

Wolf Predation and Ungulate Populations

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SYNOPSIS. Studies of the interaction of wolves and their prey during the past twenty years have demonstrated that ungulates are the primary prey of wolves both in winter and summer and that predation in summer tends to be concentrated on the young of the year while in winter it is concentrated on animals in older-age classes. There appears to be intrinsic control of wolf numbers and there is evidence which suggests that a wolf per 10 square miles may approach the maximum density that is attainable in most ranges. The adaptations between ungulates and their predators may have evolved in relatively stable forest environments which could not support high-density prey populations. This could explain why wolves do not appear to be capable of controlling moose and deer populations in environments that have been drastically altered by man.

Studies of wolf (*Canis lupus*) ecology have become fairly common during the past two decades. In many instances the programs were stimulated by "... apprehension concerning the welfare of the big game herds," as Adolph Murie phrased it in the foreword to his classical study, "The Wolves of Mt. McKinley" (1944).

Murie's was the first of the studies that dealt intensively with the interaction of wolves and their prey. Since he completed his field work, Cowan (1947), Thompson (1952), Stenlund (1955), Mech (1966), and Shelton (1966) have also reported on the wolves of North America. Pulliainen (1965) has presented an account of the species in Finland. In addition to these published accounts other work has been in progress, some of which will be reported for the first time at this meeting.

Although virtually all the studies which have been mentioned have dealt, at least in part, with the effects of predation by wolves on the population levels of the animals on which they prey, quantitative data in many cases have been sparse and their lack has precluded a very detailed consideration of the subject. Murie (1944) obtained considerable data on predation on Dall sheep (*Ovis dalli*) and on caribou (*Rangifer rangifer*). Mech (1966) and Shelton (1966) published data on predation on moose (*Alces alces*), and studies in Ontario (Pimlott, *et al.*, 1967) presented data on predation on white tailed deer.

In most cases a considerable element of

the problem has been, and continues to be, the difficulty that is encountered in obtaining sufficiently detailed data on the population levels of both the wolf and its principal prey species. The studies on Isle Royale, which are directed by Durward Allen, and which have been conducted by Mech (1966), Shelton (1966), and Jordan (unpublished) have come the closest to laboratory studies of any big-game species which have been undertaken. They, and similar future studies, will undoubtedly provide a much firmer quantitative basis from which the principles of wolf predation will be developed.

Although we have not yet reached the stage where a broad definitive statement can be made on the role of wolf predation in controlling the populations of species on which they prey, the studies that I have mentioned have added a great deal of fresh insight on the question.

My objective in this paper is to review the state of our knowledge on wolf predation, to attempt to clarify some of the areas where thinking on the subject has not been clear and, finally, to present my preliminary thoughts on the interaction of wolves and their prey.

VARIABLES AND COMPONENTS OF PREDATION

The literature on predation and its influence on prey populations is extensive. The great majority of the detailed studies have, however, been conducted on situations

where both predator and prey were insects (Thompson, 1939) or where a vertebrate predator was preying on insect prey (Tinbergen, 1955, 1960; Holling, 1959, 1961; Morris, *et al.*, 1958; Kendeigh, 1947).

Studies of predation that have been reported make it apparent that many variable factors can influence, moderating or intensifying, the effect of predation. Leopold (1933) classified the factors into five groups: (1) the density of the prey population, (2) the density of the predator population, (3) the characteristics of the prey, *e.g.*, reactions to predators, (4) the density and the quality of alternate foods available to the predator, (5) the characteristics of the predator, *e.g.*, food preferences, efficiency of attack, and other characteristics.

Holling (1959, 1961) has developed a comprehensive theory of predation, based on his studies of small-mammal predation on the European pine sawfly; following the scheme proposed by Leopold (1933) he classified the factors into basic and subsidiary variables. The variables that are always present, predator and prey density, he referred to as universal variables. Since they are part of every predator-prey situation he considered that "... the basic components of predation will arise from these universal variables" (Holling, 1961, p. 164). The remaining variable factors (environmental characteristics, prey characteristics, and predator characteristics) are either constant or absent, so he called them subsidiary variables and the components represented by their effects as subsidiary components.

To describe the dual nature of predation he adopted terminology proposed by Solomon (1949) and used the term "functional response" to indicate the numbers of animals consumed per predator and numerical response to indicate the change in the population level of the predators. The basic components of predation that he described are the functional response to prey density, the functional responses to predator density, and the numerical response, which arose from the functional response and from other population processes.

Holling (1961) considers that there are

two types of functional response to prey density. In one type more prey, or hosts, are attacked as host density increases. The relationship is curvilinear and the slope of the curve decreases until the curve becomes level. In the second type, predators attack more prey as prey density increases; however, the rising phase of the curve has an S-shape. Holling documented the form of the curve by his studies, both in the laboratory and in the field, of small mammals preying on the cocoons of the European pine sawfly. However, he also stated (Holling, 1961) that the curve for functional response of vertebrate predators to the density of their prey seemed in general to be of this type. He pointed out that Leopold (1933) predicted this type of response when he suggested that vertebrates attack scarce prey by chance but develop the ability to find a greater proportion when the prey becomes abundant.

The curves of both types ultimately level off because of satiation of the predator or, if for no other reason, simply because of the time expended in finding, attacking, and killing prey. In reviewing the components of the equations which describe the two types of curve Holling (1961, p. 170) stated, "The two types of functional response to prey density therefore can be explained by combinations of the five components: time predator and prey are exposed, searching time, handling time (including identification, capture, and consumption), hunger, and stimulation of predator by each prey discovered. The first three are universally present and hence basic and, by themselves or in conjunction with the effects of hunger, can explain those response curves that rise with a continually decreasing slope to a plateau. If stimulation by prey discovery is added to those four components, an S-shaped response results."

The third type of response curve which Holling (1961) stated might be expected in response to prey density is a domed type which may result from a predator attacking fewer prey, when the prey are very abundant. In some cases at least this may result from the "confusion effect" described by Allee (1951) as a result of studies, by

J. C. Welty, of goldfish feeding on *Daphnia*.

Holling (1961) pointed out that, in the past, studies of predation have concentrated on direct numerical responses. He cited the works of Lack (1934) and Andrewartha and Birch (1954) in which survival, fecundity, and dispersal are related to consumption of food. Holling (1961) pointed out that studies of vertebrates preying on insects (*e.g.*, Kendeigh, 1947; Morris, *et al.*, 1958; Holling, 1959) have demonstrated direct and inverse responses, as well as no response, to increasing density of prey species.

I suggest that this scheme, or structure, of predation that has been proposed by Holling (1959, 1961) is worthy of detailed consideration by students of vertebrate predation. It does a great deal to clarify this area of population dynamics that has long been a rather nebulous one. It could be valuable in guiding our thought as we seek to understand the background principles of predation by wolves on the large ungulates.

WOLF POPULATIONS

Obtaining accurate data on the two basic variables, predator and prey densities, have proven to be the principal stumbling block to understanding the influence that wolves have on prey populations. It is mandatory, if we are to gain an understanding of the processes involved, that we continue our efforts to develop census methods that will provide accurate data at costs that are economically feasible.

The early estimates of numbers of wolves were based to a considerable extent on impressions that the individual investigators obtained as a result of their observations on the occurrence of wolves and as a result of packs reported to them by other individuals. When areas of moderate size were involved the estimates were probably quite close to the actual population. When very large areas were involved too many unknown factors entered the picture and the "estimates" could hardly warrant being called anything but guesses.

Cowan (1947) worked for three years on wolves and ungulates of the Rocky Mountain National Parks of Canada. He had the close cooperation of the wardens and made estimates of the wolf populations of Banff and Jasper Parks. In the latter, the wardens regularly patrolled the principal wolf ranges and provided him with details of their observations. The area of the park is 4200 square miles; the minimum and maximum estimates of the wolf population made by Cowan were 33 and 55 wolves (Table 1). Based on summer range he estimated the population density at between one wolf per 87 and one wolf per 111 square miles. He stated (Cowan, 1947, p. 150), "At the time of maximum winter compression, however, this population is present on an area that averages approximately 10 square miles per wolf."

An estimate of wolf numbers that has been quite widely quoted is the one made by Clarke (1940) for the range of the barren-ground caribou, which he estimated at 600,000 square miles. He considered that

TABLE 1. *Estimated densities of wolf population in North America.*

Location	Author	Area (sq. miles)	Population	Density	
				General range	Winter range
N.W. Territories (Canada)	Clarke (1940)	600,000	36,000	16+	
N.W. Territories	Kelsall (1957)	480,000	8,000	60	
Mt. McKinley (Alaska)	Murie (1944)	2,000	40-60	50±	
Jasper Natl. Park (Canada)	Cowan (1947)	4,200	33-55	87-111	10
Superior Natl. For. (Minnesota)	Stenlund (1955)	4,100	240	16+	
Isle Royale (Michigan)	Mech (1966) Shelton (1966)	220	20-22	10±	
Algonquin Park (Ontario)	Pimlott, <i>et al.</i> (1967)	1,000	90-110	10±	

there probably was a pack (6 animals) for every 100 square miles and on this basis estimated the wolf populations at 36,000 animals. It has been suggested by both Banfield (1954) and Kelsall (1957) that the estimate was too high. Kelsall (1957) suggested, on the basis of observations made in the course of 43,624 miles of transit flying on caribou surveys, that a population of 8,000, or one wolf per 60 square miles of caribou range, would be more realistic (Table 1). Kelsall also pointed out that the kill of wolves (2000 to 3000 annually) made during the height of the control program would not have had any influence on a population of 36,000 but did appear to have considerable influence on the population that was present.

The relationship of the area occupied by a species to its population density can be most accurately appraised where the area occupied is essentially the same at all periods of the year. Three of the more recent studies conducted in white-tailed deer and moose range of eastern North America were in areas where this situation applied. In Minnesota (Stenlund, 1955), Isle Royale (Mech, 1966; Shelton, 1966), and Algonquin Park (Pimlott, *et al.*, 1967), the density of the wolf population was determined, primarily, by the use of aerial surveys during the winter (Table 1). Isle Royale has proven to be a particularly excellent area and the study there has provided accurate data on the density of the wolf population. On the island the population has remained at a level of approximately one wolf per 10 square miles. During this period the wolves were completely protected, a moose population of high density (approximately three per square mile) was present and, as far as could be determined, there was no movement of wolves from the island.

In Algonquin Park, the boundaries of the study area were fairly well delineated but those of the wolf ranges rarely coincided with them. Because of this, it was not possible to state with as high a degree of certainty what the relationship was between the number of wolves and the size of the study area (Pimlott, *et al.*, 1967).

The work, however, was quite intensive, and extended over several years, so that the estimate of the density of the wolf population at between one wolf per 9 and one wolf per 11 square miles was considered to be very close to the actual size of the population. During the greater part of the study the wolves were protected as was the principal prey species, white-tailed deer, and the secondary prey species, moose and beaver.

Another study of a wolf population in Ontario indicated that this high density of wolves does not occur generally throughout the province. Aerial surveys in an area of 10,000 square miles of moose range, in conjunction with an experimental wolf control program, suggested a population density of between one wolf per 100 and one wolf per 200 square miles (Pimlott, *et al.*, 1961; Shannon, *et al.*, 1964).

In summary, data on wolf populations in North America indicate that densities of one wolf per 10 square miles are high, and they show that populations of a much lower density are common over very large areas.

FOOD HABITS OF WOLVES AND SELECTION OF PREY

The evidence from the studies of the food habits of wolves in Alaska (Murie, 1944), western Canada (Cowan, 1947), Wisconsin (Thompson, 1952), Minnesota (Stenlund, 1955), Isle Royale (Mech, 1966; Shelton, 1966) and from work in Algonquin Park (Pimlott, *et al.*, 1967) shows clearly that wolves are dependent to a very marked degree on large mammals for their food.

Summer Food

It has been fairly generally accepted that large mammals serve as prey in winter; however, it is often stated that in summer wolves utilize small animals to a considerable degree. For example, Olson (1938, p. 329), writing about the wolf in the Superior National Forest in Minnesota, stated that, "The major portion of the food of the wolf during the summer is grouse, wood-

mice, meadow voles, fish, marmots, snakes, insects, and some vegetation. In fact anything that crawls, swims, or flies may be included in their diet." His conclusions have not been borne out by quantitative studies.

The greatest degree of uncertainty about the food habits of wolves in summer is for tundra areas, the range of the barren-ground caribou. Banfield (1951) stated that the observations of Farley Mowat, made near Nueltin Lake in Keewatin, N. W. T., "indicated a drastic change in diet between the denning period and the nomadic period."

He stated that there were no caribou in the vicinity of the wolves between June 17 and August 20, and during that period the wolves were observed hunting for small mammals and eating dead fish and a dead gull. Unfortunately, an intensive study of their food habits was not undertaken, and only 61 scats were examined (Kelsall, 1957). In spite of the apparent absence of caribou, 42 of these contained caribou remains, while the remains of small mammals occurred in 17. Kelsall (1957) pointed out that almost all wolf scats collected in caribou country contain caribou hair; however, he suggested that much of this may be the result of scavenging activity by the wolves.

One aspect of the uncertainty about the importance of caribou in the summer diet of wolves is caused by the comparative behavior of the two species. Barren-ground caribou are highly migratory and, it would seem, must often leave the wolves behind during the period when the pups are young and relatively immobile. Possibly under such circumstances the wolves are much more dependent on small animals, or if there are such breaks in the contact with the primary prey, they may constitute an important limiting factor to populations of tundra wolves.

It is also possible that Murie's work (1944) may provide an answer to the question that was not apparent to Mowat and other investigators. In the area of Mt. McKinley Murie found that even after the main movement of the caribou through the zone there were usually stragglers left behind. The wolves were able to locate these

animals and thus subsist on caribou long after the main herds had disappeared. It is possible that such a situation exists in caribou range much more frequently than has been realized.

In a study of the food habits of wolves in Algonquin Park during the snow-free period of the year, white-tailed deer comprised 80% of the food items that occurred in 1435 scats; moose comprised 8% and beaver 7%. The remaining 5% included snowshoe hare (*Lepus americana*), muskrat (*Ondatra zibethica*), marmot (*Marmota monox*), porcupine (*Erethizon dorsatum*), raccoon (*Procyon lotor*), and three species of mice (Pimlott, *et al.*, 1967).

In addition to Algonquin Park, studies were conducted in a number of areas in other parts of Ontario. In two of these which lie west and north of Algonquin Park (the Pakesley area of Parry Sound Forest District and the Marten River area of the North Bay Forest District) and where the same species of prey occurred, the collections were compared with the data from Algonquin Park. For the Pakesley area (206 scats) the frequency of occurrence of the three most important species was beaver, 59%, deer, 27%, and marmot, 7%. For the Marten River area (226 scats) the frequency of occurrence of the three most important species was deer, 42%, beaver, 37%, and moose 17%. The deer population had undergone a marked decline in the Marten River area as a result of losses during the severe winters of 1958-59 and 1959-60 and was very low the year when the study was conducted. The relatively high occurrence of deer hair in wolf scats suggested that predation on deer may have been disproportionate to their abundance in the area.

The data from Pakesley are the only ones, of which I am aware, that indicate that ungulates have comprised less than 50% of the summer food of wolves. However, even in this area beaver cannot be considered to be a primary food for they are unavailable three to five months of the year; wolves could not persist in the area during this period if deer and moose were not available to them.

Selection of Prey in Summer

In Ontario the percentage of wolf scats in summer (July 1 to September 30) that contained fawn hair and calf moose hair was high. Fawn hair comprised 71% of the occurrences in the scats that contained deer hair, and calves 88% in the scats that contained moose hair (Pimlott, *et al.*, 1967). It has not been shown to what extent the frequency of occurrence of juvenile and adult remains reflects the proportion of animals in the age classes that are killed by wolves. However, Pimlott, *et al.* (1967) considered that the best assumption is that the proportion of remains in scats approaches the actual proportion in the kill; in this respect we disagreed with the conclusion of Mech (1966) that juveniles in the kill are over-represented by the occurrence of their remains in scats.

Selection of Prey in Winter

The food habits of wolves in winter on Isle Royale and in Algonquin Park were known primarily from the remains of animals found during the aerial searches. In the latter the remains of 676 deer, that were believed to have been killed by wolves, were located and the mandibles of 331 (47%) were collected.

The age distribution of the deer killed by wolves was not a normal one. Animals under five years of age included 42% of the specimens while those five years of age and older comprised 58%. The comparable percentages for a sample of 275 deer that were killed by cars or collected for research purposes were 87% and 13%. The comparative percentage of fawns, the age class most likely to be under-represented in the collection from wolf kills, was 17% and 20%, respectively.

The only other data on the age classes of deer killed by wolves were reported by Stenlund (1955) for the Superior National Forest. The collection (33 deer) did not show the preponderance of animals in the older age class, but the sample was too small for statistical comparisons to be valid.

The data on the kill of moose by wolves on Isle Royale show a somewhat similar

trend to those from Algonquin Park. Of 80 animals examined, 50 by Mech (1966) and 30 by Shelton (1966), 22 were calves, one was a yearling, and 57 were 6 years of age (Age Class VI, Passmore, *et al.*, 1955) or older.

In Alaska, Burkholder (1959) tracked a pack of wolves from the air and reported on the ages of eight caribou and eight moose. Six of the moose that were killed were calves, one was a yearling, and one an adult of unknown age. The caribou were all adults, three of unknown age, four were between two and six, and one was over 10 years of age.

Fuller (1962) stated that the evidence from stomach samples of wolves (95) and an analysis of 63 scats, collected in Wood Buffalo Park, indicated that bison (*Bison bison*) form a staple food of wolves in both summer and winter. He found the remains of eight animals that had been killed by wolves and he observed wolves attacking bison on three occasions. Five of the bison killed were very old animals, three were calves, and three were in middle-age classes. All three of the latter animals were injured or diseased. He could not determine whether the leg of one had been broken before or during the attack by the wolves.

Food Requirements of Wolves

The studies on Isle Royale (Mech, 1966; Shelton, 1966) have permitted an estimation to be made of the food requirements of wolves. Mech (1966) obtained data on 48 moose that were killed over a total period of 110 days. He estimated the average daily consumption at 12.3 pounds per wolf (Mech, 1966). Scrutiny of his data suggested that he overestimated the size of moose and underestimated the amount of wastage. Pimlott, *et al.* (1967) recalculated Mech's data and concluded that 10 pounds per day would be a better estimate. The suggested daily rate of consumption was 0.14 pound of food per pound of body weight (winter conditions). In their calculations they arbitrarily lowered the per diem rate to 0.12 pounds per pound for the summer (June to September) period.

THE DYNAMICS OF WOLF PREDATION

The most intensive studies of vertebrate predation were conducted by the late Paul Errington (1934, 1943, 1963; Errington, *et al.*, 1940). A fundamental aspect of his theory of threshold phenomena is that vertebrate predators take a high toll of prey only when the prey are living in insecure situations, in marginal or submarginal habitats. However, he frequently referred to predation by the genus *Canis* on the ungulates and indicated that he considered that there were at least some occasions when it might be of a non-compensating nature. In his major review of the topic he stated (Errington, 1946, p. 158):

"Intercompensations in rates of gain and loss are evidently less complete in the life equations of the ungulates, however, than in the muskrats. There is vastly more reason that I can see for believing that predation can have a truly significant influence on population levels of at least some wild ungulates."

"Without losing sight of the fact that much more than predation or lack thereof may be involved in the great changes recorded for American deer populations of recent decades . . . , we may detect pretty strong indications of the depressive influence of predation upon the numbers of the deer."

He summed up:

"Most examples of predation upon wild ungulates showing a reasonably clear evidence of population effect have one thing in common: the predators involved had special abilities as killers—indeed were usually *Canis* spp., members of a subhuman group inferior as mammals only to man in adaptiveness and potential destructiveness to conspicuous, relatively slow-breeding forms."

The environments in which wolf predation occurs in North America are extremely variable. The rigorous arctic environment of Ellesmere Island, where the wolves prey on musk oxen and caribou, contrasts sharply with the mixed forests of the Superior National Forest in Minnesota, where the wolves prey on white-tailed deer, and with Isle Royale National Park, where the wolves prey on moose. The nature of the universal variables of predation, predator, and prey density, and the nature of the subsidiary variables are very different in the various environments. The studies that

have been or are being conducted suggest that we are likely to find that the interaction of the variables of predation produce such complexities that few generalizations are possible on the influence of predation by wolves on populations of prey.

Influence of Wolves on Ungulates in North America

In the case of the caribou, Murie (1944) suggested that predation was apparently an important limiting factor on a population in Alaska through predation on fawns. However, Banfield (1954) suggested that the mortality caused by wolves in the western Canadian Arctic did not exceed 5% of the population. Kelsall (1957) stated that an annual kill of four caribou was a likely average kill of a tundra wolf, although he estimated that it would take 14 caribou to sustain a wolf for a year. Banfield's and Kelsall's estimates, which are of approximately the same magnitude, will be subject to upward revision if future studies indicate that caribou, and particularly fawns, are primary prey of tundra wolves, in summer, in northern Canada, as they are in Alaska. However, if future studies confirm that small mammals are a primary component of the summer diet of wolves, then the estimates of Banfield and Kelsall may be quite realistic. Dall sheep are prey of wolves in Mt. McKinley National Park in Alaska (Murie, 1944). Although the data from scat analyses suggested that they were not as important as caribou, Murie considered that the wolves were controlling the population. The control appeared to be exercised through periodic, heavy predation on yearlings. When Murie (1961) returned to the Park in 1945, after an absence of four years, he found that the population of sheep had declined to 500 from a minimum of 1000 to 1500 in 1941. He considered that poor survival of the young, combined with the loss of old sheep that had been predominant in 1941, had caused the decline. The wolf population had also declined but, unfortunately, there was no knowledge of their role in the decline of the sheep population.

The sheep quadrupled in numbers by

1959, but the wolf population did not show any parallel increase. Murie (1961) believed that predator control operations, conducted outside the Park, were the factor that prevented an increase in wolf numbers.

Cowan (1947) gave rough estimates of the population of elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) in Jasper National Park. His data suggest that the ratio of wolves to the combined populations of elk and mule deer was of the order of 1:100. In addition to these two species, moose, bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*), and caribou occurred in the area and were utilized to a lesser degree by the wolves. Their numbers would appreciably increase the ratio of predator to prey. Cowan (1947) discussed the overpopulations of ungulates that existed in the park and pointed out that, in addition to not removing the net increment of the populations, the wolves were not even removing the diseased and injured animals, which he referred to as the "cull group," from the population.

The work of Thompson (1952) in Wisconsin, though covering the ranges of only two packs of wolves, provides informative data. He showed that the two areas in which he studied wolves developed the same symptoms of an overpopulation of white-tailed deer as did areas where there were no wolves. Data on the deer population indicated that their density increased very rapidly in the late 1930's, from 10 to 30 per square mile, following extensive changes in habitat that resulted from fire and logging. The density of the wolf population was of the order of one per 35 square miles so that the ratio of wolves to deer would have been greater than 1:300.

Mech (1966) estimated the population of moose in Isle Royale, in late winter, at approximately 600 animals, and, as mentioned previously, the wolf population at 20 to 22. The ratio of wolves to moose in this case was approximately 1:30. Mech (1966) and Shelton (1966) concluded that the wolves were controlling the moose population. They estimated that the control was being accomplished by the kill of

between 142 (Mech, 1966) and 150 (Shelton, 1966) moose, or approximately 25% of the late winter population.

The data on the deer population in Algonquin Park suggest a density of 10 to 15 per square mile, or a ratio of wolf to deer of between 1:100 and 1:150. The deer are primary prey of the wolves and predation may have been important in preventing major irruptions such as those that have occurred in many deer ranges where wolves are absent (Leopold, *et al.*, 1947). The population of deer has not been in perfect balance with the environment, however, for there have been periodic reductions caused by starvation during severe winters (Pimlott, *et al.*, 1967). The interpretation of the influence of wolves on the deer population in Algonquin Park is made difficult by the fact that wolves in the Park were subject to control by Park personnel for many years prior to the inauguration of the research program. The deer, however, were protected from hunting.

Calculations based on the data on rates of food consumption by wolves, and on the data obtained from studies of food habits of wolves in Algonquin Park, suggest that a population of a wolf per 10 square miles would require and would utilize 3.7 deer per square mile per year. This would require a deer population of a minimum density of 10 per square mile and a productivity rate of approximately 37% to support the wolf population (Table 2) (Pimlott, *et al.*, 1967).

DISCUSSION

Since Errington's review (1946) of vertebrate predation, there has been a great increase in knowledge of the population dynamics of both wolves and the ungulates. The marked variation in reproductive performance that has been shown to exist among the ungulates permits considerable compensation for adverse or favorable environmental factors (*e.g.*, Cheatam and Severinghaus, 1948; Pimlott, 1959). It is conceivable that predation is a factor in triggering an increase in the reproductive rate, and, if so, it could be considered to be of a compensatory nature.

TABLE 2. Calculation of number of deer required to support a wolf population of one per 10 square miles.

Basic Assumptions		
Size of area	100	sq. miles
Wolf population	10	
Gross food consumption by wolves (avg. wt. 60 lbs.)		
Oct.-May	8.4	lbs./day
June-Sept.	7.2	" "
Wastage	20%	
Species other than deer—winter	10%	
summer	20%	
Age-composition and weight of deer killed		
winter—Fawns	30%	80 lbs.
Adults	70%	150 lbs.
summer—Fawns	80%	40 lbs.
Adults	20%	150 lbs.
Total kill of deer—winter	177	
summer	190	
	367	deer
Density of 10 deer/sq. mile, productivity of 37% is required to support 1 wolf/10 sq. miles.		

In the discussion of the selection of prey by wolves it has been shown that predation tends to be concentrated on the very young and the very old. When the old animals in a population are eliminated it probably has very little influence on the population level of the prey species for they, like animals in submarginal habitats, would soon have died of other causes anyway. Predation then on the old animals in the population also appears to be of a compensatory nature.

A great weakness that exists in the study of wolves in summer is that there does not appear to be any way of making concrete determinations about the condition of the young that are eaten by wolves. A number of studies show conclusively (Thompson, 1952; Murie, 1944; Mech, 1966; Shelton, 1966; Pimlott *et al.*, 1967) that wolves feed heavily on the young of the year—but, what percentage of these animals was actually killed by wolves? To what extent is the feeding on young animals a scavenging activity? What percentage of those killed by wolves would have survived in the absence of wolves? Studies in a number of areas where wolves have been extirpated indicate that a significant mortality of young ungulates occurs between spring and

fall. To the extent that predation by wolves removes young that would have died anyway, as in the case of old adults, it is of a compensatory nature.

Although Murie's (1944) work indicated that predation fell heavily on young animals, I do not think that the full import of this fact has been realized. If a considerable portion of this predation is non-compensatory, a population of wolves of high density would exercise a considerable influence on ungulate populations. Allee, Emerson, Park, Park, and Schmidt (1949) listed a series of principles that arose from their review of predation. The third is of particular interest to this discussion: "predation is frequently directed against the immature stages of the prey and as such may constitute an effective limiting factor." (p. 374).

The question of whether or not wolves constitute an effective limiting factor on ungulates, and particularly on deer, moose, and caribou, is one that has only been partially answered. In considering the population dynamics of some big-game species, deer and moose in particular, the question arises, as to why intrinsic mechanisms of population control have not evolved to prevent them from increasing beyond the sustaining level of their food supply. It seems reasonable to postulate that it may be because they have had very efficient predators, and the forces of selection have kept them busy evolving ways and means not of limiting their own numbers but of keeping abreast of mortality factors.

Contemporary biologists often have a distorted viewpoint about the interrelationships of ungulates and their predators. We live in an age when there is a great imbalance in the environments inhabited by many of the ungulates. In the case of deer and moose the environmental changes, or disturbances, have been favorable and populations are probably higher than they have ever been. Under such circumstances it is not much wonder that we have been inclined to argue that predators do not act as important limiting factors on deer and moose populations. I doubt, however, that it was a very common condition prior to

intensive human impact on the environment. In other words, I consider that adaptations between many of the ungulates, particularly those of the forest, and their predators probably evolved in relatively stable environments that could not support prey populations of high density.

The history of wolves and moose on Isle Royale is an interesting example. There, as I have mentioned, in the presence of abundant food and complete protection, the wolf population stabilized at a level of one wolf per 10 square miles. In Algonquin Park the estimates indicated a population of the same magnitude; there was no significant difference between 1959 and 1964, although during most of this period the wolves were protected (Pimlott, *et al.*, 1967). These examples suggest that a wolf per 10 square miles is close to the maximum density that can be attained by a population.

The data from Isle Royale suggest that a state of equilibrium has been reached between the wolves and the moose at a ratio of approximately one wolf per 30 moose. A similar calculation, based on the data from Algonquin Park, suggests that a ratio of one wolf per 100 deer may be close to an equilibrium. On the basis of these data, and on the basis of the previous discussion of the evolution of wolf-prey population mechanisms, I suggest that wolves may not be capable of exercising absolute control of white-tailed deer at ratios that exceed 1:100. I also suggest that predation by wolves may cease to be an important limiting factor when densities of deer exceed 20 per square mile.

The fact that no animal smaller than the beaver has been shown to be the predominant food of wolves for any significant period is not surprising. Their size, and the complex social organization of the packs, are such that it would rarely be efficient for them to live on small animals. The organization of the pack is undoubtedly an adaptation which has developed because wolves prey on animals larger and often fleetier than themselves. Such an organization would be unlikely to persist if small animals became their primary source of food.

Energy relationships are undoubtedly also involved. An adult wolf may weigh between 50 and 150 pounds and it would rarely be efficient to obtain the energy to maintain this biomass by the utilization of animals that weigh a few ounces or even a few pounds, especially when these are often difficult to capture.

I suggest that energy demands alone make it very unlikely that tundra wolves regularly subsist on small animals during the summer. When the question is studied intensively it is likely that the successful rearing of a litter will, in the great majority of cases, be found to be dependent on the availability of caribou or of other large ungulates as food for the wolves.

A study of the interaction of wolves and their prey indicates that there are a number of characteristic aspects of predation that are worthy of review. They serve to sum up this discussion of the dynamics of wolf predation; a knowledge of their existence may also contribute to the further development of understanding of the underlying principles of vertebrate predation.

1. In all but one instance, intensive studies of the food habits of wolves indicate that the large ungulates are the primary prey of wolves both in summer and in winter. It remains to be demonstrated that wolves can live and raise young in areas where they must subsist on small animals.
2. The process of wolf predation does not come about simply as a result of random contacts between predator and prey but is complicated by a process in which the ability of the prey to escape is tested. The dynamic aspects of the process have been observed in a number of areas (Murie, 1944; Crisler, 1954) and have been particularly well documented on Isle Royale (Mech, 1966; Shelton, 1966).
3. Among the ungulates, wolves prey primarily on the young-of-the-year and on animals in older age-classes. Predation is most heavy on the young during the summer but is less intensive during the winter, when old animals are vulnerable.
4. Intensive utilization of prey animals that are captured is a characteristic of wolf predation. One study (Pimlott, *et al.*,

1967) has demonstrated, however, that utilization was less complete during a winter when severe snow conditions prevailed.

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