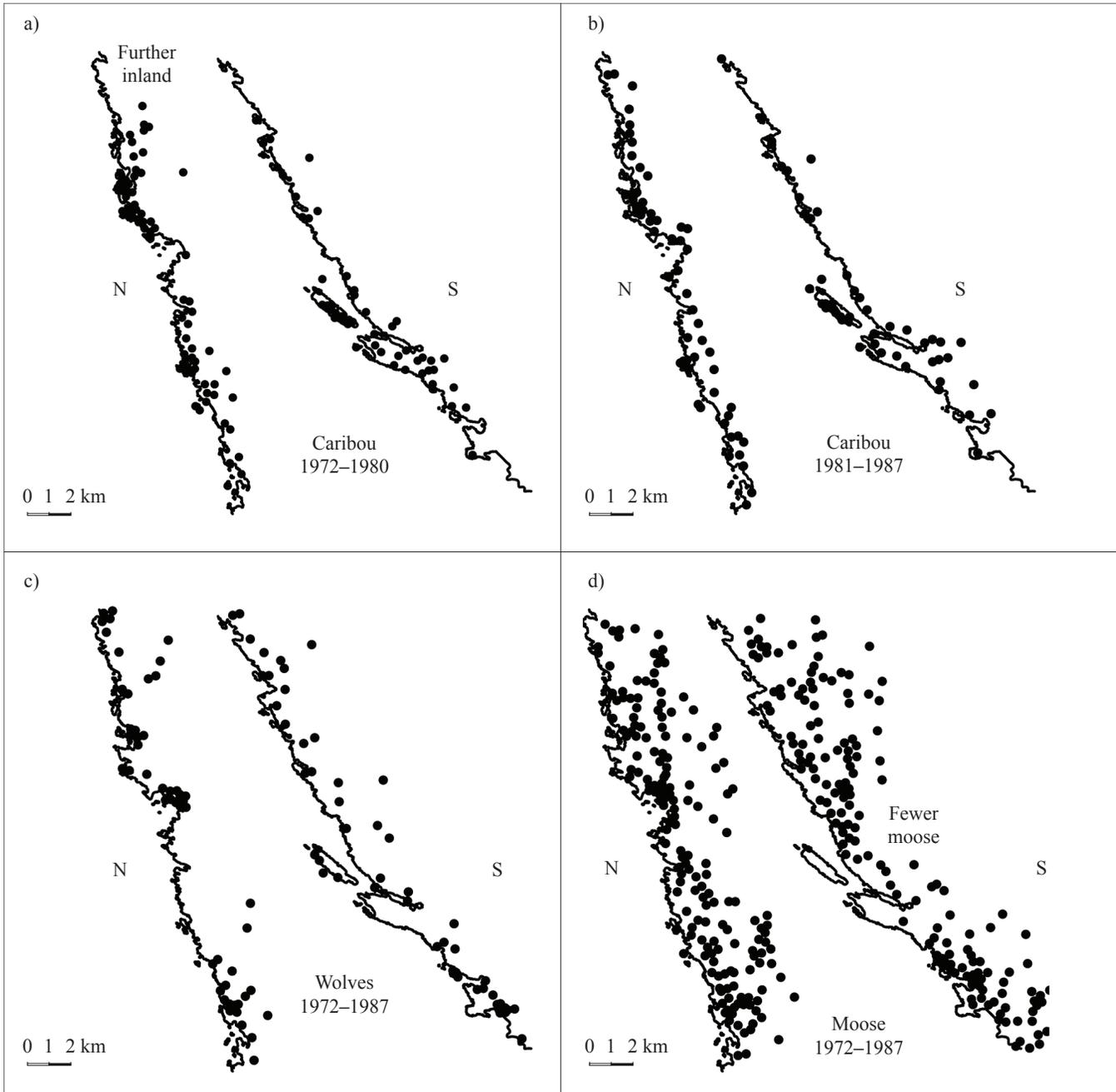


FIGURE 4. Distribution of caribou (a, b), wolves (c), and moose (d) during the DD period in Pukaskwa National Park, plotted from the annual winter census surveys <5 km of the northern (N) and southern (S) portions of the shoreline, separated at Simons Harbour (see Figure 1).

TABLE III. Tests for differences in winter predation and year-round behaviour of Pukaskwa National Park caribou and environmental factors during their density-dependent (DD) years, 1975–1988, and their inverse density-dependent (IDD) years, 1989–2009. Means and standard errors of the means (\pm SE) are shown.

Parameter	DD years	IDD years	Test for differences
Probability of winter predation on caribou			
Wolf track aggregations (km ⁻²)	2.2 \pm 0.5 (<i>n</i> = 9) ^a	4.8 \pm 0.7 (<i>n</i> = 8)	$t_{14} = 2.86, P = 0.02$
Wolves seen in caribou surveys	9 in 11 y	39 in 9 y	$\chi^2_{1,2} = 7.74, P < 0.01$
Behaviour and winter range sizes for caribou			
Range and mobility	Along entire shoreline	Small, restricted	
Size (km ²) of female home range	2.9 \pm 0.6 (<i>n</i> = 8)	Females found only on Otter Island	
Size (km ²) of male home range	4.4 \pm 1.0 (<i>n</i> = 4)	1.8 \pm 0.7 (<i>n</i> = 7)	$t_7 = 2.50, P < 0.05$
Distance (m) females to shoreline	535 \pm 64 (<i>n</i> = 50)	252 \pm 70 (<i>n</i> = 70)	$t_{116} = 6.75, P < 0.01$
Distance (m) males to shoreline	672 \pm 60 (<i>n</i> = 50)	253 \pm 27 (<i>n</i> = 90)	$t_{93} = 6.34, P < 0.01$
Percent on Otter Island in summer	38% (170 / 494)	64% (296 / 463)	$\chi^2_{1,2} = 220, P < 0.01$
Percent on Otter Island all year	na	67% (273 / 408) ^b	
Environmental factors			
Snow depth (cm) in February ^c	56.9 \pm 4.1 (<i>n</i> = 12)	58.5 \pm 6.4 (<i>n</i> = 22)	
Occurrence of land-fast ice	9 of 13 y	5 of 11 y	No differences
Mean January temperature (°C) ^c	-9.0 \pm 0.6 (<i>n</i> = 12)	-7.1 \pm 0.7 (<i>n</i> = 22)	

^a Three years of heavy snow and land-fast ice, 1978, 1980 and 1985, are excluded.

^b Based on Neale (2000).

^c Data from Environment Canada, Wawa (Ontario) weather station.

were recorded further inland, especially where the shallow snow contour extends further inland on the northern part of their range (Figure 4a). Caribou occurred north of Oiseau Bay in 12 of 15 y, with a mean group size of 5.8 \pm 0.9 individuals. Wolves were most commonly observed in this area during the early years of the study, especially in years of land-fast ice, e.g., 1980 and 1989; this north end of the caribou distribution was the first area where caribou declined (Table I; Figure 1). Refuge Island was a second safe place for calving, and Otter Head and Point Isacor to the south of PNP were safe mainland locations, with dispersed escape habitats, including inland lakes and, in the case of Otter Head, smaller offshore islands.

Caribou occurred closer to the shoreline in years with heavier snow, their distance inland from Lake Superior being negatively correlated with midwinter snow depth ($R = -0.637, n = 12$). In 2 of the years with extensive land-fast ice, 1980 and 1989, caribou were observed farther inland than at any other time in the study, at distances of 1.5–12.0 km. During 1974–1988, 59% of caribou aggregations >200 m from the shoreline were on “balds” (*n* = 73), a much higher percentage than that of wolf aggregations (18%; $\chi^2_{1,28} = 21.1, P < 0.01$). Caribou and moose sign were significantly correlated, both in winter and in summer, at scales of 4 km (Table IV; $P < 0.01, n = 11$) and 2 km (winter: $R = 0.537, P = 0.03, n = 22$; summer: $R = 0.629, P < 0.01, n = 22$). In only 5 (6%) of 88 grid cells (0.5 km) was moose sign absent in winter where caribou had been present. Wolf sign was not correlated with either sign of moose or sign of caribou. During 1982–1986, caribou were observed at 66 locations along the coast, moose co-occurring at 73% of these locations. Overlap of caribou and moose along the shoreline and on coastal islands was less than on the coastal trail, and moose did not use the smaller islands to the same extent as caribou. Wolf tracks were concentrated at the mouths of rivers, areas caribou avoided, with the exception of White Gravel River opposite Refuge Island (Figure 1). What typified the early years of our

TABLE IV. Correlation matrix^a for moose, caribou, and wolf sign (fecal pellets and tracks) observed from Pic River to the North Swallow River (44 km)^b, during May (winter sign) and September (summer sign), 1984–1986.

UTM range (m)	Number of observations					
	Moose		Caribou		Wolf	
	Winter	Summer	Winter	Summer	Winter	Summer
5383 999–5380 000	1	7	0	3	4	8
5379 999–5376 000	5	22	1	10	7	22
5375 999–5372 000	1	9	3	5	4	7
5371 999–5368 000	6	13	12	7	7	5
5367 999–5364 000	13	27	9	11 ^c	4	4
5363 999–5360 000	13	31	9	36	6	7
5359 999–5356 000	9	19	1	22	4	13
5355 999–5352 000	9	21	8	22 ^d	1	0 ^e
5351 999–5348 000	12	26	5	15	9	3
5347 999–5344 000	9	27	3	15	3	8
5343 999–5340 000	20	42	17	30 ^f	5	4
Total	98	244	68	176	54	81

^a Correlation coefficients: moose and caribou sign in the same grid cell, winter, $R = 0.72$; summer, $R = 0.77$.

^b Locations are recorded from north to south in NAD 83 Universal Transverse Mercator (UTM) North (N) latitude, 4-km grid ranges, where White River crosses at 5378793 N, Willow River at 5371836 N, Oiseau Bay at 5361289 N, White Gravel River at 5350372 N, and White Spruce Harbour at 5348077 N (see Figure 1).

^c Gids Harbour calving area.

^d One Lake calving area.

^e No wolf sign, either as a result of the grid range encompassing the boundary of the Cascade and Swallow River packs or because wolves approached One Lake on the shoreline.

^f Genevieve Lake calving area.

study was high mobility of caribou along the coast of Lake Superior, a behaviour that became much less frequent in the subsequent period of caribou decline.

WOLF, MOOSE, AND CARIBOU INTERACTIONS IN THE DECLINE YEARS

Wolf track aggregations increased at the onset of caribou decline (Table III). The mean distance of wolf tracks from the shoreline on offshore ice was 2.5 \pm 0.3 km, greater

than in the early years (0.8 ± 0.1 km, $t_{16} = 5.15$, $P < 0.001$). We saw more wolves in caribou surveys, suggesting that wolves were also staying along the shoreline longer than in the past, regardless of midwinter snow depth, land-fast ice formation, or winter temperature, all of which were similar between the 2 study periods (Table III). The radio-monitored Cascade River pack moved east from the outset of the IDD period and focused its hunting along the shoreline in the vicinity of Otter Head ($n = 30$ locations), frequently ice-bound just 1.5 km from Otter Island, and in an area where a portion of the coastal moose population increased between winter surveys in 1986 and 1993. The mean map gridline for all observed caribou in 1975 was UTM 5350000, but by 1988 it had shifted to UTM 5335000, a significant southward shift of caribou by 15 km to an area <6 km north of Otter Island (Figure 1). Ranges and mobility became more restricted for both male and female caribou, and they were observed closer to the shoreline during their decline than in the DD years (Table III). One radio-collared female with a calf was observed on the mainland over a period of 3 months in an area of only 0.15 km².

Discussion

A SUMMARY OF CARIBOU AND WOLF BEHAVIOURS IN PNP

Caribou in PNP evolved a suite of behaviours that conformed to their narrow and rugged coastal range. Their long-distance migrations before calving and in early winter, as well as their fidelity to refuge areas observed during the DD period at calving, are all expected behaviours of woodland caribou (Brown & Theberge, 1985; Bergerud, Ferguson & Butler, 1990; Ferguson & Elkie, 2004). Refuges, when they function to protect prey from predators, become the resource that stabilizes the predator–prey relationship (Berryman & Hawkins, 2006). But for woodland caribou, long-distance movements are also critical to maintenance of a population, for reasons not limited to being less predictable to predators sharing the same landscape. Typically, woodland caribou and moose are spatially segregated on a landscape as part of a survival strategy for the secondary prey, explaining the evolution of long-distance migration (Bergerud, Ferguson & Butler, 1990; Cumming, Beange & Lavoie, 1996; James *et al.*, 2004). However, the restricted range in PNP does not ultimately offer this same security, because so much of the coastal zone is regularly occupied by moose, especially when snow is deeper; predictability of caribou along the coast leaves wolves with a hunting advantage.

Why did caribou restrict their range so much more during the IDD period despite environmental conditions similar to those of the previous period? Caribou commonly observed cratering for lichens on “balds” near the Lake Superior shoreline in the early years of our study apparently ceased this behaviour at the onset of the IDD period. Woodland caribou, both the boreal and mountain ecotypes, commonly go to higher elevations like the PNP “balds,” where they are spaced away from primary prey, moose, to reduce risk from wolves (Bergerud, Butler & Miller, 1984; Hatler, 1986; Pinard *et al.*, 2012). We suggest that “balds,”

previously relatively safe prey anchor sites along the Lake Superior coast (Bergerud, 1985), became places for caribou to avoid in PNP when wolves approached the shoreline more frequently. Caribou refuges became limited to offshore islands during the IDD period; almost unique to PNP compared to most of the boreal forest (Bergerud, Ferguson & Butler, 1990), these islands became the only areas where moose largely did not co-occur, but where wolves increasingly hunted when land-fast ice allowed.

How did wolves change their hunting behaviour to overlap (*sensu* Sih, 2005) with caribou range more often? Four wolf packs compete for prey in PNP (Forshner *et al.*, 2003). Their primary prey declined in 1992 to <0.18 moose·km⁻² according to our best regression estimate of a trend over the 12 survey years in PNP. According to separate surveys of the 10-km coastal strip, moose declined below this level later, in 2005. Thus, during the IDD period, wolves more often followed the routes that took them to higher densities of their primary prey. The highest density of wolves on coastal surveys was observed in 2003 and 2005, but they showed evidence of declining condition before this period: in 1994, the only observed breeding was by packs outside the park; in 14 of 22 pack years from 1994–1998 no breeding was observed; the Swallow River pack did not breed in 2 successive years (1997 and 1998), and 2 of 26 radio-collared wolves were found starved during the IDD years (Forshner *et al.*, 2003). In summary, at the beginning of the caribou decline, wolves accessing the Lake Superior coast likely experienced more prey than they did inland, and more prey than in later years, as the number of moose increased. A concurrent decline in moose recruitment suggests that the higher prey level was not maintained, and wolves likely encountered fewer prey, both moose and caribou, as the caribou decline progressed and their own condition worsened.

A LANDSCAPE OF FEAR IN PNP

The idea of a “landscape of fear” helps explain caribou behaviour in PNP. “Animals move about the physical landscape [as] they are constantly adjusting their behavior in response to changing level of predation risk, [so] we can envision then that prey individuals live in a second landscape, one with different levels of risk or fear of predation” (Laundré, Hernández & Alterndorf, 2001). PNP caribou increased their “safety net” in response to more contact with wolves during their decline phase. Brown and Chivers (2005) argued that fitness-related activities, such as foraging, must be optimized by prey confronting a landscape of fear. Caribou staying for prolonged periods on Otter Island and other small islands during the IDD period compromised their foraging opportunities by using less suitable habitat longer (Ferguson *et al.*, 1980; Ferguson, Bergerud & Ferguson, 1988; Bergerud *et al.*, 2007; Kuchta, 2012). Most importantly, returning routinely to the offshore islands led to their losing the “space race” when wolves began to find them there more often.

Wolves should hunt where it is easier to catch prey, rather than simply where prey is more abundant (Laundré, Calderas & Hernández, 2009). For wolf prey, the same habitats can be more or less risky, dependent on

context (Gervasi *et al.*, 2013). Although we describe Otter Island as a refuge site for caribou, we also suggest that wolves began hunting more on Otter Island during the caribou decline years, because there was a higher certainty of caribou being there, and because track observations on ice showed us that wolves were frequently successful in taking down caribou there. Wolves in PNP benefitted from an additional advantage in years when snows were deep and winters severe, as has been observed in other prey systems (Boertje, Valkenburg & McNay, 1996; Post *et al.*, 1999; Mech *et al.*, 2001). Varying wolf response to environmental variation and to changes in prey life history will be increasingly reported as we watch the “space race” elsewhere; wolves do not always win the race, but we will increasingly learn when conditions lend the predator the advantage (Post *et al.*, 1999; Montgomery *et al.*, 2014). Declining caribou populations facing anthropogenic disturbances may be behind many of these cases (Schaefer, 2003; Vors *et al.*, 2007; Semeniuk *et al.*, 2012).

AN ANTI-REGULATORY EFFECT OF WOLVES

Woodland caribou in PNP fluctuated for 14 y around a carrying capacity of 24 individuals, a sequence that must have played itself out for many decades. In many of the DD years, calves were >15% of the winter population, above the level required for population stability (Bergerud, 1974), and suggesting that wolves rarely hunted them. The islands served as secure summer locations for raising calves during this period, a rare situation for caribou. For example, in montane populations, 90% of calves are dead by the end of June (Bergerud, Butler & Miller, 1984). In PNP, mortality was always relatively higher in winter, determined by the effects of snow and land-fast ice. Only along the Lake Superior shoreline could wolves search for both prey species simultaneously, and there, even in winter, water was usually available as an escape habitat. If the primary prey declines, then wolves should spend more time with their secondary prey (McLellan *et al.*, 2010). In PNP, moose and caribou declined together.

Stability was eventually to be lost, not with changes in snow and ice, but rather with the arrival of wolves at the PNP coast. Modelling of the Allee effect shows that if a species becomes the secondary prey for a predator with a Type II functional response, then its death rate from predation will be IDD (Sinclair *et al.*, 1998; Courchamp, Clutton-Brock & Grenfell, 1999). We argue, as do Wittmer, Sinclair, and McLellan (2005), that this outcome is to be expected for woodland caribou in caribou–moose–wolf systems. Where caribou persist elsewhere, it is only where migration occurs prior to calving, where traumatic encounters with wolves at safe calving sites do not interfere with their security, and where greater space exists for dispersal with enough landscape heterogeneity that the efficiency of wolves searching for both ungulates simultaneously is lessened, as is consistent with the “space race” (Sih, 2005). These factors have been used to explain persistence of woodland caribou in numerous contexts (Simkin, 1965; Bergerud, Butler & Miller, 1984; Bergerud, 1985; Cumming & Beange, 1987; Bergerud, Ferguson & Butler, 1990; Cumming, 1996; Cumming, Beange & Lavoie, 1996; Stuart-Smith *et al.*, 1997; Bergerud & Elliott, 1998;

Rettie & Messier, 2001; Ferguson & Elkie, 2004; James *et al.*, 2004; Lessard, 2005; Bergerud *et al.*, 2007; Metsaranta, 2008).

Messier (1994) argued that wolves are especially effective in reducing low density moose populations, such as in PNP, where they can shift a population to an even lower equilibrium level or to a depensatory, destabilizing (*i.e.*, IDD) demographic. Messier (1994) explained that “because moose are well dispersed in their environment and spatially predictable, they are well exposed to wolf predation.” Bergerud, Wyett, and Snider (1983) presented the moose decline in PNP not just as a consequence of reduced fecundity, but also of greater predation by wolves when populations were low. The abundance of moose in PNP provided the prey base for a viable wolf population that was ultimately a factor in the decline of caribou. Caribou migrating after the Ice Age from the south reached Ontario 10 000-y-ago (Storck & Spiess, 1994). But moose did not arrive in Ontario until after the end of the Little Ice Age in 1850, almost 10 000 y after caribou (Peterson, 1955). De Vos and Peterson (1951) described the resulting sudden change in abundance of woodland caribou in Ontario: “by the beginning of the twentieth century [they] seemed to be declining rapidly across the Province.” The decline of caribou as moose and wolves increased has been documented with harvest data in British Columbia (Bergerud & Elliott, 1986). In contrast, in Newfoundland, caribou increased during 1967–1996 ($\lambda = 1.08$) in the presence of high numbers of moose in a heavily disturbed environment. The difference between Newfoundland and British Columbia or Ontario is that wolves had become extinct in Newfoundland several decades earlier. Bergerud and Elliott (1986) presented models that show IDD for caribou whenever moose reach densities exceeding 0.11 per km² and wolves exceed 6.5 per 1000 km². Thomas (1995) suggested the critical density is 7.0 wolves per 1000 km², and Lessard (2005) has modelled caribou decline at 8.0 wolves per 1000 km² for Alberta.

With hindsight we postulate that the arrival of moose to Ontario has been a significant factor in the recent extirpation of woodland caribou from areas of Ontario and elsewhere. A common component of caribou declines is an increase in primary prey, either moose or American elk (*Cervus elaphus*), that results in an increase in wolf density and thus in higher predation on caribou. Caribou–moose–wolf systems are seldom stable; too many moose is a common recipe for caribou declines (Bergerud, 2007). These conclusions are now routinely part of modeling exercises (Courtois & Ouellet, 2007; Boan, Malcolm & McLaren, 2014). The caribou–moose–wolf system must be managed, including protection of lakeshores and islands to permit successful calving and persistence of caribou, if we are to reverse the extinction equation.

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