Changes among Caribou (*Rangifer tarandus*) in Slate Islands Provincial Park following successive arrivals of Gray Wolves (*Canis lupus*)

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Abstract
From observations of Caribou (*Rangifer tarandus*) during 1974–2017 on the Lake Superior archipelago that makes up Slate Islands Provincial Park, we infer direct and indirect effects of the arrival of Gray Wolves (*Canis lupus*) in the winters of 1993–1994, 2002–2003, and 2013–2014. Arrivals consisted of wolf pairs in the first and third cases, and, in each instance, wolves survived at least one additional winter. Wolves created conditions that led to behavioural changes in Caribou consistent with avoiding predators. Caribou did not frequent calving locations near shoreline areas, nor did they use water to escape from wolves. Wolves occupied a Red Fox (*Vulpes vulpes*) den, and its general location, at one time frequented by Caribou, became the most common area to find Caribou carcasses and was avoided by Caribou when wolves were present. Caribou were functionally extirpated by wolves, with just two to four males remaining in 2017. Wolves also appear to have caused extirpation of American Beaver (*Castor canadensis*) and Red Fox from the archipelago, while Snowshoe Hare (*Lepus americanus*) populations were unaffected by wolves.

Key words: American Beaver; *Canis lupus*; Caribou; *Castor canadensis*; Gray Wolf; *Lepus americanus*; *Rangifer tarandus*; Red Fox; Slate Islands Provincial Park; Snowshoe Hare; *Vulpes vulpes*

Introduction

Quantifying ecological patterns with adequate precision at appropriate spatial and temporal scales and inferring causal relationships from complicated sets of correlations are among the chief challenges in studying natural ecosystems (Peterson *et al.* 2014). Island ecosystems offer several advantages for study: some control on immigration and their limited size and diversity simplify food webs.

Most of the effect of large carnivores on ungulate population demographics is direct (Mech and Peterson 2003). Indirect effects occur when ungulates avoid predation. The "leapfrog effect" (Sih 2005) has been used to describe part of the spatial game of predator and prey, where a predator's distribution matches the distribution of its prey's preferred food resources, while its prey sacrifices time spent in areas of high-est food resources to reduce predation risk. The direct and indirect relationships among Caribou (*Rangifer tarandus*), Moose (*Alces americanus*), and wolves in boreal forest systems has been described in tracking studies by Rettie and Messier (2000), Bergerud *et al.* (2014), and Courbin *et al.* (2014).

The direct effects of Gray Wolves (*Canis lupus*) on Caribou adults and calves have been previously described for the island ecosystem of Slate Islands Provincial Park (SIPP), Ontario, Canada (Bergerud *et al.* 2007). In this follow-up paper, we summarize observations of Caribou on SIPP during and after three periods of wolf colonization using long-term Caribou survey data, locations of Caribou calving sites, wolf kill sites, and scat analyses. As a nationally Threatened species (SARA Registry 2019), the Boreal population of Woodland Caribou is managed

controversially in several parts of Canada by lethal wolf control (Hebblewhite 2017). Recovery of many populations may depend on a better understanding of direct and indirect effects of wolves. Here, we summarize demographic effects on Caribou and examine the leapfrog effect during the first two periods with wolves present and describe the outcome of the third colonization by wolves. We also include some incidental observations of Red Fox (*Vulpes vulpes*), Snowshoe Hare (*Lepus americanus*), and American Beaver (*Castor canadensis*) on SIPP before and during wolf arrival.

Study Area

SIPP is an archipelago of eight islands and some islets in Lake Superior, centred at 48°39′01″N, 87°00′32″W, about 10 km south of Terrace Bay, Ontario (Figure 1). Occasional connectivity of the otherwise isolated archipelago to the mainland 9 km away occurs across winter ice, which allows large mammals to cross in either direction. Caribou are frequently observed swimming between islands of the archipelago, especially between Mortimer Island, the second largest island and the farthest northwest

(6.8 km²), and the northeastern peninsula of Patterson Island, the largest and most southerly island (28.4 km²), using McColl and Bowes islands as stopovers. Caribou have not been observed swimming to or from the mainland, and their sign is rare on the more distant Leadman Islands to the northeast.

In 1907, J. King, a lighthouse keeper, saw Caribou tracks crossing on ice to SIPP (Euler *et al.* 1976). With more extensive ice in the first part of the 20th century (Assel 2009), both Caribou and wolves might have moved back and forth frequently between SIPP and the mainland. Although Euler *et al.* (1976) assumed occupation of SIPP by Caribou since 1907, Parsons (1918) conducted extensive mineral explorations of the islands in the decade following and noted no Caribou. Wolf tracks were spotted in February 1965 on Delaute Island (J. Chappel pers. comm. 21 May 1975), but a lighthouse keeper confirmed the absence of wolves during his tenure from 1948 to 1978 (J. Bryson pers. comm. 3 August 1974). Cringan (1956) also saw no sign of wolves during his studies in SIPP in the 1950s. During 1974–1993, we observed no wolf sign on SIPP. Therefore, wolves were likely absent and Caribou were likely free from predators on
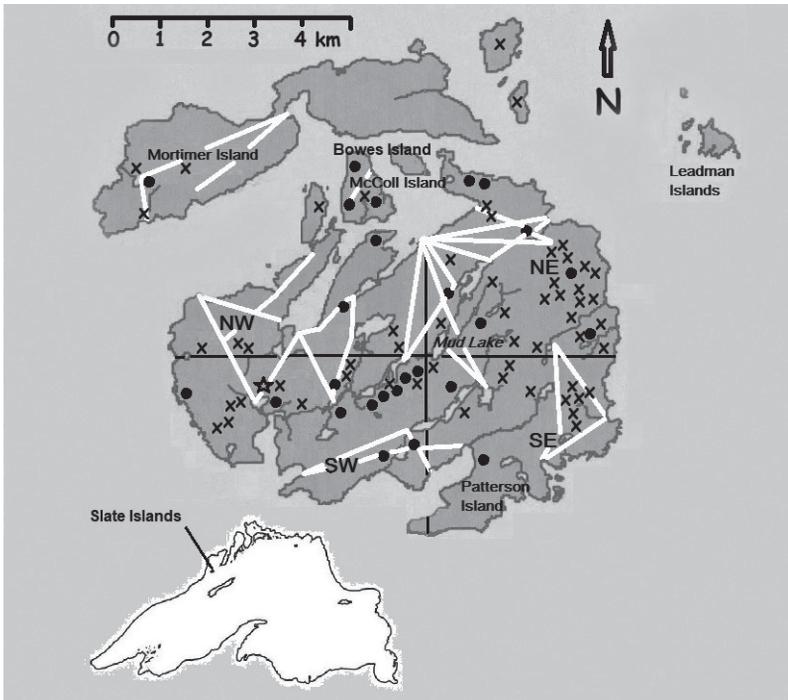

FIGURE 1. Slate Islands Provincial Park in Lake Superior, Ontario, showing the four survey quadrants on Patterson Island and locations where we observed Caribou (*Rangifer tarandus*) calving during 1976–1992 (✘), locations where we encountered a wolf-killed Caribou during 2004–2005 (●), and the Red Fox (*Vulpes vulpes*) den site where we observed Gray Wolves (*Canis lupus*) denning during 1994–1996 and 2004–2005 (☆). The white lines show examples of Caribou survey transects from Carr *et al.* (2012).

SIPP from at least 1948 to 1993. Subsequently, a pair of wolves crossed on ice to the islands in the winter of 1993–1994, and at least one wolf did the same in the winter of 2002–2003 (Bergerud *et al.* 2007). More recently, during the winter of 2013–2014, wolves and Caribou were seen moving back and forth between the mainland and SIPP (B. Patterson pers. comm. 23 October 2017).

SIPP is within the southern range of Ontario's Boreal Forest region (Rowe 1972) and supports plant communities that are generally characteristic of the region. However, as a result of its small size (a total of 36 km²) and relatively large distance from the mainland, the archipelago supports a fractured boreal fauna. Mammals listed in 1949 by Cringan (1956) include Caribou, Red Fox, Snowshoe Hare, American Beaver, Muskrat (*Ondatra zibethicus*), Southern Red-backed Vole (*Myodes gapperi*), Meadow Vole (*Microtus pennsylvanicus*), Short-tailed Weasel (*Mustela erminea*), and Little Brown Myotis (*Myotis lucifugus*). We have also observed that Northern River Otter (*Lontra canadensis*), Moose, American Black Bear (*Ursus americanus*), and Canada Lynx (*Lynx canadensis*) are absent, although Cringan (1956) reported a black bear skull on Bowes Island in 1949.

Methods

Strip transects to estimate Caribou density

A more detailed description of our Caribou survey method using strip transects (King 1937) can be found in Bergerud *et al.* (2007) and Carr *et al.* (2012). Single observers, but not the same observer each year, and usually in teams spread over the transect routes, walked transects in May and June 1974–2001 and again in 2006, 2008, and 2016. Routes for strip transects were chosen to include practical landmarks and turning points (topographic features, lakes, bays, points, etc.) and easy boat access (see Figure 1). The walking schedule coincided with the period after calving, but when vegetation least obscured the view, and the routes were chosen to avoid areas that had been visited the previous day. Using a measuring tape, observers recorded the angular distance to a Caribou spotted or flushed from the transect route; the longest distance each year was considered the maximum line of sight through the vegetation (Table 1). Mortimer Island was always included in the survey transects.

Other Caribou observations

Cringan (1956) mentioned a natural salt lick at the outlet of Mud Lake in the centre of Patterson Island (Figure 1), the island where most Caribou resided during summer. We started placing additional salt at the Mud Lake lick in 1976 and made daily observations of Caribou from this point from mid-May to mid-June each year from 1977 to 1999 and in 2004. These ob-

servations allowed a spring classification of Caribou by sex and age, estimates of pregnancy, and a different method for estimating the population, all of which are reported in Bergerud *et al.* (2007); here, we report the directions that Caribou travelled as they entered and left the salt lick during 1988, 1991, and 1992 (our three best observation years before wolf arrival) and during 1994–1996 (three years after wolf arrival).

We divided Patterson Island into four quadrants using Mud Lake as the centre (Figure 1). We labelled them NE (a quadrant of 8.4 km²), NW (5.0 km²), SE (7.3 km²), and SW (7.7 km²). Six main trails led from each quadrant: from the north, northeast, and east to the NE quadrant; from the northwest to the NW quadrant; from the south to the SE quadrant; and from the west to the SW quadrant. From a watchtower, 5 m in height and ~35 m from the salt lick, we observed Caribou as individuals (see next section), including multiple observations of the same individual, entering or leaving the salt lick, and we recorded the trail each used. We used the same quadrants to report calving locations during 1976–1992, based on capturing neonates, observing their tracks, or hearing characteristic grunting by female Caribou for their young calves. We also used the quadrants to report the locations of Caribou aggregations, defined as two or more adult Caribou that we spotted or flushed together, while walking on the survey transects. We also described changes to Caribou distribution across all survey transects using the four quadrants.

In 19 of the study years during 1974–1998, we visited SIPP for a brief period in March to compile age composition tallies (previous-year calves, yearlings, and adults) based on track and sign characteristics. In 20 years during the same period, we obtained age composition tallies (current-year and previous-year calves and adults) from boat and foot surveys in September. During the summers of 2003–2005, we recorded all locations where we encountered a wolf-killed Caribou.

Caribou capture and tagging

We captured Caribou during each fall of 1975–1995 in traps baited with salt, setting two to four box traps and two walk-through traps along regular travel routes. We also herded Caribou from boats toward drive traps at water crossings, and we occasionally used drop nets from trees or from boats when we spotted individuals swimming. During 1980–1995, we tagged captured Caribou with Duflex ear tags (Destron Fearing, Dallas, Texas, USA), numbered in a manner identifiable with binoculars. We released all Caribou at their capture site, after taking measurements including total body weight, estimated by slinging individuals from a collar using a pulley attached to a spring scale. During subsequent summers,

TABLE 1. Demographic parameters of the Caribou (*Rangifer tarandus*) population in Slate Islands Provincial Park, 1974–2017. Years when Gray Wolves (*Canis lupus*) were present are shown in bold; wolf pairs were seen in 1994–1996 and 2014–2017.

Year	Caribou density from strip transect surveys*				Minimum overwinter survival from tracking tagged individuals†				% calves in classifications‡	
	Total transect length, km	No. Caribou seen	Maximum line of sight, m	Caribou density, no./km²	No. adult females tagged	Tags (♀) spotted following year, %	No. adult males tagged	Tags (♂) spotted following year, %	Sept. survey	March survey
1974	99	22	29	3.9	—	—	—	—	12	—
1975	105	20	26	3.6	—	—	—	—	12	10
1976	80	41	34	7.5	—	—	—	—	14	—
1977	169	72	38	5.6	—	—	—	—	15	—
1978	65	16	27	4.5	—	—	—	—	18	25
1979	130	43	32	5.1	—	—	—	—	16	17
1980	101	46	33	6.9	17	88	10	70	11	18
1981	162	68	29	7.2	30	93	11	100	18	10
1982	140	74	30	8.7	46	91	25	88	17	—
1983	133	107	31	13.0	50	80	36	84	20	25
1984	83	88	31	16.9	38	84	37	76	15	22
1985	158	96	33	9.3	32	88	38	82	11	5
1986	154	73	33	7.2	24	83	27	93	19	13
1987	62	57	33	13.9	26	85	30	80	16	—
1988	93	41	30	7.3	28	86	29	72	—	6
1989	57	34	36	8.3	26	15	17	12	15	13
1990	168	35	36	2.9	14	100	30	80	—	3
1991	135	24	28	3.2	23	91	6	83	—	4
1992	40	14	50	3.5	23	100	8	100	—	19
1993	55	37	39	8.6	28	89	19	89	25	23
1994	157	54	30	5.7	34	71	38	87	3	28

TABLE 1. *Continued.*

Year	Caribou density from strip transect surveys*				Minimum overwinter survival from tracking tagged individuals†				% calves in classifications‡	
	Total transect length, km	No. Caribou seen	Maximum line of sight, m	Caribou density, no./km²	No. adult females tagged	Tags (♀) spotted following year, %	No. adult males tagged	Tags (♂) spotted following year, %	Sept. survey	March survey
1995	190	70	27	6.7	26	81	57	91	5	5
1996	133	58	30	7.2	—	—	—	—	22	2
1997	57	25	29	5.7	—	—	—	—	—	21
1998	43	30	49	7.1	—	—	—	—	11	—
1999	29	16	26	10.6	—	—	—	—	—	—
2000	22	14	45	7.0	—	—	—	—	—	—
2001	59	27	36	5.9	—	—	—	—	—	—
2002	—	—	—	7.4	—	—	—	—	—	—
2003	—	—	—	6.8	—	—	—	—	—	—
2004	—	—	—	7.6	—	—	—	—	—	0.1
2005	—	—	—	7.5	—	—	—	—	—	—
2008	63	11	—	3.6	—	—	—	—	—	—
2014	—	—	—	1.4	—	—	—	—	0	—
2016	114	3	34	0.4	—	—	—	—	—	0
2017	—	—	—	0.1	—	—	—	—	—	0

Note: — = missing data. Data up to 2005 are from Bergerud *et al.* (2007).
*Population density estimates from 2002 to 2008 and 2016 are based on a "best estimate" of line of sight of 33.6 m. Population density estimates in 2014 and 2017 are based on approximate number of Caribou seen during summer field visits and not on strip transect surveys.
†Tagging during 1980–1995 was with ear tags numbered in a manner identifiable with binoculars. Minimum survival is calculated from relocating tagged individuals up to four years after capture ($n = 602$) or recapture ($n = 27$).
‡Classifications in September were by boat and in March from snow track surveys. Absence of calves in 2017 was determined from camera traps (B. Patterson pers. comm. 23 October 2017).

we were able to see and record most tagged individuals at the Mud Lake salt lick.

Observation of other mammals

In 1994 and 1995 during May and June, we counted wolf tracks along the Caribou survey transects by quadrant on Patterson Island. We collected wolf scats during 1995–1998 ($n = 45$) and fox scats in 1986 ($n = 26$) on all spring and summer excursions and examined them for remnants of prey by suspension in water. We regularly observed the fox den at Horace Cove Lake (Figure 1) during 1974–1996, including when it was occupied by wolves during 1994 and 1995. We recorded Snowshoe Hares and approximated their flushing distances during 1974–2001, when we encountered them along the Caribou survey transects. W.D. regularly observed beavers and attempted to count all beaver lodges in the summer during the entire study period, 1974–2017.

Data compilation and analysis

During 1997–2001, L.C. measured the angular distance of Caribou from the walking transects more accurately than in previous years and also measured angle from perpendicular, to create a "best estimate" line of sight to use in density and population-size estimates from 2002 to 2008, a period when none of us was involved in the surveys. We compared this average to the average for all previous years using a two-sample t test. We used the estimate of line of sight to calculate the line transect width for input to estimates of density. We calculated an annual Caribou population by multiplying the number of individuals spotted or flushed in the strip transects by the area of the archipelago (36 km^2), divided by the estimated transect area (transect length × twice line of sight estimate). That is, we applied the density estimate from transects to the entire archipelago.

An estimate of annual adult survival was based on second sightings of tagged Caribou individuals in a following summer, on the last year an individual was seen, waiting three additional years to decide whether the individual had been overlooked, and on estimated date of death for any tagged carcass. If an individual was later seen with tags in good condition, it was added back to the tagged, live pool.

We recorded distances of Snowshoe Hare sightings from the walking transects less accurately than for Caribou sightings, but we adopted the same approach to estimating their abundance for 27 years in the period 1974–2001, when at least three hares were spotted; we substituted a fall survey for the June survey in 1978 when only three hares were spotted in what was part of a series of years of high abundance. We also substituted a best estimate line of sight for 13 years when five or fewer hares were spotted, which

we calculated as the mean line of sight for the other 14 years. We made all calculations and t tests using Statistical Package for the Social Sciences, version 25.0 (IBM Corp. 2017).

Results

Caribou demographics

Our best estimate of line of sight in the Caribou surveys was 37.0 m ± 1.0 m (SE), measured most accurately during 1997–2001 (Table 1), when an average of 6.4 ± 0.6 km^2 or ~18% of the archipelago was surveyed; it was not significantly different from the estimates of line of sight during the previous 23 years, 32.4 m ± 1.1 m ($t_{26} = 0.56$, $P = 0.14$). The corresponding mean perpendicular distance from the 1997–2001 measurements, 33.6 m, served as an outer bound of the strip transects in all density calculations during 2002–2016, when lines of sight were not estimated.

Caribou density before wolf arrival ranged from a low of 2.9/km^2 (1990) to a high of 16.9/km^2 (1984; Table 1). Caribou density was 5.7 and 6.7/km^2 in the two springs following the first winter of an observed wolf pair (1994–1995), not much below the average for 1974–2001 of 7.2/km^2. Caribou density was above average, 7.6 and 7.5/km^2, in the two years following the second wolf arrival (2004–2005), but then fell to among the lowest density estimates, 3.6/km^2 in 2008. We visited the archipelago in 2014 and estimated that 50 Caribou remained and we found no calves. In estimates of abundance, this first spring following the second arrival of a wolf pair in 2014 was the first time we observed the population fall below 100 (Figure 2). In September 2016, the second fall after the arrival of the second wolf pair, we walked 114 km searching for Caribou and encountered just three females, all on McColl Island. By summer of 2017, at most four males and no females were photographed with remote cameras deployed throughout the archipelago (B. Patterson pers. comm. 23 October 2017).

Mean calf fraction in the Caribou population in March, excluding the springs of 1995 and 1996, was 15% ± 2% (for 17 years, mean sample size 123 track observations; Table 1). In March 1995 and 1996, the second and third years following the first wolf pair arrival, Caribou calf fractions were just 5% and 2%, respectively. These low fractions corroborated estimates of just 3% and 5% of the population in the previous September, unlike the other low March estimates of 5% (1985) and 3% (1990), which followed years of above average population density and September estimates of 15% calves (both years). In March 2004, the only spring after 1998 when we classified the population, and the first spring after the arrival of the third wolf, our sample comprised 132 females, 36 males, one yearling, and one calf.
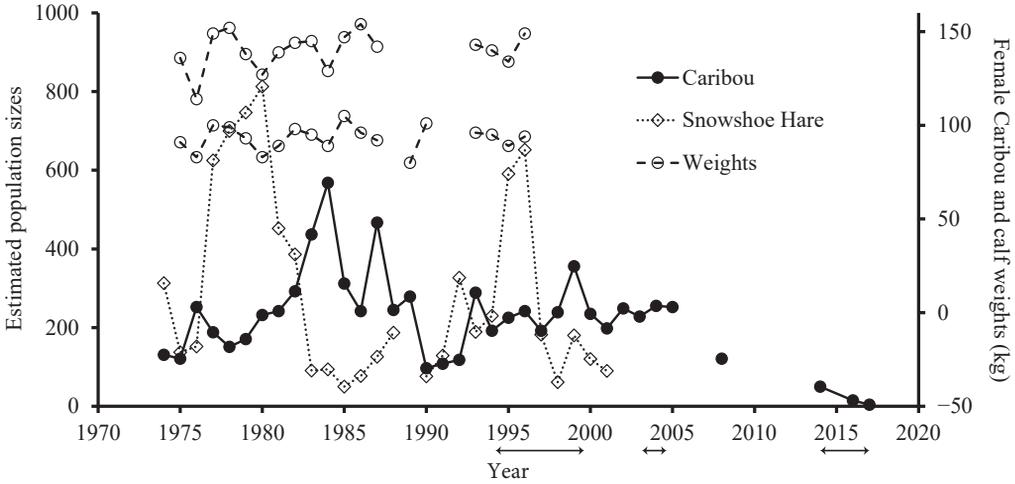
FIGURE 2. Effect of three Gray Wolf (*Canis lupus*) occupancies of Slate Islands Provincial Park (arrows below the x axis) on Caribou (*Rangifer tarandus*) population size; estimated Snowshoe Hare (*Lepus americanus*) population size; and average weights of female Caribou (lower series of open circles) and female Caribou with their calves (upper series) in September. Caribou population estimates up to 2005 and weights are from Bergerud *et al.* (2007). We acknowledge that the transect method could result in overestimates of abundance given that the line transects were conducted over one month and individual Caribou could have been counted more than once.

During 1974–1995, there were 628 adult Caribou capture events, mostly in fall: 602 unique individuals, 13 of which were relocated as carcasses and were included as deaths in the survival analysis. The mean fraction of tagged Caribou seen in the year subsequent to tagging, 1980–1995, was 82% for both females and males (Table 1). The year with lowest adult survival occurred before wolf arrival, in 1989–1990, 15% for females and 12% for males. After the first winter when wolves were spotted, in 1994, only 24 (71%) of 34 tagged adult female Caribou were spotted the following year, the second lowest fraction we recorded for females. Male Caribou, on the other hand, were spotted again in higher fractions after each of the first two winters with the wolf pair

present: 33 (87%) of 38 in 1994, and 52 (91%) of 57 in 1995.

Caribou behaviour

Before 1994, Caribou entered the salt lick at Mud Lake most frequently on a trail from the west that took them from the SW quadrant, northeast along the shores of Peninsula Lake, and then just west of Mud Lake (Table 2). After wolf arrival, Caribou rarely used this trail and also substantially reduced their use of trails from the south and northwest. A trail from the east, rarely used before wolf arrival, became among the heavier used in 1994 and 1995; the heaviest used trail was from the northeast during these years.

The distribution of 54 Caribou calving sites on Patterson Island encountered during 1976–1992 was

TABLE 2. Percentage of total Caribou (*Rangifer tarandus*) observations by trail direction leaving/entering the Mud Lake salt lick in three years without Gray Wolves (*Canis lupus*) and in three years following the arrival of a wolf pair that denned southwest of Mud Lake.

Trail	% Caribou with no wolves			% Caribou after arrival of wolf pair		
	1988 ($n = 340/352$)	1991 ($n = 328/334$)	1992 ($n = 558/563$)	1994 ($n = 980/952$)	1995 ($n = 321/288$)	1996 ($n = 316/365$)
South	8/20	14/15	11/15	3/1	2/3	8/1
West	39/34	57/47	43/24	2/5	7/4	10/13
Northwest	44/23	16/14	12/8	5/8	6/10	5/4
North	5/5	1/5	4/6	20/9	12/7	56/21
Northeast	4/16	12/19	30/47	54/56	63/66	12/55
East	0/2	0/0	0/0	16/22	10/10	8/7

Note: Multiple observations of the same individuals are included.

not even, with more than expected in the NE quadrant ($\chi^2_3 = 33.6$, $P < 0.01$; Figure 1; Table 3). More than 50% of calving sites were >1 km from the Lake Superior shoreline and only three sites were adjacent to small inland lakes. Few females calved on Mortimer Island during the pre-wolf years; only during two of 20 spring surveys from 1974 to 1993 did we see calves there (in 1983 and 1984, the first period of unusually high Caribou density). During the first three wolf years, 1994–1996, more Caribou occupied the NW quadrant of Patterson Island, as well as Mortimer Island, and, except in 1995, Caribou aggregations were encountered least often in the SW quadrant (Table 3). In 1994 and 1995, only seven calves were seen during Caribou surveys, and only one of these was in the SW quadrant.

We found no Caribou carcasses after 1996, the first year without a wolf pair, until the arrival of the third wolf in winter of 2003–2004. We then found 26 Caribou carcasses during 2004–2005, 20 of which were on the shorelines or shoals of inland lakes and Lake Superior, the remainder inland at longer distances (Figure 1). Eleven of the carcasses were in the SW quadrant on Patterson Island, and three were on McColl Island. New calving sites were identified on Mortimer Island during these two years. In 2006, we observed another shift in distribution of Caribou, when many occupied the east side of the NW quadrant and the west side of the NE quadrant. This combined area is only 5 km², but we encountered 16 Caribou aggregations in 9.5 km walked in 2006, compared with the rest of Patterson Island, 23 km² (4.6 times the size), where we encountered only 18 aggregations in 26.0 km of walking (1.7 times the distance).

Observations of wolves

The wolf pair arriving in winter 1993–1994, the

TABLE 3. Percentage of Caribou (*Rangifer tarandus*) calving sites encountered during 1976–1992 on Patterson Island and percentage of aggregations of two or more adult Caribou encountered on survey transects in the years following the arrival of a Gray Wolf (*Canis lupus*) pair in winter of 1993–1994, by quadrant of Patterson Island. Quadrants are by compass direction from Mud Lake. Wolves denned SW of Mud Lake.

Quadrant	% calving sites ($n = 60$)	% aggregations		
		1994 ($n = 151$)	1995 ($n = 110$)	1996 ($n = 36$)
SW	25	15	29	11
NW	10	33	41	42
NE	35	27	14	28
SE	30	25	16	19

Note: n = the total number of calving sites or the total number of aggregations each year.

third wolf arriving in winter 2002–2003, and the second wolf pair arriving in winter 2013–2014 all adopted the same Red Fox den on the northern shore of Horace Cove Lake (SW quadrant); the first pair also used it as a rendezvous site. Wolves were most active around this den, and wolf tracks were most frequent in the SW and SE quadrants during our spring surveys in 1994 and 1995 (SW quadrant) and at Sunday Harbour (SE quadrant). Both wolves of the first pair were observed in March 1996, but from May 1996 only one wolf was observed; until 1999, there was continued wolf sign near the fox den, as well as at Sunday Harbour. Sign of the third wolf persisted only until 2004. Following the winter of 2013–2014, a wolf pair was observed and photographed for three seasons, with one wolf remaining until 2017 (B. Patterson pers. comm. 23 October 2017).

Wolf scats contained hairs of Caribou calves (21 cases), adult Caribou (13), Snowshoe Hare (12), beaver (12), and Red-backed Vole (two), and berries of Showy Mountain-ash (*Sorbus decora* (Sargent) C.K. Schneider); four), feathers of birds (two), insects (one), and grass (one).

Observations of other mammals

We observed Red Fox using the same den at Horace Cove Lake for 32 years of the study period, including during 1999–2013; we did not find any sign of foxes in SIPP from 2014 onward. The fox scats we collected in 1986 contained hairs of Caribou (four cases), Snowshoe Hare (two), beaver (four), Red-backed Vole (two), and Muskrat (11), as well as feathers of birds (four). Near the den in 1977, we found remnants of 8–10 hares, 6–10 small birds, one Muskrat, two ducks, one Common Raven (*Corvus corax*), one beaver, and one newborn Caribou calf. On another visit in 1985, we found four recent and one older Caribou calf skulls, portions of a Caribou calf pelvis and hindfoot, and the tarsus of a young adult Caribou, along with remnants of Muskrat, beaver, vole, frog, snails, and several birds.

On our Caribou survey transects, maximum flushing distances for Snowshoe Hare varied from 4.0 to 8.9 m, with an average maximum of 6.9 m ± 0.4 m applied to the calculation of strip width during years when five or fewer hares were flushed. In seven years during 1974–2001, more than 15 hares were flushed, and, in those years, population estimates for the archipelago exceeded 450 hares (Figure 2). These high-hare years occurred in two periods: 1977–1981 (15–36 observed, 0.15–0.26/km walked, 450–750 estimated) and 1995–1996 (31 and 46 observed, 0.23/km walked, 600–650 estimated). The second high-hare period corresponded with the wolf pair occupying the archipelago. The average number of hares flushed per km walked was 0.31 ± 0.07 during the six

years with at least one wolf present, while in the 22 years of observation without wolves, the same average was only 0.09 ± 0.01 hares, a statistically significant difference ($t_{26} = 9.33$, $P < 0.001$). In the 21 years not identified as high-hare periods, only two cases of more than 10 flushed hares were recorded, and estimates of the number seen per km walked never exceeded 0.10 hares.

Before the arrival of wolves, some beavers constructed their lodges on very shallow creeks, creating just small ponds. Frequently, they did not cover their lodges with mud, and, in some years, they left their lodges in winter to forage over land when their food caches froze to a lake or pond bottom. Their foraging ranged to >400 m from water during 1974–1976. There were 36 active lodges in 1974 ($1/km^2$) and beavers could have searched for forage over 95% of Patterson and Mortimer islands at that time. By 2006, only six colonies remained, their lodges only occurring on the shores of inland lakes. In 2014, we could not find any sign of beavers in SIPP.

Discussion

Summary of demographic effects of wolves on Caribou

Bergerud *et al.* (2007) concluded that, in the years before the arrival of wolves, Caribou in the SIPP ecosystem were regulated by the availability of summer forage, although they did not experience starvation. Caribou occurred at very high densities compared with other forest-dwelling Caribou populations subject to wolf predation, where densities <$0.12/km^2$ are expected (Bergerud 2001). Support for density dependence in Caribou is summarized from Bergerud *et al.* (2007) and relates the SIPP population size and weights of female Caribou in September, which we reproduce in Figure 2: weights are negatively correlated with population size for the previous year. Bergerud *et al.* (2007) also found that Caribou weights were negatively correlated with the number of Caribou carcasses encountered in March of the following year and that the number of carcasses had a positive, exponential regression effect on the Caribou population size in the previous year.

Following the density-dependent period described by Bergerud *et al.* (2007), the Caribou population size did not diminish during or after the first occupancy of SIPP by wolves, nor immediately during or after residence by the third wolf during 2004–2005 (Figure 2). However, arrival of a second pair of wolves in 2014 resulted in Caribou kills throughout Patterson Island and on McColl and Mortimer islands, eventually reducing the number of Caribou to very few, in part because of departures from SIPP beginning at least in the winter of 2013–2014 (InfoSuperior 2017). Why was the Caribou population driven to functional ex-

tirpation only after the third wolf colonization? The simplest explanation is that this colonization by two wolves coincided with a much lower Caribou population than what was present in 1994. Alternatively, indirect effects of wolves on Caribou behaviour could have contributed to the final demise of the SIPP population, as we describe below.

Effects of wolves on Caribou behaviour

We propose that the arrival of wolves resulted in Caribou shifting their distribution to the NE quadrant of Patterson Island to reduce their contact with wolves in behaviour conforming with the leapfrog effect (Sih 2005). Bergerud *et al.* (2014) documented a similar effect on Caribou by wolves in Pukaskwa National Park, also on the Lake Superior shoreline. Wolves occupying SIPP were less active in spring and summer in the NE quadrant of Patterson Island, likely because of our activities (at Mud Lake) and that of fishermen and tourists in McGeevy Harbour, between McColl and Patterson islands. But by moving to these smaller islands and the NE part of the archipelago to avoid wolves, Caribou were likely compromising their access to food in an already food-limited environment and becoming more vulnerable to starvation as well as predation, as observed on other Lake Superior islands (Ferguson *et al.* 1980). Concurrently, Caribou increased their contact with people in SIPP, especially on McColl Island. With fitness consequences unknown, such contact has been shown to increase cortisol concentrations in Caribou (Ewacha *et al.* 2017).

Other forest-dwelling Caribou will disperse to higher mountain slopes (Edmonds 1988; Bergerud *et al.* 1990; Nobert *et al.* 2016) or to fen, bog, or island habitats, where escape from predators by swimming is available during calving (Shoesmith 1978; Bergerud 1985; Bergerud *et al.* 1990; Ferguson and Elkie 2004; Carr *et al.* 2007). From the calving locations we documented, many of which were well inland and not near water, we suspect that pre-parturition female Caribou in SIPP never did seek the increased safety of calving near water. Possibly they lost this behaviour after decades without predation. On the other hand, kills of Caribou appeared to have occurred predominantly near inland lake shorelines, consistent with the effectiveness documented for wolves, or even a single wolf, seeking to kill ungulates by wearing them down while they swim in small bodies of water that wolves easily circumnavigate (Jordan *et al.* 2010; Kiss *et al.* 2010). To summarize the leapfrog effect on SIPP, Caribou missed opportunities with summer food in the southern and western part of the archipelago, as they moved north and east to avoid wolves because wolves hunted in the Caribou's preferred space.

Other ecological effects of wolves

Although wolf scats did contain the hairs of Snowshoe Hare, we observed the second highest peak in the hare population during the occupation of the SIPP archipelago by the first wolf pair; thus, wolves did not appear to affect the Snowshoe Hare cycle in SIPP. In contrast, we infer direct and near-complete effects of wolves in reducing an American Beaver population and possibly also a Red Fox population. Our many years in SIPP show that both food limitation (bottom up) and predation (top down) can direct the behaviour and population dynamics of herbivores.

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Writing – Original Draft: A.T.B.; Writing – Review & Editing: B.E.M. and W.D.; Conceptualization: A.T.B. and H.B.; Investigation: A.T.B., W.D., L.C., H.B., and R.S.F.; Methodology: A.T.B., H.B., and R.S.F.; Formal Analysis: A.T.B. and B.E.M.; Funding Acquisition: A.T.B.

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