Functional Changes to the Slate Islands Provincial Park Ecosystem with Successive Arrival of Wolves, *Canis lupus*,from the Lake Superior Coast

**Running title:** Slate Islands after Wolf Arrival

**Article**

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**Abstract**

Observations from 1974-2016 of Caribou (*Rangifer tarandus*) on the archipelago that comprises Slate Islands Provincial Park allowed us to infer direct and indirect effects of the arrival of Wolf (*Canis lupus*) pairs in winters of 1993-94 and 2003-04. Wolves created conditions that led to the near demise of Caribou from the islands, including some, but not all, behavioural changes in Caribou consistent with avoiding predators. Caribou on SIPP did not appear to return to calving locations near shoreline areas, nor use them to escape from Wolves by entering water. Shorelines and locations of Patterson Island near a Wolf-occupied Red Fox (*Vulpes vulpes*) den were the most common Caribou kill locations. Wolves also functionally shifted the ecosystem in Slate Islands Provincial Park via direct and indirect effects on North American Beavers (*Castor canadensis*), Red Foxes and Snowshoe Hares (*Lepus americanus*).

**Key Words:** *Canis lupus*, *Castor canadensis*,Caribou,*Lepus americanus*,North American Beavers, *Rangifer tarandus caribou*, Red Foxes, Slate Islands Provincial Park, Snowshoe Hares, Interactions, *Vulpes vulpes*, Wolves.

**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 study of large ecosystems (Peterson *et al.* 2014). Attention in study of large ecosystems is also dominated by an anthropocentric perspective focused on changes easily seen with the naked eye or measured with a ruler. Notwithstanding, island systems offer important observations of the more obvious animals, as they offer some control on immigration and their limited size simplifies food webs. Corroborating observations of direct and indirect effects of large carnivores like Wolves (*Canis lupus*) in well-studied systems with occasional observations on islands, where their effect on a less diverse food web may be more obvious, seems to us an important role for natural history.

The direct effect of predation by large carnivores captures most of their role in the demographics of ungulate populations (Mech and Peterson 2003). Examples of indirect effects of large carnivores are usually about what happens when ungulates avoid predation, which can be costly in terms of reproductive physiology: in Yellowstone National Park, after Wolves were reintroduced, American Elk (*Cervus canadensis*) retreated into woodlands, where they were safer, but they were also forced to consume poorer-quality forage (Mayo *et al.* 2005; Creel *et al.* 2007). The “leapfrog effect” is the name used to describe this part of the spatial game of predator and prey, in which a predator distribution matches the distribution of its prey’s resources, while its prey sacrifices resources to reduce predation risk (Sih 2005), discussed for the Caribou (*Rangifer tarandus*)-Moose (*Alces alces*)-Wolf system in boreal forest from data collected in at least two tracking studies (Bergerud *et al.* 2014; Courbin *et al.* 2014).

Our objectives in documenting some of our observations in Slate Islands Provincial Park (SIPP) were to summarize the demographic effects of the arrival of a pair of Wolves in 1993-94 on the archipelago’s Caribou, which have been reported in more detail elsewhere (Bergerud *et al.* 2007), to update briefly on effects of a second Wolf pair arrival in 2003-2004, to describe some of the changes to the spatial distribution of Caribou that we associate with the arrivals of Wolves, and to list briefly some of the proposed indirect effects of the arrivals of Wolves on other SIPP mammals. We conclude with a statement on the persistence of Caribou along the Lake Superior coast.

**Study Area and Methods**

SIPP constitutes an archipelago of eight larger islands and some islets (Figure 1; total 36 km²) in Lake Superior about 10 km south of Terrace Bay, Ontario and the same distance to any of the mainland coast. SIPP falls within the southern range of Ontario’s boreal region and has plant species and communities that are generally characteristic of the province’s southern boreal forest. In most winters, but not all, an ice bridge forms between SIPP and the mainland for brief periods between late January and early March. In the 1880s-1920s extensive ice-cover existed on Lake Superior (Assel 1990).

SIPP supports a fractured boreal fauna: Moose (*Alces alces*), American Black Bear (*Ursus americanus*) and Canada Lynx (*Lynx canadensis*) are absent. Smaller mammals include the Red Fox (*Vulpes vulpes*), snowshoe hare (*Lepus americanus*), North American Beaver (*Castor canadensis*), and Muskrat (*Ondatra zibethicus*). In 1907, Peter King, a lighthouse keeper, saw Caribou crossing on ice to SIPP. With more extensive ice in this period, Caribou and Wolves both might have moved back and forth frequently between SIPP and the mainland. John Bryson, a lighthouse keeper from 1948 to 1978, confirmed the absence of Wolves during that period, and Cringan (1956) also had not seen Wolf sign during his studies in SIPP the 1950s. From 1974-93 during our studies, no Wolf sign occurred on SIPP. Therefore, Wolves were likely absent and Caribou predator-free on SIPP from at least 1948-93. Then, a pair of Wolves crossed to the islands in the winter of 1993-94, and a second pair in the winter of 2002-03. More recently, during the winter of 2014-15, Wolves and Caribou were seen moving back and forth from the mainland to SIPP.

Cringan (1956) mentioned a salt lick at the outlet of Mud Lake in the centre of Patterson Island, the largest and most southerly island (28.4 km²), where most Caribou have resided (Figure 1). Observers frequently see Caribou 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, using McColl and Bowes islands as stepping stones between the larger islands. Caribou have not been observed swimming to the mainland and their sign is rare on the more distant Leadman Island to the northeast.

More detailed description of our Caribou survey methodology can be found in Bergerud *et al.* (2007) and in Carr *et al.* (2012), who tested it in 2007 and found it reliable. Essentially, it followed distance sampling methodology (Buckland *et al.* 2015) and abundance indices based on Caribou flushing distances that were developed for waterfowl (Lincoln 1930) and upland birds (King 1937). Our area searched annually was 6.4 ± 0.6 km2 or 18% of the archipelago. Single observers walked in May and June on compass courses at a normal pace and on routes chosen for practical turning points (topographic features, lakes, bays or points, etc.) and for boat drop-off and pick-ups. Walking schedule was selected to coincide with the period when vegetation least obscured view, and walking routes were selected to avoid areas disturbed in recent days and with the goal to have maximal line dispersal for effort invested. We also recorded Snowshoe Hares and their flushing distances as we them encountered in the Caribou surveys.

We started placing additional salt at the Mud Lake lick in 1976 and made daily observations of Caribou and Wolves from mid-May to the mid-June each year from 1977-1999 and in 2004. Patterson Island was divided using UTM coordinates into four straight-line quadrants using Mud Lake as the centre. The coordinates were from this centre to directions NE (8.4 km²), NW (5.0 km²), SE (7.3 km²), and SW (7.7 km²) to quadrants of Patterson Island with the land areas indicated (Figure 1). A watchtower 5 m in height was located approximately 35 m from the salt lick. Caribou habituated to observers when they remained in the tower. Observers recorded sex and age, tag number for tagged Caribou, and time in and out of Mud Lake, and in certain years (1988, 1991, 1992, 1994-96) the direction travelled (trail used). We counted as many uniquely identified Caribou as possible in each of the four quadrants during these years.

During Wolf years 1993-1995, Wolf tracks were also systematically counted during May and June in each quadrant of Patterson Island. In 19 of the study years during 1974-1998, we visited SIPP for a brief period in March (late winter) to locate carcasses for indications of die-off and to compile age composition tallies based on track and sign characteristics. We plotted calving locations across Patterson Island based on capturing neonates, observing their tracks, or hearing characteristic grunting by female Caribou for their young calves.

Captured Caribou were tagged with ear tags and released after certain measurements. Captures were in salt-baited box traps (2-4 traps each fall), boat herding to drive-traps at water crossings, a walk-through travel route trap, occasional use of drop-nets, and from boats for swimming Caribou. There were 628 capture events during 1974-1998, mostly in fall, capturing 602 unique individuals. We were able to see most tagged individuals most years at the Mud Lake salt lick. The survival of individual tagged individuals was based on the last year an individual was seen, after waiting three additional years to decide if the individual had been overlooked. If an individual was later seen with tags in good condition it was added back to the tagged pool. Recaptures were retagged with fresh tags.

**Results**

**Summary of Demographic Effects of Wolves on Caribou**

Mean annual survival rates of tagged Caribou females and males were both 82%. The year with lowest adult survival occurred before Wolf arrival in 1989-90, 15% for females and 12% for males. Prior to the arrival of Wolves, the number of Caribou carcasses encountered in March was negatively correlated with the weights of female Caribou captured the previous fall (*R*2 = 0.43, *n* = 16, 1975-94), and mean female weights in turn were negatively correlated with our estimates of the population size (*R*2 = 0.23), so we inferred that years of low survival prior to the arrival of Wolves could be attributed to starvation.

When Wolves were present in 1994-95, only 24 (71%) of 34 tagged female Caribou survived, the second lowest survival rate we calculated for females. Males, on the other hand, had high survival in both winters when Wolves were present: 33 (87%) of 38 in 1994-95, and 52 (91%) of 57 in 1995-96. Consequently, the sex ratio of classified adult Caribou changed from 56% females in 1993 to 43% in 1996.

Our estimate of the calf fraction in the Caribou population in March, excluding the springs of 1995 and 1996, was 15 ± 2% (*n* = 17 years, mean sample size of *n* = 123 track observations). In March 1995 and 1996, the years following Wolf arrival, the calf fractions were 5% (*n* = 165) and 2% (*n* = 129). Our population estimate in 1994 was 343 and in 1996 it was 190. The only year after 1998 when we classified the population in 2004 our sample comprised 132 females, 36 males, one yearling and one calf.

Our last systematic survey estimate in 2006 was 233. The Ontario Ministry of Natural Resources and Forestry conducted counts during 2008-10. Their transect census estimate was 134 (Carr *et al.* 2012). We visited in 2014 and estimated 50 individuals left and found no calves. In September 2016, we walked 114 km searching for Caribou and encountered just three individuals, all on McColl Island.

**Effects of Wolves on Behaviour of Caribou**

The flushing distance of 33 ± 1 m (*n* = 30 years) during our surveys did not differ significantly when Wolves were present in 1994-96. The first major change in spring behaviour with Wolves was larger sizes and frequency of groups of Caribou coming to the Mud Lake salt lick, eight per hour in 1994, higher than in any other year (Table 1). In 1995 the trend was reversed with just two visits per hour. Individuals, presumably recognizing safety near the watchtower, returned for a second time in the same day 253 times in 1994, compared to only 82 times in 1995. In 1994 and again in 2004, both times just after Wolf arrival, a substantial fraction of visits to Mud Lake were over an hour in duration, while in other years, few visits were this long (Table 1).

Wolves were most active at their den near Horace Cove Lake (SW quadrant of Patterson Island) and at Sunday Harbour (SE quadrant; Figure 1). Prior to 1994, Caribou entered the lick most frequently on a trail from the west that took them from the SW quadrant, northeast along the shores of Peninsula Lake, just west of Mud Lake, to the salt lick. After Wolf arrival, Caribou rarely used this trail and also substantially reduced their use of trails from the south and NW (Table 2). A trail from the east, rarely used before Wolf arrival, became among the heavier used in 1994-95, and the heaviest used trail was from the NE during these years. Wolf tracks, on the other hand, were most frequent in the SW and SE quadrants.

The distribution of 60 calving sites on Patterson Island encountered during 1976-92 was relatively even, with fewer in the smaller NW quadrant (Table 3). Few females calved during the pre-Wolf years on Mortimer Island. From transect data collected during the Wolf years 1994-96, more Caribou aggregations began to occupy the NW quadrant of Patterson Island as well as Mortimer Island. Except in 1995, Caribou aggregations were encountered least often in the SW quadrant and second most often in the NE quadrant during the Wolf years (Table 3). New calving sites were identified on Mortimer Island. The major shift in movement was in 2006, when many Caribou occupied the east side of NW quadrant and the west side of the NE quadrant. This combined area is only 5 km², with 16 Caribou aggregations encountered in 9.5 km walked in 2006, compared to the rest of Patterson Island, 23 km² (4.6 times the size), with 18 aggregations (only two more) encountered in 26.0 km (1.7 times the distance).

We found 26 Caribou carcasses during 2003-05, twenty 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 of Patterson Island, three on McColl Island.

**Other Ecological Effects of Wolves**

Wolf pairs arriving in 1993-94 and 2003-04 independently adopted the same Red Fox den on the northern shore of Horace Cove Lake and used it as a rendezvous site (Figure 1). By 2014, this den that been used by Red Foxes for 32 years had been deserted; we were also unable to find any sign of foxes in SIPP. Wolf scats we collected from 1995-98 (*n* = 45) contained hairs of Caribou calves (21 cases), of adult Caribou (13), of Snowshoe Hares (12), of Beavers (12), of Red-backed Voles (*Myodes gapperi*; 2), and berries of Showy Mountain Ash (*Sorbus decora*; 4), feathers of birds (2), insects (1) and grass (1).

High populations of Snowshoe Hares were estimated for SIPP in 1979, 1988, 1995 and 1996. In the presence of Wolves during 1994-96 and 2003-05, hares flushed sooner. The number of hares flushed per km of survey transect was 0.31 ± 0.07 during the six years with Wolves, while in the years without Wolves, the same index was only 0.09 ± 0.01, a statistically significant difference (*t* = 9.33, *P* < 0.001).

Before the arrival of Wolves, some beavers dug their own small ponds or built lodges on shallow creeks. 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 bottom. Their foraging range from water often exceeded 400 m during 1974-76. There were 36 active lodges in 1974 (one per km2) and with their long-range mobility free from predation we estimated they could have searched for forage over 95% of the habitat on Patterson and Mortimer islands. By 2006, only six colonies remained, only on the shores of inland lakes. In 2014 we could not find any sign of heavers in SIPP.

**Discussion**

Our interpretation of the SIPP ecosystem during the years 1974-93 was that Caribou were regulated by the availability of summer forage (Bergerud *et al.* 2007). Caribou often occurred during these years at very high densities, commonly 8-10 per km², compared to other forest-dwelling Caribou populations subject to Wolf predation, where densities are <0.12 per km² (Bergerud 2001). Residence by one pair of Wolves in 1994-96 (reduced to one wolf by 1996; Bergerud *et al.* 2007) produced these direct effects: consumption of adult and calf Caribou, leading to reduced recruitment, a smaller component of females in the population, and a diminished population size. Arrival of a second pair of Wolves in 2004 resulted in Caribou kills throughout Patterson Island and on McColl and Mortimer islands, eventually reducing the number of Caribou to very few, in part due to departures from SIPP beginning at least in the winter of 2014-15.

Caribou shifted their distribution to the NE quadrant of Patterson Island to reduce their contact with Wolves in the classic “space race” (Sih 2005) that has been documented for Caribou with Wolves in Pukaskwa National Park (Bergerud *et al.* 2014). Wolves in SIPP were likely less active in the spring and summer in the NE quadrant of Patterson because of our activities (at Mud Lake) and that of fishermen and tourists in McGeevy Harbour between McColl and Patterson islands. Kills did occur in these locations. But by avoiding Wolves and moving to occupy less space and smaller islands in an already food-limited environment, Caribou were likely also compromising their access to food, and becoming more vulnerable to starvation as well as predation, as observed on other Lake Superior islands (Ferguson *et al.* 1980). Concurrently, Caribou also increased their contact with people in SIPP, especially on McColl Island. With fitness consequences unknown, such contact does increase cortisol concentrations in Caribou (Ewacha *et al.* 2017).

It is not clear whether a Wolf pair could be sustained in SIPP (one Wolf was likely poisoned in 1996; Bergerud 2007), but their frequent departures from the archipelago, their unusual prey base, and our observed depletion of their major prey sources suggests that it is not possible. Other forest-dwelling Caribou will disperse to higher mountain slopes (Bergerud *et al.* 1985, Edmonds 1988, Nobert *et al.* 2016) or fen, bog or island habitats, where Moose and Wolves are rare and where water escape 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, 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, or possibly food limitation did not allow them the extra energetic expense. They also did not imprint to their birth sites as they do elsewhere (Shoesmith 1978, Wittmer *et al.* 2005, Bergerud *et al.* 2014). As a result, females and calves in SIPP appeared particularly vulnerable to the arrival of Wolves, and kills of Caribou appeared to have occurred predominantly near shorelines, consistent with the “leapfrog effect.” In sum, if Wolves had persisted on SIPP, Caribou would now be extinct, because to persist with Wolves they need the increased safe space provided by water.

Caribou on the SIPP were observed to be much more solitary than in other forest-dwelling populations, perhaps also because of food limitation. Their behaviours changed immediately the first spring following Wolf arrival. We documented similar changes in behaviour in Snowshoe Hares with Wolf arrival, and we infer direct and near-complete effects of Wolves in reducing a North 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 in herbivores.

We assisted the Ontario government in 1982 with an introduction of seven SIPP Caribou Michipicoten Island Provincial Park (188 km²), also in Lake Superior. A pellet count in 2011 estimated 680 caribou (3.6 per km²), a rate of increase, λ = 1.17, over 29 years (Kuchta 2012). Wolves are now established visitors to Michipicoten Island. Will we lose the last Caribou population in southern Ontario, a population which may be as naive as its ancestors in SIPP about the safety of water, caught between “bottom-up” and “top-down”?

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Figure 1

Figure 1. Slate Islands Provincial Park, showing the four survey quadrants on Patterson Island, locations where we encountered Wolf-killed Caribou (dots) during 2003-05, and the Wolf den site (star) during 1994-96 and 2003-05.

Table 1. Percent of total Caribou observations by time spent during mid-May to mid-June at the Mud Lake salt lick, Slate Islands Provincial Park, in three years without Wolves, 1988, 1991 and 1992, and in years following the arrival of Wolf pairs in winters of 1993-94 and 2003-04.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Time at lick (min) | 1988 | 1991 | 1992 | 1994 | 1995 | 1996 | 2004 |
| < 6 | 15 | 23 | 14 | 10 | 21 | 19 | 18 |
| 6-20 | 43 | 55 | 42 | 29 | 59 | 49 | 30 |
| 21-45 | 32 | 18 | 32 | 32 | 13 | 27 | 30 |
| 46-60 | 6 | 1 | 5 | 9 | 4 | 3 | 10 |
| >60 | 4 | 3 | 7 | 20 | 2 | 3 | 11 |
| Total observations 1 | 404 | 329 | 564 | 980 | 299 | 319 | 193 |

1 Multiple observations of the same individuals are included.

Table 2. Percent of total Caribou observations by trail direction leaving/entering the Mud Lake salt lick in three years without Wolves, 1988, 1991 and 1992, and in three years following the arrival of a Wolf pair in winter 1993-94 that denned southwest of Mud Lake.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trail | 1988 | 1991 | 1992 | 1994 | 1995 | 1996 |
| 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 |
| Totals 1 | 340/352 | 328/334 | 558/563 | 980/952 | 321/288 | 316/365 |

1 Multiple observations of the same individuals are included.

Table 3. Percent of Caribou calving sites encountered during 1976-92 on Patterson Island, and aggregations encountered on survey transects in the years following the arrival of a Wolf pair in winter 1993-94, by quadrant of Patterson Island. Quadrants are by compass direction from Mud Lake. Wolves denned SW of Mud Lake.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Quadrant | Calving sites | | Aggregations | | |
| 1994 | 1995 | 1996 |
| SW | 25 | 15 | | 29 | 11 |
| NW | 10 | 33 | | 41 | 42 |
| NE | 35 | 27 | | 14 | 28 |
| SE | 30 | 25 | | 16 | 19 |
| Total | 60 | 151 | | 110 | 36 |