

Predation rate by wolves on the Porcupine caribou herd

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Abstract: Large migratory caribou (*Rangifer tarandus*) herds in the Arctic tend to be cyclic, and population trends are mainly driven by changes in forage or weather events, not by predation. We estimated daily kill rate by wolves on adult caribou in winter, then constructed a time and space dependent model to estimate annual wolf (*Canis lupus*) predation rate (P_{annual}) on adult Porcupine caribou. Our model adjusts predation seasonally depending on caribou distribution: $P_{\text{annual}} = \sum K_{\text{daily}} * W * A_p(2) * D_p$.

In our model we assumed that wolves killed adult caribou at a constant rate (K_{daily} , 0.08 caribou wolf⁻¹ day⁻¹) based on our studies and elsewhere; that wolf density (W) doubled to 6 wolves 1000 km²⁻¹ on all seasonal ranges; and that the average area occupied by the Porcupine caribou herd (PCH) in eight seasonal life cycle periods (D_p) was two times greater than the area described by the outer boundaries of telemetry data (A_p /1000 km²). Results from our model projected that wolves kill about 7600 adult caribou each year, regardless of herd size. The model estimated that wolves removed 5.8 to 7.4% of adult caribou as the herd declined in the 1990s.

Our predation rate model supports the hypothesis of Bergerud that spacing away by caribou is an effective anti-predatory strategy that greatly reduces wolf predation on adult caribou in the spring and summer.

Key words: *Canis lupus*, kill rate, *Rangifer tarandus*, Yukon.

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Introduction

Migratory barren-ground caribou (*Rangifer tarandus*) herds show wide population fluctuations that have been explained by changes in forage, climate, predation and harvest (as reviewed in Klein, 1991). Various researchers have pointed out the difficulty of separating interactions of forage-climate-predation when trying to determine the cause of change in caribou abundance (Gauthier & Theberge, 1986; Thomas, 1995; Adams *et al.*, 1995; Bergerud, 1996; National Research Council, 1997). The effects of wolf (*Canis lupus*) predation on migratory barren-ground caribou were poorly understood in the past, mainly because arctic wolves were migratory and difficult to follow (Kuyt, 1972; Stephenson & James, 1982). Recent studies in arctic Alaska (Dale *et al.*, 1994; Ballard *et al.*, 1997) and Canada (P. Clarkson, Government of the Northwest Territories, unpubl.; R. Hayes, unpubl.) provide new data about arctic wolf movements, range use and their killing rates on caribou. These data were required their to

develop quantitative models for estimating predation rates on migratory caribou herds.

In this paper, we present data on winter kill rate by wolves on adult caribou when Porcupine numbers were high. We construct a simple predation rate model that includes constants for wolf density and kill rate that are applied to changing seasonal range use and densities of caribou. We discuss why predation by wolves is not the main force limiting the size of the Porcupine herd in the 1990s.

Study area

We conducted our predation rate research in 1989 in a 14 450 km² study area in the Northern Richardson Mountains. Predation studies that winter were part of a larger study of wolf ecology conducted between 1987 and 1993 in the northern Yukon (R. Hayes, unpubl.).

Our study area straddled the northern boundary of the Yukon and Northwest Territories (NWT). The main study area included the Northern

Richardson Mountains and the eastern part of the Yukon Coastal Plain. The study area was bounded by the Blow and Bell Rivers to the West, the MacKenzie Delta to the East, the Rat River to the South, and the Arctic Coast to the North. The study area included two communities in the NWT, Aklavik (population 801) and Fort MacPherson (878, Statistics Canada 1996).

We studied winter kill rate across 3 ecoregions (Oswald & Senyk, 1977): the Northern Mountains, the Coastal Plain, and Berry Creek. We have paraphrased descriptions of physiography and vegetation from Oswald and Senyk (1977). Most of the northern Yukon was a glacial refugia that now lies within the zone of continuous permafrost. The Northern Mountains Ecoregion includes the Richardson Mountains where elevations commonly exceed 1500 m above sea level (asl). Most of the Coastal Plain Ecoregion lies below 150 m asl. The eastern part of the Yukon Coastal Plain include four watersheds: the Peel, Big Fish, and Blow Rivers and Rapid Creek. The Richardson Mountains are drained by the Willow, Rat, Fish and Bell Rivers.

The Berry Creek Ecoregion forms the southwestern flank of the study area, and ranges from flat to gently rolling terrain with uplands below 600 m asl, and valleys below 300 m asl. The area is drained by the Bell, Porcupine, Eagle and Driftwood Rivers.

Most of the study area is open tree-less tundra, except along protected valleys where there are isolated stands of black spruce (*Picea mariana*), white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*). The main vegetation is sedge (*Carex* sp.) and cottongrass (*Eriophorum* sp.) tussock tundra. Dwarf birch (*Betula* sp.), willow (*Salix* sp.) and alder (*Alnus* sp.) are found on warmer sites. Cooler sites support ericaecious shrubs, willows and various forbs. Riparian spruce and balsam poplar forests are found on the Bell, Driftwood and Porcupine Rivers. Shrub birch and willow dominate most openings and the forest understory. Sedge and cottongrass tussocks dominate most poorly drained open areas.

Four ungulate species inhabit the study area: caribou, moose (*Alces alces*), Dall sheep (*Ovis dalli*) and muskoxen (*Ovibus moschatus*). The PCH increased from 135 000 caribou in 1983 to 178 000 in 1989; an annual finite rate of increase of 1.048 (λ). Between 1989 and 1992 the herd declined to about 160 000 caribou ($\lambda = 0.965$, Fancy *et al.*, 1994). The PCH traditionally calves on or near the Arctic National Wildlife Refuge in northeastern Alaska, then spends the post-calving and summer

periods along the Yukon Coastal Plain. The herd then migrates to various traditional wintering areas in the Richardson Mountains, Eagle Plains, Ogilvie Mountains and southern Brooks Range in Alaska. During the winter 1988-89, a large number of Porcupine caribou wintered in our study area.

Moose density is low and most moose winter in the limited riparian forests along the Bell River (Smits, 1991). Few moose wintered in the north slope drainages, where we conducted most of predation studies. In the same area, Barichello *et al.* (1987) counted about 900 sheep in 1986. C. Smits (Yukon Fish and Wildl. Br., unpubl.) counted 157 muskoxen on the Yukon Coastal Plain in 1993, mainly to the west of our study area.

Other large predators in the study area include brown bear (*Ursus arctos*) (Nagy, 1990), black bear (*Ursus americanus*) in the taiga, lynx (*Lynx canadensis*) and wolverine (*Gulo gulo*). Arctic fox (*Alopex lagopus inuitus*) are restricted to coastal areas (Youngman, 1975). Ravens (*Corvus corax*) are the main scavengers that compete with wolves at kills.

Materials and methods

We used radiotelemetry techniques (Mech, 1974) to study predation behaviour of wolves. After we first located a wolf pack by fixed-wing aircraft, we dispatched a helicopter (Bell 206B) and immobilized wolf pack members with Capchur (Palmer Chemical and Equip. Co., Douglasville, Ga.) equipment. Most wolves received a dose of Zoletil (A. H. Robins) at 8 mg/kg, based on an estimated average wolf weight of 40 kg. We attached conventional VHF radio-collars on wolves (Telonics, Mesa, Arizona).

We studied kill rates by monitoring the daily activities of seven radio-collared packs from 23 March to 16 April 1989 from a Maule LR7 aircraft. We defined pack size as the mean number of wolves seen in the period (Messier, 1994; Dale *et al.*, 1994; 1995; Hayes *et al.*, 2000). We defined kill rate as the number of caribou killed per wolf per day. The total biomass (kg) of caribou killed was used to measure consumption rates of wolves. Based on data from Skoog (1968) we estimated the live weights of adult caribou: male 107 kg, female 79 kg and unknown caribou 86 kg. We assumed the consumable biomass was 75% of caribou live weight (Ballard *et al.*, 1987; 1997).

Each day, we located six wolf packs (2-6 wolves) once in the morning (9:00-12:00h). We located the

Table 1. Killing rates by wolves on caribou in our study, March and April 1989.

Pack name	Pack size	Period (days)	No. wolf days	No. of caribou killed	Total kg. killed	No. caribou killed/wolf/day	Kg. caribou killed/wolf/day	Kg. caribou consumed/wolf/day
Blow River	12	25	300	9	776	0.03	2.59	1.94
Bell River	2	7	14	3	274	0.21	19.57	14.68
Blow R. 450	3	6	18	2	195	0.11	10.83	8.13
Rat River	6	25	150	4	406	0.03	2.71	2.03
Rat River II	3	24	72	1	109	0.01	1.51	1.14
Trail River	3	14	42	2	195	0.05	4.64	3.48
Two Ocean	2	19	38	2	172	0.05	4.53	3.39

12 member Blow River pack twice a day, in the morning and evening (18:00 to 22:00 h). We compared kill rate for morning-only sightings of Blow River wolves, and for the combined morning and evening to test for temporal bias in our ability to detect caribou kills by locating other packs once daily.

Most packs traveled in the north slope drainages where snow conditions were heavily windblown in 1989. Wolves and their prey carcasses were difficult to see because of the contrasting mosaic of open ground and snow fields. Snow was usually too wind-packed to backtrack wolves to determine their activities between location points. We located radio-collared wolves, then systematically searched for any kills in a 2-3 km² area, until we either found kills or we were confident wolves had not made a kill nearby.

We estimated annual *predation rate* as the proportion of adult Porcupine caribou killed by wolves. To determine the rate of wolf predation on the Porcupine herd we needed a model that was based on reasonable ecological assumptions about wolves and caribou. From wolf surveys in the northern Yukon (R. Hayes *et al.*, unpubl.) and in other parts of the PCH range (Stephenson, 1994; Carrol, 1994), we estimated a mean density of about 3 wolves/1000 km², giving a population of 725 wolves in the entire range of the herd. Not all wolves have caribou available to them each year, and the number must vary with the area caribou occupy during different phases of their annual life cycle (*e.g.*, spring migration, calving, winter). This means that we cannot estimate predation rate by simply applying a fixed kill daily rate to the entire wolf population. To account for changing distributions of caribou and wolves, both in space and time, we constructed the model for estimating annual predation rate (P_{annual}):

$$P_{\text{annual}} = \sum K_{\text{daily}} * W_i * A_p(2) * D_p.$$

We assumed that wolves killed adult caribou at a constant rate (K_{daily}); that wolf density (W) doubled to 6 wolves per 1000 km² on all seasonal ranges; and that the average area occupied by the PCH each year in eight seasonal life cycle periods (D_p , see Table 2) was twice as large as the average area described by the outer boundaries of satellite telemetry data (A_p /1000 km²; Int. Porcupine Caribou Board 1993).

Results

Kill rate by wolves

We followed the daily activities of seven wolf packs for 17.1 ± 3.1 (standard error of the mean) days (Table 1). Traveling pack size was 4.4 ± 1.4 , ranging from 2 to 12 wolves per pack. We found 23 wolf-killed caribou and we examined 13 carcasses in situ. All were adults (8M, 5F). The mean age of killed caribou was 6.1 ± 0.7 years-old. The lowest kill rate was for wolves in the Rat River II pack (Table 1) which scavenged from many hunter kills in the area. After excluding this pack, we estimated the wolf kill rate was 0.08 ± 0.03 caribou per day per wolf; or 7.5 ± 2.7 kg of caribou killed per wolf per day. Wolves consumed 5.6 ± 2.0 kg caribou each day in winter.

We did not find a difference in the number of kills seen for morning-only sightings of Blow River wolves compared to the combined morning and evening sightings ($n=9$ kills, 0.36 caribou per pack per day). We conclude that twice daily locations did not improve our ability to detect kills made by study packs.

Predation rate by wolves

Based on a daily kill rate of 0.08 adult caribou (K_{daily}), our model projected that wolves killed 7600 adult caribou from the Porcupine herd each year. About 84% of the adults were killed during fall and

Table 2. Variables and values used in modeling annual wolf predation rate on Porcupine caribou herd. Values for D_p and A_p were provided by Inr. Porcupine Caribou Board (1993).

Caribou life cycle Period	D_p No. of Days	Mean Area ¹	A_p Area of Available Caribou ¹	W Wolf Density ²	K_{daily} Daily Kill Rate by Wolves on Caribou
1. Late Winter	120	25.9	51.8	6	0.08
2. Spring	62	27.4	54.8	6	0.08
3. Calving	11	8.8	17.6	6	0.08
4. Post Calving	22	7.5	15	6	0.08
5. Early Summer	16	3.4	6.8	6	0.08
6. Mid Summer	22	5.99	11.98	6	0.08
7. Late Summer and Fall Migration	62	12.8	25.6	6	0.08
8. Rut and Late Fall	50	37.1	74.2	6	0.08

¹ in 1000 km² units.

² number of wolves per 1000 km².

winter (Table 2, Fig. 1) when caribou use the largest areas, allowing more wolves to concentrate on fall and winter range. The remaining 16% of adults were taken in spring and fall when the herd's range is substantially compressed, and their availability to wolves is lowest (Table 2, Fig. 1).

Because our predation model does not depend on herd size, we applied it to Porcupine census data in 1992, 1994 and 1998. Each year the herd was censused with photo counts in July (D. Russell, unpubl.). The percent calves was annually estimated in March (D. Cooley, Yukon Fish and Wildl. Br., unpubl.). Our model estimated that wolves removed 5.8% of adults in 1992 when herd size was 160 000; 6.3% in 1994 when herd size was 152 000; and 7.4% when herd size fell to 129 000 in 1998.

Discussion

Kill rate by wolves

The daily kill rate of our study wolves was similar to caribou-killing wolves in Alaska (0.08 caribou per wolf per day, Dale *et al.*, 1994) and Northwest Territories (0.05 caribou, P. Clarkson, unpubl.), although our pack kill rates were more variable. We studied wolf kill rate in mainly small packs of 2-3 wolves (Table 1). Hayes *et al.* (2000) found wolves in small packs had much wider variation in kill rate of moose compared to larger packs, which could also explain our caribou predation data.

The mean daily consumption rate was 4.9 kg of caribou per wolf, above the range of 1.7 to 4.0 kg

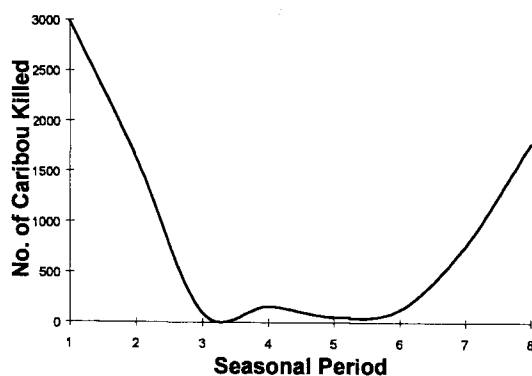


Fig. 1. Seasonal predation rate by wolves on PCH based on model. Seasonal periods correspond with numbers shown on Table 2.

required for survival (Mech, 1977; Thurber & Peterson, 1993) and above the 3.2 kg required for reproduction (Mech, 1977). Similar consumption rates were recorded for arctic wolves in northwestern Alaska (5.3 kg of moose and caribou, Ballard *et al.*, 1997) and NWT (4.4 kg, P. Clarkson, unpubl.).

Previous estimates of wolf consumption rate are probably higher than actual, because biologists usually assumed that wolves eat all available biomass of their kills (Carbyn, 1983; Messier & Crete, 1985; Ballard *et al.*, 1987; Fuller, 1989; Hayes *et al.*, 1991; Thurber & Peterson, 1993; Dale *et al.*, 1995). Hayes *et al.* (2000) adjusted kill rates to account for raven scavenging, estimating that ravens can remove up to half of consumable moose biomass

from small wolf packs (2-3 wolves). Five of our study packs were small and we commonly saw ravens at caribou kills. However, we agree with Ballard *et al.* (1997) who estimated that wolves lost less of their caribou kills to ravens because wolves can consume caribou carcasses more rapidly than they can consume moose - leaving less caribou biomass for scavengers.

By back-tracking wolf trails, Dale *et al.* (1994) increased their estimate of kill rate because wolves killed then left the caribou carcasses before the next radio location. Hayes *et al.* (2000) underestimated kill rate by wolves on woodland caribou by locating packs once daily, and recommended back-tracking whenever possible. Clarkson and Liepens (unpubl. data) believed that arctic wolves remained close to their kills in order to protect them from other migratory packs, therefore, back-tracking was not useful in tundra areas. Without backtracking we recorded a similar kill rate as Dale *et al.* (1994) did with backtracking. We had the advantage of studying small migratory packs that traveled in open tundra areas, which probably remained near kills for defense purposes (P. Clarkson, unpubl. data). Increasing our observation rate to each morning and evening did not increase our ability to detect caribou kills made by a pack of 12 wolves. Despite the windblown conditions, we reasonably estimated kill rate of our study packs on Porcupine caribou winter range.

Predation rate model

We verified our model assumptions by looking at caribou and wolf studies elsewhere. Our study, Dale *et al.* (1994) and P. Clarkson (unpubl.) reported kill rates of 0.05-0.08 caribou wolf⁻¹ day⁻¹. Thus, we believe that substantial changes to the value for variable K_{daily} are not justified. Our study, Parker (1973), Kuyt (1972), Thomas (1995) and Clarkson & Liepins (unpubl.) all found a two-fold increase in wolf density on winter range. We had substantial telemetry data to evaluate seasonal PCH distribution for over twenty years. Thus, we could not justify increasing the areas of available caribou more than two-fold. Our model does not incorporate changing vulnerability to predation, which Mech *et al.* (1998) found was an important function of wolf predation rate on the Denali caribou herd.

We next examined how our predation rate fit current knowledge of Porcupine caribou ecology. Fancy *et al.* (1994) found mean adult mortality rate for ≥ 3 -year-old caribou was 15% for females and 17% for

males. Using our 1992 wolf predation rate estimate of 5.8%, our model projects that wolves were responsible for about 1/3 of the adult mortality in the early 1990s.

According to Fancy *et al.* (1994) and Walsh *et al.* (1995) the growth of the PCH is most sensitive to the survival rates of females three years and older, followed by production and survival rates of calves. Fancy *et al.* (1994) speculated that the decline of the PCH after 1989 was related to a combination of low parturition rate of ≥ 3 -year-old females in 1991, and lowered calf survival in March 1992. Using stochastic modeling, Walsh *et al.* (1995) showed that a survival rate decline of about 3% among adult females or 4% among calves could be enough to cause the Porcupine herd to decline. Our model projects that wolves would have to nearly double their predation rate to account for an additional 3% decline in adult female survival.

Using different predation rate models, Dale *et al.* (1994) and Ballard *et al.* (1997) also determined that predation by wolves was not the main factor limiting caribou in northwestern Alaska. Ballard *et al.* (1997) estimated that wolves annually removed about 6-7% of the Western Arctic caribou herd.

Predation by wolves is an important factor limiting smaller caribou herds in Canada and Alaska (Gasaway *et al.*, 1983; Bergerud & Elliot, 1986; Edmonds, 1988; Seip, 1992; Hayes & Gunson, 1995; Mech *et al.*, 1998). Current knowledge suggests wolf predation acts in a depensatory fashion (i.e., it increases as herd size declines) where caribou are secondary prey to wolves that rely primarily on moose. Wolf predation does not appear to be the main cause of population change for large migratory caribou herds in the arctic (Messier, 1995; Crete & Huot, 1993; Thomas, 1995). Large migratory caribou herds tend to be cyclic, and previous population trends have been linked to changes in forage or weather events (Crete & Huot, 1993; Fancy *et al.*, 1994; Messier, 1995).

The low effect of predation by wolves is supported by the hypothesis of Bergerud (1974), who has argued that the migratory behavior of caribou evolved as a predator-avoidance strategy. Bergerud (1992) believes that migratory caribou calve on small remote areas to 'space away' from predators. By doing so, they can flood a large number of young in a small area where the per capita risk to being killed by any predator is lowest.

Our model does not estimate predation rate on calves, however, it does support that 'spacing away'

is also an effective anti-predatory strategy of adult caribou (Bergerud, 1974; 1992; Thomas, 1995). In late spring and summer, Porcupine caribou concentrate on the coastal plain of Alaska and Yukon, where they occupy the smallest seasonal range, thereby reducing their exposure to predators (Table 2). Adult wolves are limited in their ability to travel there due to their requirement to feed pups at dens (Thomas, 1995; R. Hayes, unpubl. data).

Fryxell *et al.* (1988) developed a similar time-space dependent model for estimating African lion (*Panthera leo*) predation rate on migratory wildebeeste (*Connochaetes taurinus*) that supports the 'spacing-away' advantage. They concluded that large migratory wildebeeste herds could not be regulated by lions, mainly because lions could not maintain contact with herds year-round, reducing annual predation rate.

We believe that the variables of our model are useful at various Porcupine caribou herd sizes because: 1) the area that caribou used seasonally was similar in the 1970s when the herd was about 100 000 caribou (Le Resche, 1975); and 2) as the herd declines we should not expect a strong density-dependent change in the wolf functional response (Dale *et al.*, 1994). Thus, wolf kill rate should remain constant. Also, taiga wolves can readily switch to low density moose prey to survive (Ballard *et al.*, 1997) reducing the negative effect of declining caribou abundance on wolf numerical response.

Data quality

Although our estimate of mean daily kill rate was similar to other studies, it was bounded by a wide standard error. This could be because the sample size of packs was small, or the kill rate was underestimated for some packs due to terrain or weather constraints.

We acknowledge some shortcomings with our predation rate model. Although the model fits current indices of the PCH, components of the model need further validation. First, we assumed that K_{daily} in the summer period was the same as for winter. Wolves are reported to surplus kill neonatal and adult caribou (Miller *et al.*, 1983; 1988; C. Gardner, Alaska Dep. Fish and Game, pers. comm.). The effect of wolf predation rate on changing calf recruitment rates of the Porcupine herd remains unknown, and we did not include this important population process in our model.

Second, the estimates of the area that caribou occupy seasonally are based on radiotelemetry loca-

tions. There is a declining gradient outward from these areas where low density caribou will still be available to wolves. We estimated caribou-available areas to be twice the areas described by caribou telemetry, but the area might be even larger. However, we needed to increase the caribou available area in our model by five-fold before wolves took 10% or more of the adults. Third, arctic wolves show strong preference for caribou, and wolves probably continue to search for caribou even when caribou appear to be absent (P. Clarkson, pers. comm.). If PCH wolves behave this way, then our estimates of seasonal predation rates could also be low.

Nevertheless, our results are consistent with other arctic wolf studies that found a uniquely migratory behaviour among wolves associated with barren-ground caribou, naturally low wolf densities, a preference for caribou prey, and moderate daily kill rates by wolves. The model we present is based on detailed knowledge of a dynamic seasonal range use pattern by Porcupine caribou that was available only after decades of radiotelemetry studies. Future predation research should be conducted to investigate whether the assumptions of our model hold in this period of declined herd size.

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