SCAVENGING AND ITS POSSIBLE EFFECTS UPON PREDATION - A SELECTIVE REVIEW OF LITERATURE

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Abstract: A literature search and personal communication with many field workers across North America suggests that predation may be affected to varying degrees by scavenging. Scavenging as a phenomenon practiced by predators and non predators is discussed. A clarification of terminology associated with predation and scavenging is attempted and examples from the literature are summarized. Factors affecting recognition and importance of scavenging are discussed.

ALCES 22 (1986)

Keywords: scavenging, predation, natural mortality, consumption, utilization, surplus killing, caching, competition.

A literature search and personal communication with many field workers across North America indicated that with the exception of studies conducted in Africa and Alaska, little is known regarding the importance of scavenging as it relates to predator-prey relationships. Reference to scavenging in the literature is often oblique in nature and qualitative rather than quantitative, yielding few reliable data regarding competition for prey carcasses.



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DEFINITION OF TERMS

Probably because little work has been done relating to secondary uses of prey carcasses, there appears to be a tendency in the literature to generalize regarding carcass disposition. Terminology relating to predation and scavenging is defined in Table 1 and subsequently discussed. When no definition could be found in the literature, one was inferred.

Table 1. Definition of terms.

Term	Definition	Reference
D. Latter		
Predation	The act of one animal (predator)	
	killing another (prey) by inflict-	
	ing wounds such that the prey dies	(inferred)
	immediately or at a later date	
	of wounds inflicted at the time of	
	attack.	
Non-predatory	The death of an animal resulting	
natural	from any natural cause other than	(inferred)
mortality	predation.	
Hunting	Number of prey animals killed by	
success rate	a predator or group of predators	
	expressed as a function of the	Mech, 1966

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Table 1. Definition of terms. (cont'd)

Term	Definition	Reference
	number of prey animals tested	
	by the predator or predators.	
Predation	The rate at which prey are killed	
rate	by a predator or group of predators.	
(Killing rate)	May be expressed as prey animals	inferred, and
	killed (preferably equating to a	Ballard pers.
	common biomass to avoid ambiguity),	comm.
	per predator or group of predators	
	as a function of time.	
Consumption	Rate at which prey animals killed	
rate	by predators are consumed by the	inferred
	predators. May be expressed as prey	
	weight (kg) consumed per predator	
	per day.	
Initial	The amount of a prey carcass utilized	
utilization	as food by the predator or predators	inferred
	which killed it, from the time of death	
	until the predator or predators cease	
	feeding on the carcass for the first	
	time.	

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Table 1. Definition of terms. (cont'd)

Term	Definition	Reference
Surplus	The killing by a predator of prey,	
killing	without the killing individual or its	Kruuk, 1972
	offspring or members of the same	a & b
	social unit eating anything from the	
	kill, although there is free access to)
	the carcass, and usually the particula	ır
	prey species would be eaten by that	
	predator.	
Killing with	Very similar to surplus killing,	
partial	except, the predator proceeds to	Mueller &
consumption	eat a part of the prey item.	Hastings, 197
Guarding	When a predator or group of	
	predators kills and feeds upon a	
	prey item but remains at the	
	carcass to prevent consumption by	(inferred)
	other animals while part of the	
	edible portion of the carcass	
	remains intact.	
Scavenging	Feeding on the carcass of any dead	
	animal by any live animal which	(inferred)



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 $\label{eq:total_continuity} {\mbox{Table 1. Definition of terms. (cont'd)}}$

Term	Definition	Reference
	did not participate in the killing of that animal.	
Caching	When a predator kills and stores a prey item with the possibility of retrieving it at a later date. May consist of burying, covering or scraping.	Mueller & Hastings, 1977
Inter- scavenger competition	Utilization of a prey carcass by any animals other than the predator or predators may constitute competition and may occur directly as a result of confrontation (displacement) or indirectly as a result of stealing. Competition may be inter or intraspecific.	(inferred)



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SELECTED LITERATURE REVIEW OF DEFINITIONS

Predation

Predation upon ungulates in North America is well documented in the literature, with timber wolf (<u>Canis lupus</u>), brown or grizzly bear (<u>Ursus arctos</u>), and black bear (<u>Ursus americanus</u>) the three major predator species of importance to moose (<u>Alces alces</u>) managers. (Mech 1966, Murie 1968, Ballard et al 1981, Wilton, 1983).

Non-predatory Natural Mortality

Natural mortality of ungulates aside from predation may be caused by many factors, but very often results from starvation or deteriorating habitat in conjuction with severe winter conditions and deep snow (Peterson 1977, Pimlott et al 1969).

Hunting Success Rate

On Isle Royale it was found that wolves were successful in 6 out of 77 (7.8%) attempts on moose (Mech 1966) and from 1972 to 1974 were successful in 1 out of 38 (2.6%) attempts on moose (Peterson 1977). Shelton (1966) observed during 1962 and 1963 on Isle Royale the testing of 9 moose of which 1 (11.1%) was killed. Kolenosky (1972) estimated success rates for wolves in Algonquin Park on white-tailed deer (Odocoileus virginianus) of 25% and 63% in 1968 and 1969 respectively.

Predation Rate

The following table (Table 2) summarizes predation rate as established by various studies.

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				ŝ	30 01			Individual	
Prey species	Predator species	Location	Year	Duration (days)	no. or prey killed	Days/ kill	Pack size	predator days/kill	Reference
400se	Wolf	Isle Royale	1959 1960 1961	28 45 37	9 15 12	3.1	15 15 14.9	46.5 45.0 46.2	Mech, 1966
foose/Caribou	Wolf	Alaska	1975-1976	1	70	10.5	8.6	102.9	Stephenson, 1978
hite-tailed Jeer	Wolf	Algonquin Park	1969	37	29	1.3	80	10.4	Kolenosky, 1972
Moose/Caribou	Wolf	Alaska	1958	35	21	3.9	6	35.0	Burkholder, 1959
loose	₩olf	Alaska	1977–1979	179 80 85 51 85	12 13 10 16	14.9 6.2 8.5 3.2	2.0 7.0 8.2 16.3	29.8 43.4 69.7 52.2 79.5	Peterson et al, 1984
)eer/Moose	Wolf	Minnesota	1972-1976	121	14.5	8.3	က	25.0	Fritts, 1979
loose	Wolf	Isle Royale	1962 1963	50 52	15 14	3.3	14 14	46.2 51.8	Shelton, 1966
.lk/Deer/Moose	Wolf	Manitoba	1978 1979	94 153	14 23	6.7	3.2	20.1	Carbyn, 1983
.lk/Moose/Deer .heep/Horse	Wolf	Alberta	1984-1985	109	17	5.2	5.5	28.5	Schmidt & Gunson, 1985
1k	Grizzly	Yellowstone	1969-1970	19	200	0.3	*08	10.0	Cole, 1972
oose/Caribou	Brown Bear	Alaska	1978	437	78	5.6	23**	23.3	Ballard et al, 1981
oose/Caribou	Wolf	Alaska	1975-1980	1735	352	6.4	variable (17 packs)	!	Ballard and Spraker, 1981

Estimated number of Grizzlie

Consumption Rate

Mech (1966) defined one "prey unit" as 100 pounds (45.45 kg) and assigned the following prey units to various ages and species of big game: moose calf, 3; cow, 8; bull, 10; deer, 1; elk (Cervus elaphus), 6; caribou (Rangifer tarandus), 3. Even though there are substantial differences in moose weights across North America (Ballard pers. comm.), I have adapted these units for the sake of consistency. The following table (Table 3) summarizes consumption rate of prey by predators (only).

Utilization

While some authors found that (winter) carcass utilization by the predator(s) was generally complete (Mech 1966, Kuyt 1972), others felt that initial carcass utilization might not be complete, but that the predators might return (Pimlott et al 1969, Kolenosky 1972, Burkholder 1959) at some later date to feed on the carcass again. Kolenosky (1972) further stated that scavenging may take place in the interim.

Smith (1980) witnessed a wolf killing a caribou on the ice in a small bay on Baffin Island and during 42 hours of observation the entire carcass was utilized by the wolf, two Glaucous Gulls (Larus hyperboreus) and one raven (Corvus corax). He estimates that the gulls and the raven utilized about 10 (23%) kg while the wolf utilized the remaining approximately 33 (77%) kg.

able 3. Summary of consumption rate.

Species Predator Location Hoose Wolf Isle Royale II White-tailed Wolf Alaska II White-tailed Wolf Minnesota II	Year 1959 1960 1961	Ouration (days) 28 45 37	kg prey consumed 2,525 3,182 3 518	pack/ day	Pack	Kg prey/	Ko prev/ko		
Wolf Isle Royale -tailed Wolf Algonquin Park Wolf Alaska -tailed Wolf Minnesota	1959 1960 1961 1961	28 45 37	2,525 3,182		size	predator/day	predator/day	Reference	
-tailed Wolf Algonquin Park Wolf Alaska -tailed Wolf Minnesota	1960 1961 1969	37	3,182	90.2	15	6.0	0.08	Mech, 1966	
-tailed Wolf Algonquin Park Wolf Alaska -tailed Wolf Minnesota	1969		2	70.7 95.1	16 15	4.4	90.0		
Wolf Alaska Wolf Minnesota	9	63	1,851	29.4	89	2.94	0.10	Kolenosky, 1972	
Wolf Minnesota	1978-79	i	ł	ł	1	1	0.12	Peterson et al, 1984	1984
	1972-77	ŀ	ł	1	}	2.9	1	Fritts, 1979	
Moose Wolf Isle Royale	1	;	;	1	1	2.34.5	3 3	Allen, 1979	163
Elk/Moose Wolf Manitoba	ł	i	;	34	ιn	;	0.21	Carbyn, 1983	



Parker (pers. comm.) believes that when prey are plentiful, wolves and coyotes (<u>Canis latrans</u>) will utilize 1/4 to 1/3 of the carcass in the first 12-24 hours and then desert the carcass which will be rapidly scavenged by ravens, marten (<u>Martes americana</u>) and gray jays (Perisoreus canadensis).

Jolicoeur (pers. comm.) observed ravens and eagles scavenging on white-tailed deer carcasses between the killing time and the second visit (of the wolves), but felt that it was "impossible to calculate how many pounds of meat they (the ravens and eagles) removed from the carcass and so considered that all the meat had been eaten by wolves".

Surplus Killing

Evidence of surplus killing of barren-ground caribou calves was documented in 1970 on the Kaminuriak calving grounds, Northwest Territories (Miller and Broughton 1970), where 18 of 51 dead calves were judged to have been killed by wolves and 6 of those were left with "no part of the carcass being eaten". Predation over a 2 week period in 1973 of 40 reindeer (Rangifer tarandus), 8 of them in one night, is attributed to two wolves in Sweden (Bjarvall 1976). Of 34 wolf killed barren-ground caribou calves found in a 3 km area in the Northwest Territories, 1982, wolves had not fed on 17 of the carcasses and had only partially eaten the other 17 (Miller et al 1985). On March 31, 1979, seven caribou carcasses were observed within a 1 km radius along the Copper River near its confluence with the Indian River, Alaska. Tracks and puncture marks suggested the caribou had been killed by a pack of two to four gray wolves (Eide and Ballard 1982). While it is suspected that surplus killing by bear may occur, no reference to this was found in the literature.

Killing With Partial Consumption

In the early 1970s, Isle Royale wolves exhibited an immediate response to high moose vulnerability (deep snow) by increasing their kill rate (Peterson 1977). As kill rate went up, wolf utilization of carcasses declined, leaving a bonanza of food for foxes (<u>Vulpes fulva</u>) and ravens (Peterson and Allen 1974). Pimlott et al (1969) found that in Algonquin Park, Ontario, utilization of white-tailed deer carcasses was less complete in winters of extreme snow depth when killing was easier. Carbyn (1983) found that in Riding Mountain National Park, Manitoba, wolves left approximately 40-50% of available elk and moose carcasses respectively, unconsumed.

Guarding

Murie (1968) and Cole (1968) have described how grizzlies in Alaska and Yellowstone, respectively, will rest on or near a carcass after feeding on it. Burkholder (1959) describes a pack of 10 wolves guarding a recent caribou kill, and Allen (1979) describes the feeding sequence on a moose kill of a pack of 15 to 18 wolves on Isle Royale, which may last up to 3 days, and during which the pack may move off a short distance to rest and allow subordinates and scavengers to feed. A gray wolf was observed chasing a raven from the carcass of a caribou killed by the wolf on Baffin Island, Northwest Territories (Smith 1980). Peterson (1977) observed a wolf kill a raven near a carcass.

Scavenging

There is evidence in the literature that most North American carnivores will scavenge if the opportunity presents itself. (Kuyt 1972, Kelsall 1968, Magoun 1976, Kolenosky 1972, Shelton 1966, Cole 1972, Stirling and Archibald 1977, Andriashek et al 1985).



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Caching

Smith (1980) observed a gray wolf carrying the foreleg and shoulder of a caribou that it killed and surmised that this was the only portion of the caribou to be cached; the remainder being fed on at the kill site.

Magoun (1976) observed only 2 species caching meat from carcasses; the wolf and the raven. During 839 observation periods in which ravens were feeding, these birds made 382 caches. Wolves made 28 caches in 259 observation periods in which wolf feeding occurred. Ravens would often cache meat under pieces of flotsam or cover the caches with sand, small stones, or debris. Wolves nearly always cached meat in loose soil after digging a hole with the forefeet. In addition, Magoun observed grizzlies covering carcasses with vegetation and dirt scraped from the area around a carcass. Scraping occurred at four of eight carcasses that bears were known to have visited; and is also felt to provide a physical barrier to scavengers such as ravens and wolves which must remove the scrapings to feed.

Stirling (1968) observed ravens picking up whole discarded fish from a commercial fishing operation in the Athabaska area of Alberta and flying with them to nearby forest where they were cached. Cole (1972) found that in Yellowstone, individual adult grizzly bears tended to cover (with soil and vegetation), defend, and feed on an elk carcass over periods as long as a week or more. Murie (1968) observed that grizzlies at Mount McKinley (Alaska) after eating to their capacity, usually covered the carcass with sod and debris; first pawing the debris loose and then raking it back toward the carcass.

Inter-Scavenger Competition

Ballard (1982) observed interactions between gray wolves and brown bears at carcasses, when often the one species would try (occasionally successfully) to displace the other, sometimes resulting in the death of one of the antagonists.

Dean (pers. comm.) states "I firmly agree that kill rates by primary predators must be dramatically affected by what might be called "take-over" rates and pure scavenging rates. I have frequently seen brown bears either finish killing an ungulate that wolves had attacked initially (perhaps the wolves were simply resting near a wounded animal awaiting its death) or displace wolves from a carcass. In my experience, though wolves can get some meat from carcasses being used/guarded by brown bears, I do not recall seeing wolves displace single adult bears. Wolves can displace a female brown bear with cubs-of-the-year".

Murie (1968) states that "carrion in any form, is a special "delicacy" for a grizzly although not a major food source. A large carcass may attract several bears over a short period of time bringing them into closer contact than is usual. At most times, little overt strife results; larger bears have priority and others partake as temporary absence of a more dominant bear permits".

Cole (1972), who conducted grizzly predation studies on elk in Yellowstone found that there was competition among scavengers for available carcasses. These would usually be reduced to skeleton and hide within 48 hours, especially if undefended by bears. Often larger grizzlies or sows with cubs would force the (smaller) predator grizzly away from its kill, perhaps prompting it to kill again.



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Avian scavengers will usually be displaced from carcasses by mammalian scavengers, although Bowen (1980) described how golden eagles may attempt to guard carcasses from coyotes. Magoun (1976) ranked 7 scavenger species from most dominant to most subordinate as follows; grizzly bear, wolf, fox, eagle, raven, gull and jaeger.

FACTORS AFFECTING RECOGNITION AND IMPORTANCE OF SCAVENGING

1 -- Distinguishing Predation from Natural Mortality

Stephenson and Johnson (1973) developed the following criteria to distinguish between fresh kills and scavenged carcasses resulting from natural mortality.

"Wolf-kill sites are quite characteristic. They are usually in an open area, such as a frozen lake or stream or a small opening in the woods. If the kill is only a day or so old, circumstances of the kill can generally be constructed from the tracks in the snow. There are usually considerable signs of struggle, with bits of hair, blood and often rumen contents strewn over a wide area. Bounding wolf tracks, indicating extreme excitement on the part of the wolves, are usually present. There will typically be several wolf trails radiating from the kill, often ending on a prominence where the wolves rest after feeding. After feeding on a fresh carcass, wolves "preen" themselves by wallowing in the snow near the kill site. After a few days scavenging birds, especially ravens and eagles, smaller carnivores (fox, coyotes and wolverines) and repeated visits of the wolf pack usually obliterate the tracks at a kill site.

Examination of very recent kills reveals that wolves kill large animals, especially moose, by attacking their rear quarters and flanks as the animals are standing or running (see also Mech, 1970 and Burkholder, 1959). The hair around the calcanei typically is saturated with blood on a large animal killed in this manner. The lower hind legs are usually the last portion of a carcass to be eaten or removed by wolves so skeletal remains which have a blood soaked calcaneus are good evidence of a wolf kill. Such a blood soaked leg is recognizable for several weeks after death of the animal. Skeletal remains with reasonable fat reserves in the long bone marrow indicate that the animal did not die of malnutrition.

The carcass of a wolf-killed animal is usually on its side with all four legs extended. On the other hand, animals scavenged by wolves also show typical characteristics. Animals dying from malnutrition frequently seek solitude in dense brush just prior to death. They often freeze solid before scavengers, including wolves, find them. When such a carcass is scavenged, often only the uppermost portion is eaten. The calcanei do not show blood saturation. There are fewer indications of wolf excitement and preening signs are scarce. There is seldom any blood around the carcass. Winter-killed moose generally reflect total utilization of all fat reserves. An animal dving of malnutrition/starvation reclines in the position typical of large herbivores, its legs doubled up under its body and its body in an upright position. If it freezes before it is scavenged, the folded-up position is recognizable until the skeleton is disarticulated. Careful examination of skeletal remains of animals killed and not salvaged by humans but



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scavenged by wolves usually will reveal ax or saw marks, bullet wounds or other marks not made by wolves. Bone marrows of such kills usually show good fat reserves."

Ballard et al. (1979) describe characteristics used to identify predation on moose calves by brown bears, black bears and wolves, while Haynes (1982) describes in detail methods by which carcass utilization and skeletal dismemberment may be used to determine if the prey died as a result of predation or from natural mortality.

2 -- Winter Versus Summer Scavenging

Kuyt (1972) found that whereas caribou killed in winter are completely utilized by wolves, in summer, parts of carcasses are often left to scavengers. Peterson et al (1984) reported that the carcasses of moose killed during the winter were incompletely utilized, but that summer observations indicated wolves frequented old winter kills and probably scavenged extensively. Haber (1977) found the extensive winter use of carrion to be in contrast to what appeared to be almost negligible summer use.

3 -- Prey Susceptibility as a Function of the Time and/or Severity of Winter

Degree of deer carcass utilization by wolves was found to decrease during the later more severe stages of winter in Algonquin Park as predation became easier (Pimlott et al 1969). The predation rate of wolves on moose on Isle Royale was found to increase directly with corresponding decrease in carcass utilization as-snow depths increased and moose were forced into

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shoreline conifers, which also serve as travel routes for wolves (Peterson and Allen 1974). Carbyn (1983) observed killing with partial consumption by wolves in Manitoba in late winter. Morrison (pers. comm.) observed frequent wolf killed white-tailed deer carcasses in central Ontario during the severe winters of 1970-71 and 1971-72, when crusting conditions supported wolves but not deer. During that period only partial consumption by wolves was noted with abundant material left for scavengers.

4 -- Status of the Prey Population

Morrison (pers. comm.) feels that scavenging probably does cause heavier predation in certain cases. In healthy prey populations, the added resulting predation probably will not cause problems with the overall welfare of the prey population. When prey populations are depressed, however, the increased predation on the population may act to prevent an upswing in numbers and the additive effect of scavenging may compound the depression.

Peterson (1977) found that as moose range on Isle Royale deteriorated, moose became more vulnerable to predation and killing with partial consumption occurred giving rise to lower carcass utilization by wolves. This in turn not only gave rise to an increased food supply for scavengers, but eventually led to the formation of 2 new wolf packs subsequent to the raising of large pup litters.

5 -- Prev Size as a Function of Pack Size

Shelton (1966) felt that small packs of 2-3 wolves were unlikely to successfully kill a moose whereas large packs of



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15-16 wolves could do so with ease. Schmidt and Gunson (1985) speculate that one wolf pack altered prey selection from moose to deer and elk as a result of the alpha male being shot; this not only reduced the pack size but may have removed the "moose specialist". Carbyn (1983) states that in Riding Mountain National Park, Manitoba, in a mild winter with low snowfall, a pack of 3 wolves killed elk and deer but not moose. Wolfe and Allen (1973) found that in the period 1967 to 1970 the common size for major wolf packs on Isle Royale was six or seven, and that packs of this size did not evidence any decrease in predation efficiency on moose relative to that observed for a large pack of 16 prior to 1967.

DISCUSSION

Many scavengers are predators, but all predators are scavengers. This makes it important for workers to be able to differentiate between carcasses resulting from predation and those resulting from other mortality, if the relationship between these two activities is to be properly understood.

It is scarcely surprising that wolves depending on moose as their chief prey species must sometimes scavenge for nourishment considering their low hunting success rates. It appears that 5-6 may be the optimal pack size for wolves to successfully predate moose; larger packs do not appear to experience greater killing efficiency, while packs smaller than this may only succeed in predating smaller species such as deer or caribou.

Predation rate appears to be quite variable depending upon such factors as pack size, condition of prey species and winter conditions.

Some workers, assuming that carcass utilization by the primary predator is complete, have calculated consumption rate based solely upon the number of prey units represented by the prey carcasses found. This method has two possible shortcomings; first, care must be exercised in deciding whether or not the carcass is truly a predator kill, and second, care must be exercised in deciding whether or not the primary predator(s) were the only animal(s) feeding on the carcass. Failure to recognize carcasses resulting from other mortality or failure to accurately assess the percentage of the carcass removed by scavengers can result in inflated consumption rates. There is evidence in the literature indicating that in the majority of cases scavengers have shared in the utilization of predator killed carcasses.

While surplus killing appears to only occur occasionally as a result of an unusual set of circumstances, killing with partial consumption occurs fairly frequently, often as a result of high prey vulnerability. While the rare instance of surplus killing would probably not affect scavenger abundance, it is possible that killing with partial consumption may. Newton et al (1982), demonstrated that annual variation in the mean number of eggs laid per raven pair was correlated with the amounts of sheep carrion available in winter/spring, and that ravens depended on carrion and bred nearest the time of peak supply. This implies that in situations such as on Isle Royale described by Peterson (1977), where deteriorating range led to increased moose vulnerability, raven populations may respond



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(as did wolves) by increasing their numbers. This could in turn give rise to greater interspecific competition for carrion after stabilization of the prey population. Magoun (1976) feels that numbers of ravens in an area are directly related to the predator population that provides the carrion.

While predators may often guard carcasses against other predator/scavenger species, often avian scavengers are allowed to feed at the carcass while the predators rest. There is a tendency for workers to discount avian predators because of their size, as being incapable of removing much of the carcass. Magoun (1976) noted strong caching behaviour among ravens which visited carcasses she was studying. This implies that ravens may remove more from a carcass than that needed to meet their immediate food demands.

Some workers (Cole 1972) feel that inter and intraspecific displacement of the primary predator from carcasses by a more dominant predator/scavenger may lead to increased predation by the displaced animal -- although this appears to remain as yet unproven. Ballard (1982) states that "black and brown bears have only recently been identified as significant predators of cervids. The fact that both predator species have potential to not only prey upon ungulate species, but also to scavenge and interact with one another, could greatly complicate our attempts to understand predator-prey relationships".

Competition between predators and scavengers would probably be greatest during the late fall/early winter period for the following two reasons. Firstly, prey species have not yet been subjected to the rigours of winter, so there will not be a plentiful supply of

naturally occurring carcasses for scavenging. Secondly, snow depths have not yet become restrictive to prey movement, while at the same time waterways have not frozen to provide travel routes for predators.

Where a prey population may be decreasing because of deteriorating range, predator numbers may actually increase because of increased food supply resulting from increased prey vulnerability (Peterson 1977). This in turn may give rise to increased numbers of ravens (Newton et al 1982), also because of food availability. While predator numbers may not decrease proportionately as do prey numbers (Gasaway et al, 1983), if the prey population is virtually eliminated, then predator numbers may also decrease (Strickland and Tozer pers. comm., O.M.N.R. files). Predator reduction may not be reflected in reduced numbers of avian scavengers though since the latter, being so highly mobile, can obtain their food from more distant food sources (Strickland, pers. comm.). Ultimately then, even though prey and predator populations have undergone downward stabilizing trends, highly mobile avian scavenger populations may remain at high levels, thereby providing relatively greater interspecific competition at predator kills and other natural mortality carcasses.

Ravens are communal feeders. Connor (1985) has identified 18 raven call types, some of which are associated with feeding behaviour. Being highly mobile and highly vocal, ravens compete with wolves and other predator/scavengers for carcasses. Conversely, however, ravens may alert other predator/scavengers to the presence of food in the vicinity by their flying activities and vocalizations. Magoun (1976) found that ravens were the first



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species to arrive at 73% of carcasses studied. Houston (1979) describes how predator/scavenger species in Serengeti (Africa) often follow avian scavengers in search of food sources. Harrington (1978) observed ravens reacting to wolf howling in search of food.

Thus, it seems while there is reason to believe that competition for carcasses among and within species does occur and may increase predation, cooperation of sorts also exists which could conceivably decrease predation by making predators aware of carcasses available for scavenging.

It is advisable for workers to realize that in nature no activity such as predation takes place without accompanying activities such as scavenging as a complement.

ACKNOWLEDGEMENTS

Sincerest thanks are extended to the many individuals who corresponded, relating instances of predation or scavenging.

Deepest appreciation to the staff members of the Ontario Ministry of Natural Resources libraries at Queen's Park (Toronto) and Maple, without whose help the literature search would not have been possible; and to M.D. Payne for the final typing of the manuscript.

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