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Seasonal scatology of wolves along the Dempster Highway, northwestern Canada—an introduction of pollen analysis for dating old scats

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Abstract: This study aims to renovate the method of studying seasonal variation in wolf diet by introducing simultaneous analysis of undigested residua and pollen grains in wolf scats collected regardless of their freshness over a short period of time, in which pollen grains help to identify the season the diet was taken. The present study was conducted over a range of 500 km along the Dempster Highway extending north from Dawson, Yukon Territory to Inuvik, the Northwest Territories, Canada. We collected a total of 24 wolf scats along side roads and rivers, in which as many as 14 million pollen grains/scat were found on an average. The analysis revealed that the wolves relied exclusively on the caribou during winter when scats are free of pollen grains, but increase their dependence on the beaver and other mammals up to over 50% in term of residuum occurrence in spring and summer when scats are respectively loaded primarily with arboreal and herbaceous pollen grains. This result was consistent with the local fauna of prey animals, the migration pattern of the caribou for breeding and wintering, availability of the beaver and other rodents as dictated by ice/snow cover, and breeding and cub rearing pattern of the wolves themselves. Thus it was concluded that the pollen analysis serves as a powerful and effective tool for identifying the seasonality of old scats, and therefore saves a great deal of time and effort to be devoted to finding fresh scats.

key words: wolf, pollen, undigested residuum, seasonal diet, Dempster Highway

Introduction

Among our knowledge about wildlife, their feeding and reproduction habits are of primary importance. Especially, the diet of the predators explains their relationship with prey species, and thus helps to understand the community structure. The classic yet basic method even today to study dietary habits of elusive animals on the uppermost hierarchy of the food chain is scat analysis, in which their diet is estimated from undigested remnants in the scat. The major disadvantage of this method is a considerable amount of time and effort needed to search for fresh scats year around to reveal the seasonal variation of dietary habits.

To overcome this difficulty, we have incorporated pollen analysis into scat analysis so that the seasonality of old scat can be identified from the timing of pollen production. Obviously, the wolf doesn't feed on pollen grains, but we have reasoned that they have a good chance of ingesting them involuntarily either by inhaling pollen-laden air or by eating prey whose coat has trapped a considerable amount of pollen during the pollination season.

Study area

Our study area covers a 500 km stretch across the Arctic Circle along the Dempster Highway extending northeast from Dawson, Yukon Territory to Inuvik, the Northwest Territories, Canada. The southern margin of the study area is bounded by the E-W oriented Ogilvie Mountains, its eastern margin by the N-S oriented Richardson Mountains with two drainage basins in between. Cutting across the Richardson Mts., the smaller basin toward the south drains east into the Mackenzie River, while the larger one toward the north drains north and then west *via* the Porcupine River into the Yukon River (Fig. 1).

The vegetation is characterized by boreal forests at lower elevations, with a mosaic of ecotone woodland and alpine tundra at higher elevations, culminating in bare spots and zones respectively around peaks and along ridges. More specifically, moist to mesic sites in the valley bottom are vegetated by such broad-leaved species as alders (*Alnus crispa* and *rugosa*), birches (*Betula papyrifera* and *pumila*) and willows (*Salix alaxensis*, *arbusculoides*, *arctica*, *bebbiana*, *glauca*, *myrtillifolia*, *padophylla* and *planifolia*); and drier sites on the mountain slope by such conifers as spruces (*Picea glauca* and *mariana*)

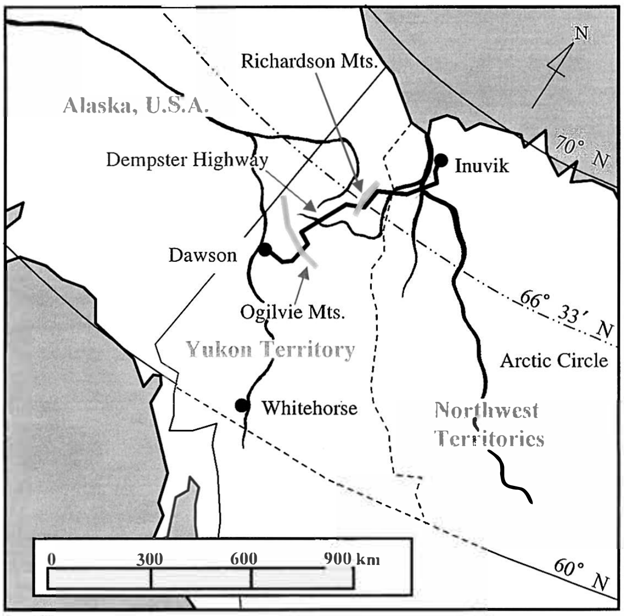


Fig. 1. Study area, from the Ogilvie Mts. to the Richardson Mts. along the Dempster Highway.

and pines (*Pinus banksiana* and *contorta*) which become stunted and open with increasing elevation and exposure. Eventually the vegetation turns into alpine meadow of Ericaceae such as blueberries (*Vaccinium myrtilloides* and *caespitosum*), cranberry (*V. vitis-idaea*), leatherleaf (*Chamaedaphne calyculata*) and common bearberry (*Arctostaphylos uva-ursi*); Caryophyllaceae species as chickweeds (*Stellaria longipes* and *longifolia*) and northern stitchwort (*S. calycantha*); Asteraceae such as yarrows (*Achillea millefolium* and *sibirica*) and canada goldenrod (*Solidago canadensis*); Cyperaceae such as bulrushes (*Scripus caespitosus* and *lacustris*) and tall cotton-grass (*Eriophorum angustifolium*); and Gramineae such as foxtail barley (*Hordeum jubatum*). Other plants commonly found are fire weed (*Epilobium angustifolium*), ground-cedar (*Lycopodium complanatum*), stiff club-moss (*L. annotinum*) and peat mosses (*Sphagnum* ssp.).

The fauna is characterized by such hoofed animals as caribou (*Rangifer tarandus*), moose (*Alces alces*) and Dall sheep (*Ovis dalli*); mid-sized rodents such as beaver (*Castor canadensis*) and porcupine (*Erethizon dorsatum*); hares such as snowshoe hare (*Lepus americanus*) and arctic hare (*L. othus*), and many species of small rodents. According to Whitaker (1998), they include muskrat (*Ondatra zibethicus*), squirrels (*Spermophilus parryii* and *Tamiasciurus hudsonicus*), least chipmunk (*Tamias minimus*), lemmings (*Lemmus sibiricus* and *Synaptomys borealis*), voles (*Clethrionomys rutilus*, *Microtus longicaudus*, *xanthognathus*, *miurus*, *oeconomus* and *pennsylvanicus*) and deer mouse (*Peromyscus maniculatus*) in our study area, though we did not see them all. Other animals which are rarely hunted, if ever, by wolves are such carnivores as coyote (*Canis latrans*), foxes (*Vulpes vulpes*, and *lagopus*), lynx (*Lynx lynx*), bears (*Ursus arctos* and *americanus*), river otter (*Lontra canadensis*), and bird species such as crane, goose and many others.

Methods

A field survey in search for wolf scat was conducted for a month in August, 2002 along the Dempster Highway and its subsidiary sideroads as well as along nearby streams, resulting in a total of 24 scats. As a precaution against parasitism by tapeworms, round-worms, flukes, etc. (Kohira, 1995), they were tightly sealed in plastic bags while out in the field and were subjected to autoclave back in Inuvik and Edmonton, and then brought back to Japan for analyses of undigested residuum and pollen.

The major constituents of the residuum were hairs, fractions of bones and occasionally teeth. What makes wolf scat so different from that of dogs, a species of the same genus *Canis*, is its heavy loading with undigested hairs and bones apparent even in the fresh state. They were extracted by dissolving scats in water and screening through a sieve of 0.25 mm mesh. Of the residua thus extracted, hairs were identified by comparison with samples from known animals and bone fractions by their size. Sample hairs prepared for comparison were of caribou, beaver, arctic hare, otter, muskrat, grizzly, black bear, lynx and red fox. The only distinction possible from the bone fractions was the size of the prey, and thus they were identified only as large, medium and small mammals with species identification in association with concomitant hairs. The large mammals cover Dall sheep and larger, medium beaver, hare and porcupine, and small the small rodents such as muskrat, lemmings, squirrels, chipmunks, voles and mice. Teeth could provide more accurate keys to species, but to be consistent identification was only by hair and bone, which were by far the most abundant evidence.

Pollen was analyzed from small fraction of the scat, weighing 0.1 to 12 g, depending on the size and the moisture content of scats. To avoid possible post-factum contamination by falling pollen grains on resting scats after defecation, the samples were taken meticulously from the unexposed portion of the scats, to each of which 48540±4380 exotic marker grains of *Eucalyptus* were added to facilitate calculation of pollen concentration later on. Basically, following the standard extraction method for modern pollen grains, they were dissolved in water, and then filtered through a 0.25 mm mesh sieve to remove large wastes. The solution was then cooked alternately in potassium hydroxide (KOH) and acetolysis solution, *i.e.* a 9:1 mixture of glacial acetic anhydride ($(CH_3CO)_2O$) and concentrated sulphuric acid (H_2SO_4), for disintegration and dissolution of non-pollen matrix. Potassium hydroxide was meant for deflocculation and removal of humic acids, while acetolysis solution for dissolving free cellulose. The solution was then centrifuged to settle the pollen grains, and the resultant 0.1–3.0 cc sediment was mixed with glycerol jelly for mounting on a microscope slide.

The subsequent pollen identification and counting on the slide were done under the microscope along parallel lines of equal spacing of 1 mm from one end to the other and from top to bottom covering the entire area of the cover glass. Along with pollen grains, the exotic marker grains were also counted to determine their relative abundance to pollen grains, from which an estimate of total pollen grains in the whole scat can be obtained. Broken pollen grains, usually into halves, were counted as 0.5. Pollen grains were identified at ×400 magnification. Pollen grains were identified with the aid of a published key (McAndrews *et al.*, 1973) and the reference collection of the Kyoto Prefectural University, to the genus level whenever possible.

In the above pollen identification and counting, the following criteria were set to economize time and effort, yet to retain as much representation of pollen occurrence as in the original sample: for each individual scat 1) to count a minimum of 20–25 pollen grains, 2) to make a full count of at least one slide even when it contains more pollen than has been specified above and 3) to judge the sample as "pollen-free" when the exotic marker count exceeds 300 without finding any pollen.

The exotic marker also serves as a factor to estimate the total number of pollen grains (X) in a given scat according to

$$X=\frac{M}{m}x\cdot\frac{W}{S}, \tag{1}$$

where x is the number of pollen grains counted, M (=48540) and m are numbers of exotic marker grains originally added to the sample scat and found in the examined slides respectively, and W and S represent weights of whole and sample scat.

Upon identification and counting, pollen grains were classified, first by their seasonal sensitivity and then by the time of production. Gramineae pollen grains and *Sphagnum* spores were discounted since they are ubiquitous throughout the growing seasons and thus not indicative of any particular season. The timing of pollen production was eventually identified by season in two steps. First, consulting local botanical field and identification guides (Johnson *et al*., 1995; Peterson and McKenny, 1968; Pratt, 1991), a list of production timing by month was prepared as in Fig. 2 at genus or family level for all the pollen grains and spores identified in the analysis. Then, as in Fig. 3, seasonal classification of the months was assigned somewhat arbitrarily but with some consideration for temperature control over plant physiology according to the 1970–1976 mean of observed monthly maximum and minimum temperatures at Dawson, near the southern margin of the study area. The seasonality of scat was then determined as the production time of the pollen grains identified in a given scat. In case two or more kinds

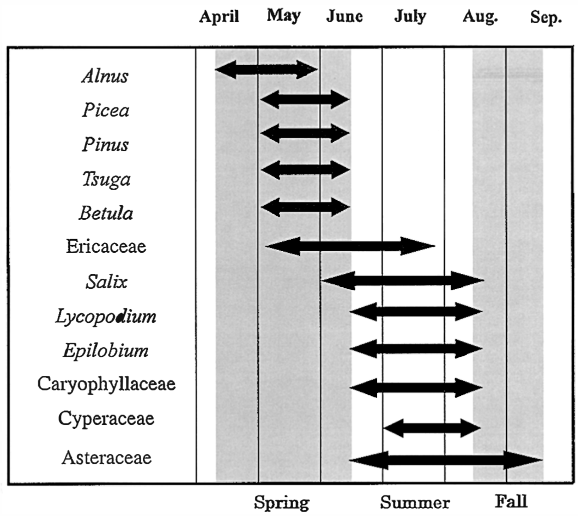


Fig. 2. Seasonal distribution of pollination time (composed after Johnson *et al*., 1995; Peterson and McKenny, 1968; Pratt, 1991).

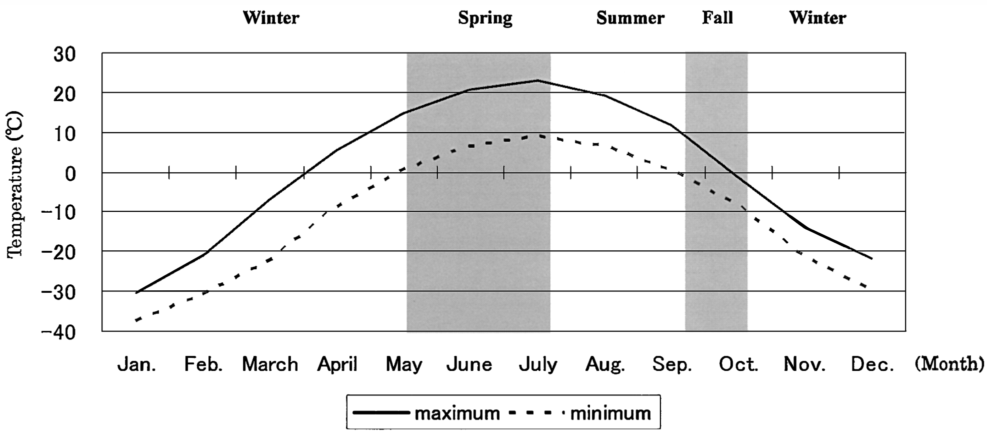


Fig. 3. Classification of seasons according to monthly maximum and minimum temperatures at Dawson, Yukon Territory.

of pollen grains from different seasons were found in a given scat, it was judged to have been defecated in the later season, reasoning that the later pollen had just been emerging while the earlier one had still been airborne or not yet settled down.

Result and discussion

Judging from the time lag of a few days at most between feeding and excretion as observed in the dog, the domesticated cousin of the wolf, the timing of defecation was naturally interpreted as that of feeding in the following discussion. Before getting into seasonal characteristics of prey species, it is necessary to discuss the results of residuum and pollen analyses separately.

In residuum analysis, the caribou appeared most frequently among diet items, followed by small mammals and then by the beaver. In other words, the caribou and the beaver were the only prey identified to specific level out of some seven possible prey species of large to medium size in the study area. This is consistent with the dietary habit of wolves mentioned by Mech (1970): *Because the wolf as a species ranges over a much wider area than any of its prey, different populations of wolves must prey on different kinds of animals. In each region, only one or two species make up most of the wolf's diet.*

In our case, the caribou in wolf scat outnumbered other hoofed mammals for several reasons. The first is the population size. Our study area coincides with the southeastern quarter of the migration range of the Porcupine caribou herd, with estimated population size of some hundred thousand, against which both the moose and the Dall sheep populations are dwarfed. Additionally, being much larger and thus more resistant than the caribou (90–130 kg), the moose (300–600 kg) seems to be less vulnerable to wolf attack. On the other hand, considerably smaller than caribou, the Dall sheep (40–100 kg) seems more susceptible, but its habitat of steep terrain in the Ogilvie Mountains is more or less out of our study area, and naturally they did not appear in our scat samples.

The result of pollen analysis is given by scat in increasing order of latitude, *i.e.* from south to north in Table 1, in which actual pollen counts are listed along with such other statistics as scat weights and marker counts to scale up the pollen count to an estimate of total pollen grains in each scat. As readily seen in the table, the scat weight varies greatly depending upon the moisture content dictated by freshness and the original scat size controlled by the amount originally defecated and lost after defecation. A total of 1228.5 pollen grains and spores were counted, of which 950.5 or 77.4% turned out to be sensitive ones effective for identification of scat's seasonality. The remaining 22.6% or 278 were either insensitive or unidentifiable. The insensitive ones include those of Gramineae and *Sphagnum*, as has been mentioned already in the Method section.

As also mentioned in Method, the actual pollen counts were scaled up to the scat basis as a reference for determining proper scat sample size for pollen analysis in future work. The total pollen content in individual scats calculated according to eq. (1) from the weight of the whole scat and a pollen-analysis sample, and the count ratio of pollen to marker, ranged from null to 23.929 million with an overall average of 1.402 million, of which 1.311 million were sensitive ones, abundant enough for pollen analysis.

These sensitive pollen grains and spores provided keys for determining the

Table 1. Actual count and estimated total number of pollen grains and spores by scat.

Scat No.	Scat Weight (g)		Number of pollen grains and spores counted		Number of exotic marker grains	Estimated number of pollen grains and spores per scat ($\times 10^3$)	
	Whole	Sample	Total	Sensitive		Total	Sensitive
1	141.1	2.6	19.5	18.5	51.0	1,007	956
2	72.1	1.3	47.5	47.5	66.0	1,938	1,938
3	73.7	2.9	22.0	22.0	67.0	405	405
4	33.3	1.0	22.0	21.0	236.0	151	144
5	20.8	2.4	46.0	16.0	434.0	45	16
6	30.6	0.6	0.0	0.0	91.0	0	0
7	41.4	0.8	0.0	0.0	102.0	0	0
8	16.9	0.1	0.0	0.0	14.0	0	0
9	4.0	0.4	0.0	0.0	41.0	0	0
10	122.6	12.0	122.0	15.0	73.0	829	102
11	38.0	0.5	10.0	8.0	682.0	54	43
12	13.4	0.3	47.0	4.0	674.0	151	13
13	70.4	1.9	35.0	20.0	309.0	204	116
14	94.5	1.8	554.0	548.0	59.0	23,929	23,669
15	168.5	3.1	26.5	22.5	534.0	131	111
16	72.0	1.0	15.5	13.5	358.0	151	132
17	86.0	7.0	38.5	30.5	97.0	237	188
18	135.0	3.1	56.0	51.0	40.0	2,959	2,695
19	10.0	0.8	53.5	26.5	51.0	637	315
20	3.1	0.2	19.0	16.0	393.0	36	31
21	52.6	1.3	22.0	17.0	68.0	635	491
22	3.7	0.3	19.0	16.0	297.0	38	32
23	12.3	0.5	17.0	15.0	529.0	38	34
24	20.5	2.0	36.5	22.5	292.0	62	38
Total	1336.5	47.9	1,228.5	950.5	5,558.0	33,637	31,469
Average	55.7	2.0	51.2	39.6	231.6	1,402	1,311

seasonality of scats. They were *Lycopodium*, *Picea*, *Betula*, *Alnus*, Asteraceae, Ericaceae, *Salix*, Caryophyllaceae, *Tsuga canadensis* type, *Pinus*, Cyperaceae and *Epilobium* in decreasing order. *Tsuga canadensis* type was found in only one of the scats (No. 1). With its pollen identifiable down to specific level due to its characteristic shape, the natural habitat of this species is confined to eastern North America. It is rather strange to find such pollen grains from the opposite corner of the continent. It is impossible that they flew all the way from the east in a climatic zone of prevailing Westerlies. Perhaps they came from ornamental plantations in Dawson or other local communities. Found only in one scat but with an impressive amount of 387000 pollen grains (41%) out of a total of 956000 they were hard to ignore and thus counted here as spring pollen. Generally speaking, arboreal pollen was significantly more abundant than herbaceous ones except for *Lycopodium*, which appeared in great number though only in one scat.

Relative occurrence of pollen species by scat is given in Fig. 4. With complete absence of pollen, the easiest to date were winter scats (Nos. 6, 7, 8 and 9). Referring to the pollen seasonality in Fig. 2, the second easiest to date is fall scats which should contain no other pollen than of Asteraceae. However, no such scat was found, indicating that the remaining 20 were either of spring or summer. They were distinguished with the key summer pollen of *Epilobium*, Caryophyllaceae and Cyperaceae, and *Lycopodium* spores. Their occurrence was taken as definite proof of summer scat since the summer pollen and spores should never appear in spring scat though it could be the other way around. The summer pollen and spores were found in six scats, namely Nos. 4, 11, 13,

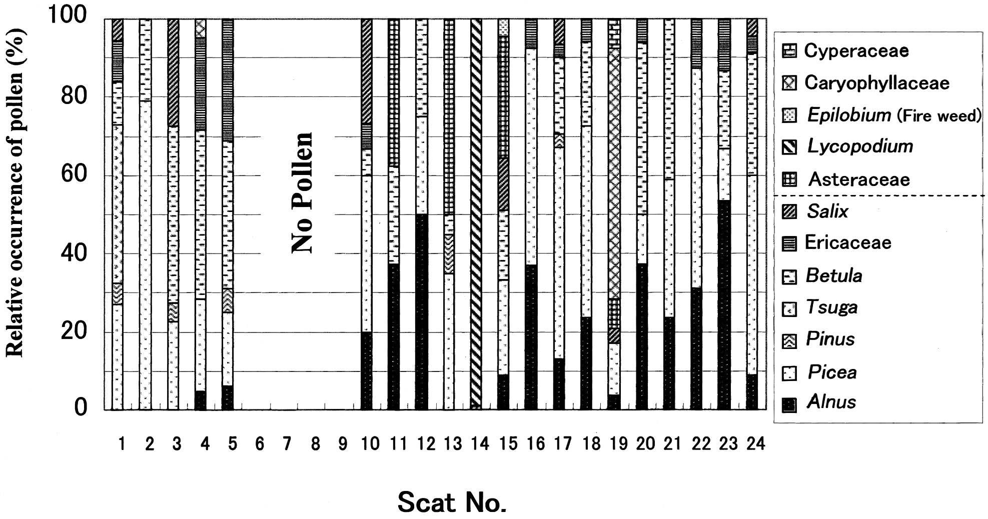


Fig. 4. Composition of pollen species in scats (sensitive pollen only).

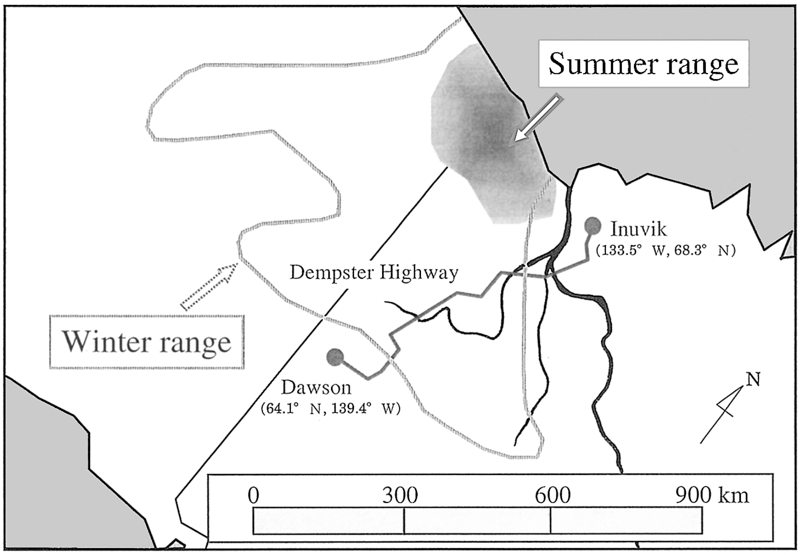
14, 15 and 19. The remaining 14 scats were, consequently judged to be of spring.

This scat seasonality is consistent with statistics of pollen count and species composition. Spring scats contained significantly more pollen, mainly of arboreal species, than summer ones, which is consistent with the spring pollination of arboreal species and their anemophilous nature. Overall mean pollen content in spring scats was 505000, while it was only 146000 in summer scats except for one exceptional case of scat No.14 that produced as many as 23433000 *Lycopodium* spores. As for the species composition, while spring scats contained 92.9% spring pollen grains and 7.1% spring-summer pollen grains on average, the summer scats contained 98.5% summer pollen grains, 1.2% spring and 0.3% spring-summer pollen grains.

There were six summer, 14 spring and four winter scats in deteriorating order of freshness, and none from last fall. With this seasonal distribution of scats, several factors are involved. They are the length of the seasons which we have allotted somewhat arbitrarily, scat disintegration and decay over time, migration patterns of prey animals and wandering patterns of the wolves themselves. The first two factors account for relatively few scats from last winter and fall. Considering that seven months were allotted for winter and only a month for fall, the tally of four scats from last winter and none from fall are virtually the same in terms of frequency.

The remaining two factors are more essential since the seasonal migration of the caribou affects the wolf's wandering pattern, and thus, the spatial distribution pattern of scats. The Porcupine caribou herd wintering in our study area and providing the single source of diet for wolves during the winter move north to their breeding ground near the Arctic coast in spring as shown in Fig. 5. This should attract some wolves when the bond of a pack is rather weak in summer due to abundance of smaller mammals which can be hunted alone. The wandering pattern of the wolf is also influenced by snow cover. Snow provides wolves more freedom to wander across the terrain, while its disappearance and the appearance of bush in spring tends to confine wolves more or less to roadsides and along streams which happened to be our search routes. However, heavier traffic of tourist vehicles and transportation trucks in July may keep some wolves away from the Dempster Highway.

With the seasonality of the scats thus determined, the occurrence and relative frequency of prey items are tallied by season in Table 2 with the former being the number of scats, and the latter the ratio to total number of scats in a given season. As has been explained earlier, "small mammals" includes all rodents smaller than the



(after Urquhart, 1983)

Fig. 5. Summer and winter ranges of the Porcupine caribou herd.

Table 2. Seasonal number and relative frequency* of scats containing prey item.

			Summer	Spring	Winter	Fall	Total
Undigested residuum	Animals	Caribou	4 (67)	10 (71)	4 (100)	0 (0)	18 (75)
		Beaver	1 (17)	0 (0)	0 (0)	0 (0)	1 (4)
		Small mammals	1 (17)	9 (64)	0 (0)	0 (0)	10 (42)
		Unknown	2 (33)	3 (21)	0 (0)	0 (0)	5 (21)
	Plants		1 (17)	3 (21)	0 (0)	0 (0)	4 (17)
	Total appearance		9	25	4	0	38
Total number of scats			6	14	4	0	24

* Relative frequency (in parentheses): percentage of scats containing each prey items to total number of scats.

porcupine. "Unknowns" found in five scats refer to unidentifiable animals whose hair did not match any of our collection of sample hairs. In two cases, long hairs most likely of wolves themselves were found, but judging from the small amount of hair, they do not seem to be cases of cannibalism. In another case, a small amount of very fine hair was accompanied by a relatively large amount of Gramineae fibers, making the scat look like of a sick wolf. In one of the remaining two cases, unidentifiable hairs were accompanied by a cat-like claw most likely of porcupine or weasel, but it was difficult to judge which. So was the last case in which a relatively large chunk of bone seemingly of a moose or a wolf accompanied unidentifiable hairs.

In the above method of tallying, a single scat was counted multiply when it contained remains of two or more different prey items simultaneously. As a matter of fact, a total of 24 scats was counted a total of 38 times, *i.e.* 14 spring scats counted 25 times and six summer ones nine times. Accordingly, the relative frequency adds up to more than 100% seasonally. As has been mentioned earlier, there was no fall scat. Winter scats are characterized by absolute dominance of caribou, while incorporation of other mammals to more than 65% of scats and admixture of some plant remains characterize spring and summer scats with increasing diet variety into summer.

These results are consistent with composition of prey animals and seasonal change in their behavior, which in turn is controlled by the seasonal climatic cycle of harsh winter of severe coldness and extensive snow cover alternating with productive and luxuriant summer green. The caribou constitutes the staple diet for wolves throughout the year since it composes the primary portion of the faunal biomass in northwestern Arctic Canada. This is especially true in winter when small mammals are either hibernating or hidden under the ice and snow cover. Their emergence in spring adds them to the wolf's diet in compensation for the decreasing opportunity of hunting the caribou, the majority of which migrate north for breeding while the wolves themselves have to be more sedentary for their own reproduction and cub rearing. Yet, the remaining members of the Porcupine and Woodland caribou herds (Urquhart, 1983) seem to contribute to the wolf's diet considerably even during the summer as seen in our result.

Conclusions

The dietary pattern of wolves as revealed by simultaneous analyses of contaminating pollen grains and undigested residua in wolf scats in the present work corresponded superbly not only with seasonal activities and migration patterns of prey species, but also with the general hunting pattern of wolves in the boreal and arctic regions, *i.e.* team hunting exclusively of large hoofed animals during winter and introduction of individual hunting of smaller mammals in summer, as reported by many wolf specialists (*e.g.* Mech, 1970; Carbyn *et al.*, 1993; Kohira, 1995) as well as by non-professional observers (*e.g.* Thomas, 1995; Mowat, 2001). This indicates that the pollen analysis in dietary studies with scat is not only valid for identifying the seasonality of old scats but also effective for saving a great deal of time and effort to be spent looking for scats the whole year around.

However, no overwintering scat from the last fall was found in the present work, indicating that even in the Arctic, where decomposition is rather slow due to the cold climate, a single scat collection trip may not be enough to cover the annual dietary cycle of an object animal. Yet, there is no doubt that the introduction of pollen analysis would lessen the demand for frequent scat collection and thus make the dietary study of animals more effective.

Acknowledgments

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