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Testing Socially Acceptable Methods of Managing Predators: Reducing Wolf Predation on Moose Through Increased Caribou Abundance

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PROGRESS REPORT (RESEARCH)

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SUMMARY

The primary objective of this study was to determine if increasing numbers of alternate prey, i.e., caribou (*Rangifer tarandus*), could reduce predation on moose (*Alces alces*) and allow moose to escape chronic low densities without predator control. However, our study design was based simply on radiocesium (Cs-137) sampling of wolves (*Canis lupus*) to estimate consumption of caribou. This study design was inadequate to evaluate the above objective. Therefore, the study was prematurely terminated. Also, the principal investigator was replaced. We conclude that long-term inventories of caribou, moose, bears (*Ursus arctos* and/or *americanus*), and wolves are needed to evaluate the above objective adequately. To date, we have not observed moose and caribou escape low densities in lightly harvested wolf-bear-moose-caribou systems.

The effect of increased caribou numbers in a wolf-bear-moose-caribou system is variable and unpredictable. We found that, as caribou increased in numbers in the Delta, Nelchina, and Fortymile herds, wolves in respective study areas consumed increased, decreased, and near constant amounts of caribou. Our data estimated only kg of caribou consumed per wolf per day using grab samples of available wolf muscle samples and did not estimate the effect of wolves on caribou or moose populations. Sampling of wolves was irrespective of caribou distribution and, except in the Fortymile herd, wolf pack identity. Even if Cs-137 data indicated that wolves consumed more caribou as caribou increased, the wolves could be killing similar or greater numbers of moose without our knowledge because average total wolf consumption rates in the literature vary 3-fold. Also, increases in caribou numbers would not necessarily decrease the effect of predation on moose because wolf numbers are highly correlated to prey biomass.

We tentatively conclude that Cs-137 sampling can adequately estimate intake of caribou (kg caribou/kg wolf/day), but list several qualifications of data that future sampling designs should consider. For example, Cs-137 sampling of wolves cannot evaluate the hypothesis that increases in caribou have a detrimental effect on moose, because wolf consumption rates of moose are not estimated. We also provide a Lotus 123 model to help managers estimate the proportions of caribou and/or moose populations killed by wolves given several input parameters; e.g., the diet and kill rates of wolves, prey and wolf densities, moose and caribou population composition, and prey body weights.

Wolves may at times have less effect on high-density than low-density prey populations, because individual wolves do not necessarily increase consumption rates as prey biomass increases, unless prey vulnerability increases. This lessened effect of individual wolves on high-density prey populations is partly offset because wolf density is highly correlated with prey density. In lightly harvested systems, moose and caribou may seldom attain densities where the effect of wolf predation is reduced because of the stochastic limiting effects of predation and adverse weather. Adverse weather increases vulnerability and can lead to dramatic declines in prey populations.

We suggest that the effect of wolf predation in lightly harvested systems is unpredictable. Therefore, managers should not expect that increases in caribou populations will predictably allow moose to escape chronic low densities. Only by substantially reducing predation can managers reliably achieve goals for increased prey and harvest in wolf-bear-moose-caribou systems. Favorable weather may be necessary to achieve such goals.

Key Words: Alaska, caribou, food consumption, moose, predation, predator-prey relationships, radiocesium, wolf.

CONTENTS

BACKGROUND

Near-natural levels of predation strongly influence moose (*Alces alces*) densities and reduce the allowable hunter harvest. Predation by wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*) appears to be the primary factor maintaining moose at densities well below food-limited or K carrying capacity (KCC, McCullough 1979:85), where moose are primary prey and predators and moose are lightly exploited (Van Ballenberghe 1987, Gasaway et al. 1990); e.g., Quebec, Ontario, Yukon Territory, and Alaska (Bergerud et al. 1983; Messier and Crete 1985; Crete 1987, 1989; Van Ballenberghe 1987; Bergerud and Snider 1988; Larsen et al. 1989; Gasaway et al. 1990). The common conceptual model for regulating moose populations in these lightly harvested multipredator systems is a single, low-density equilibrium (LDE), where moose densities fluctuate in a range well below KCC (Messier and Crete 1985; Crete 1987, 1989; Van Ballenberghe 1987; Bergerud and Snider 1988). In contrast, high-density moose populations (i.e., near KCC) in Alaska appear to be products of predator reductions (Gasaway et al. 1990). Approximate sustainable harvest yields from moose populations at a LDE are low ($\leq$18 moose/1,000 km^2), compared with those (20-140 moose/1,000 km^2) from populations at elevated densities in Alaska and the Yukon Territory (Gasaway et al. 1990).

A controversy among wildlife conservationists resulted from the intense use of lethal methods of controlling predators to elevate moose densities and harvests above levels common to populations at a LDE. On one side of the controversy are advocates for managing predation in some areas to increase prey densities and harvests; on the other side are advocates for maintaining more natural, lightly exploited and protected systems at a LDE.

Reducing the divisiveness of predator management is essential if conservationists are to unite in addressing the most serious threat to wolf-bear-moose-caribou (*Rangifer tarandus*) systems in Alaska, i.e., loss of wilderness. To reduce this divisiveness, Gasaway et al. (1990) suggested the development of more socially acceptable alternatives to intense, lethal, government-sponsored predator reduction programs. The focus of this study was to evaluate whether increasing alternate prey (i.e., caribou) can help moose to escape the LDE without predator reduction programs.

Studies in the southern range of moose support the concept that increased alternate prey reduces predation on moose (Crete 1987, Bergerud and Snider 1988). Wolves prefer deer (*Odocoileus virginianus*) and elk (*Cervus elaphus*) over moose (Carbyn 1983, Wilton 1987), and in deer– and/or elk-moose-wolf-bear systems, moose became more abundant than in areas having a scarcity of alternate prey. For example, moose are more abundant in northeastern Minnesota (≥800 moose/1,000 km^2 in 30% of 15,000 km^2 of moose range; Mech 1977; Mech and Karns 1977; P. Karns, pers. commun.), Algonquin Provincial Park, Ontario (400-700 moose/1,000 km^2 and increasing, Wilton 1987), and Riding Mountain National Park, Manitoba (800 moose/1,000 km^2, Carbyn 1983) than in Quebec (400 moose/1,000 km^2, Messier and Crete 1985), where alternate prey is scarce. However, we have no indications that caribou are universally preferred over moose or that increasing caribou numbers benefit moose populations.

Our approach for assessing whether increasing caribou abundance markedly reduced wolf predation on moose relied on measurements of radiocesium (Cs-137) in muscle tissue to determine wolf food habits (Holleman and Stephenson 1981). Nuclear tests introduced Cs-137 into the atmosphere during the 1950s and 1960s. Lichens absorb Cs-137 readily, in part because their nutrients are absorbed from the atmosphere. Lichens eaten by caribou and, consequently, caribou muscle tissue have high concentrations of Cs-137; in contrast, foods eaten by moose and muscle tissue of moose have very little Cs–137. Wolves have concentrations of Cs-137 proportional to their consumption rate of caribou (kg/day/wolf, Holleman and Stephenson 1981). Moose consumption by wolves was estimated by the difference between estimated total consumption from values in the literature and estimated caribou consumption from Cs-137. However, literature on the total consumption rates of wolves varies 3-fold. We estimated Cs-137 concentrations in muscle samples from wolves, moose, and caribou in portions of the Delta, Fortymile, and Nelchina Caribou Herd ranges. Samples were collected when caribou were at high and low numbers in their respective ranges.

OBJECTIVES

Estimate winter wolf consumption rates of caribou as caribou abundance increased in the Delta, Fortymile, and Nelchina Caribou Herds study areas from 1975 to 1990.

Develop a LOTUS 123 computer model that predicts predation rates on moose and/or caribou populations when a variety of inputs are provided, including caribou, moose, and wolf densities and wolf food habits.

Assess whether increasing or the maintaining of moderate to big caribou populations can help increase moose abundance without intense lethal predator reductions.

STUDY AREA

The study areas included the range of the Delta Caribou Herd and portions of the ranges of the Fortymile and Nelchina Caribou Herds.

METHODS

Muscle samples from wolves, caribou, and moose were purchased from hunters and trappers during several winters in the late 1980s. We solicited trappers and hunters by letter, phone, and in person to obtain muscle samples. Staff stationed in Tok, Glennallen, Palmer, Delta, Anchorage, and Fairbanks participated in specimen collections. We paid $15 for a wolf hind leg or a 1–kg meat sample from moose or caribou. Wolf and caribou muscle samples were also collected by Alaska Department of Fish and Game (ADF&G) staff beginning in the mid-1970s.

We estimated Cs-137 concentration in muscle samples following methods of Holleman and Stephenson (1981). Approximately 1 kg of fat-free, fresh muscle tissue was double-wrapped in plastic bags and frozen. Cs-137 assays of the samples were made at the Institute of Arctic Biology, Fairbanks, by D. Holleman.

Concentrations of Cs-137 in samples were standardized for a specific recent date, 1 May 1990, using estimates of the environmental half-life of Cs-137 (Holleman and Stephenson 1981) plus the amount of Cs-137 deposited by the 26 April 1986 explosion of the nuclear reactor at Chernobyl, U.S.S.R. The environmental half-life of Cs-137 is the number of years that must pass before Cs-137 declines in the environment by 50%, assuming no additional Cs-137 deposits. We estimated the environmental half-life of Cs-137 from caribou muscle samples collected in the Nelchina herd during 1969-72 ($\underline{n}$ = 8, Holleman and Stephenson 1981) and 1989-90 ($\underline{n}$ = 29) and assumed lichen biomass in the caribou diet was constant. We regressed the natural log of Cs-137 concentration in caribou muscle on the date of death. The half-life was calculated by dividing the slope of that regression line into the natural log of 2. We calculated the additional percent Cs-137 deposited from Chernobyl by estimating the ratio of Cs-134:Cs-137 in the caribou samples. The Cs-134 present in samples was deposited entirely by Chernobyl. The Cs-137 concentrations in muscle samples collected before the explosion were increased by the percentage of Cs-137 contributed by the explosion.

The kg of caribou consumed daily by each wolf or group of wolves (x) during the month before the wolves' deaths (Holleman and Stephenson 1981) was calculated using a stochastic, propagation-of-error model. A bootstrap procedure (Efron 1982) was integrated in the model to produce estimates of standard error. This model chose variables at random for each wolf using the following formula and ran 1,000 replications for each wolf or group of wolves:

$$x = [(A-B)\ .\ (C)^{-1}][(D)\ .\ (E)^{-1}(1.16)]$$

where

A = Cs-137 concentration in 1 kg of muscle from wolves,

B = Cs-137 in wolves from an area of central Alaska devoid of caribou (n = 59),

C = Cs-137 in caribou from the same study area as wolves,

D = ingesta-free wolf body weight from central Alaska (n = 390), and

E = an in vivo kinetic factor described by a 2-compartment model, which reflects the retention and elimination of Cs-137 in wolves (n = 5; Holleman et al. 1971, Holleman and Luick 1976).

The constant (1.16) adjusts for the additional percent of muscle in a wolf compared with a caribou in terms of body weight (Holleman 1974, Adamczewski et al. 1987). In the Fortymile sample, the average percent caribou in all the wolves' diets was calculated by weighting percent caribou in the diets of each wolf pack by the sum of each respective pack's early winter numbers during 1981-88. Sample sizes for individual packs ranged from 2 to 22 (= 8, Gasaway et al. 1992). In the Delta and Nelchina samples this was not possible because we did not know the pack sizes from which wolves were sampled. Sampling of wolves in these 2 areas was not characterized by known pack identities or home ranges. Also, sampling design in all 3 areas was irrespective of caribou distribution, and only qualitative assessments of winter caribou distribution were made.

Variation in the half-life of Cs-137 (= 5.4 yrs) and the additional Cs-137 introduced by Chernobyl (Table 1) was integrated into the above model using modifications of the above formula, as follows. Each Cs-137 value in the formula was multiplied by $e^{-[\ln(2)(F)/(G)]}$, where F = the number of days between the date of kill and a recent correction date (1 May 1990) divided by 365, and G = the half-life in years. If the date of kill precedes the Chernobyl explosion (26 Apr 1986), the Cs-137 value is increased by a percentage so that all Cs-137 values are corrected to a single date (Table 1).

The percent caribou in the wolf's or wolves' diet was approximated by first dividing the above value "x" by the kg edible food available/39 kg wolf/day from 22 North American studies where moose and/or caribou were the primary prey and prey were not highly vulnerable (Table 2). The resulting value is multiplied by 100 to derive percent caribou in the wolf's or wolves' diet.

RESULTS

Radiocesium (CS-137) data from the Delta herd's range indicate that wolves relied more heavily on caribou as the herd increased from about 3,000 caribou during 1976-79 to 7,000-9,000 during 1986-90. Pooling all wolves taken during 1976-79 (n = 151) suggests wolves consumed 0.2 ± 0.1 (SE) kg of caribou/wolf/day or 4 ± 2% caribou, compared with 1.9 ± 0.3 kg or 36 ± 5% during 1986-90 (n = 117). However, only "grab sampling" (Cressie 1991) of wolves was conducted. Therefore, legitimate comparisons of wolf intake of caribou during the 1970s and 1980s can only be made on a geographical basis between time periods (Fig. 1). In all such comparisons, wolves consumed more caribou during the latter period when caribou were more abundant, and in 3 of 8 geographical areas studied, wolves consumed significantly (P < 0.1, Student's t-test) more caribou when caribou were more abundant.

In contrast, wolves did not rely more heavily on caribou in a 15,500-km^2 portion of the Fortymile herd's range during this herd's increase from about 8,000 caribou during winter 1981-82 to 15,000-20,000 caribou during 1985-88. Wolves consumed less caribou as the herd increased, although differences between periods were not significant (P > 0.5, Student's t-test). During the early period (1981-82) 47 wolves were sampled from 10 packs, and during the latter period (1985-88) 61 wolves were sampled from 12 packs. Because no differences were found between periods, data were lumped during 1980-90. These data were published separately (Gasaway et al. in press). In brief, data indicated wolves were consuming 1.6 kg of caribou/wolf/day, which comprised about 33% of the wolves' diets (n = 143 wolves from 16 packs). The Cs-137 in the Fortymile herd was estimated from 42 caribou.

Data from the Nelchina herd indicated that fewer caribou were consumed in the study area as the herd grew, but the herd largely abandoned the study area during recent winters. The total effect of wolf predation on the herd may have increased, decreased, or remained the same. Data do not deserve further attention.

To date, Cs-137 sampling of wolves appears to give realistic field results of wolf intake rates of caribou. We base this conclusion on a comparison of actual predation rates observed in other studies (Table 2) with the Cs-137 data from a sample of 14 wolves, which appeared to consume only caribou as large prey (Holleman and Stephenson 1981). Because Cs-137 sampling estimates only the consumption rate of caribou, only wolves consuming essentially 100% caribou can be used to estimate total consumption rates by wolves. These wolves were from the Selawik area of the Western Arctic Caribou Herd range and were collected in 1977 (Holleman and Stephenson 1981). We assumed these wolves were consuming caribou with Cs-137 levels similar to caribou collected from Arctic Village during 1973 and 1976 (Holleman and Stephenson 1981). These data suggest the wolves were consuming 0.16 kg caribou/39 kg wolf/day which is within the range of observed predation rates (0.11 to 0.29 kg of edible food available to wolves/kg of wolf/day) for 22 study areas where moose and/or caribou were the major prey and prey were not highly vulnerable (Table 2). Samples of wolves consuming 100% caribou and observations of predation rates before sampling are needed to verify our tentative conclusion that Cs-137 sampling can give realistic approximations of actual wolf intake rates.

Finally, we completed a Lotus 123 computer model that predicts the percentage of caribou and/or moose populations killed by wolves during a specified time given specified densities of wolves, caribou, and moose and various other inputs. This model and an example of the inputs and outputs are provided in Appendix A. This model is available from the senior author at the Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701.

DISCUSSION

We summarize here several qualifications of Cs-137 sampling to assist future potential studies of Cs-137.

1. Cs-137 sampling of wolf muscle estimates only the kg of caribou consumed per wolf per day, not percent caribou or percent moose unless assumptions are made on total daily intake rates, which can vary 3-fold (Table 2). Because consumption of moose is not measured, Cs-137 sampling is incapable of evaluating the hypothesis that an increase in caribou is detrimental to moose. Only long-term inventories of wolves, bears, moose, and caribou in several areas will provide answers to the original question of whether increased caribou can allow moose to escape chronic low densities without predator control.

2. Cs-137 sampling of wolf muscle only estimates kg of caribou consumed during the 28 days before the wolf's death, so caribou movements and distribution are important to interpreting data and sampling design must reflect this importance.

3. Cs-137 sampling must be conducted on wolf, caribou, and other major prey simultaneously, and study design must reflect this need.

4. Background data are needed on each Cs-137 muscle sample. For wolf samples, pack size, territory location, and date killed are needed. Wolf samples need to be collected throughout the caribou herd's range. Samples collected in this manner can be weighted by pack size to estimate kg caribou consumed by the population. "Grab sampling" (Cressie 1991) of wolves will be more meaningful if analysis is weighted by pack size. Pack identity is also important, e.g., wolves following migratory caribou could be sampled in a study area and could confound estimates of caribou intake by local wolves. For caribou samples, length of time in the study area is important if lichen quantity varies between adjacent areas. Time in

the study area should exceed 28 days. In brief, "grab sampling" (Cressie 1991) and lumping of wolves and caribou should be avoided if possible.

As caribou increased in the 3 study herds, the wolf populations studied either increased, decreased, or did not significantly ($P > 0.5$) change their consumption of caribou (kg caribou/wolf/day). Apparently the effect on the moose population from increased caribou numbers could be beneficial, detrimental, neutral, or, most likely, variable. For example, increased numbers of caribou in a wolf-moose system might benefit moose if wolf numbers remained stable and wolf kill rates remained stable. However, these are unlikely events. Wolf numbers do not remain stable with increased prey. In fact, wolf and prey densities are highly correlated in lightly harvested systems (Fuller 1989, Gasaway et al. in press). Also, average kill rates of wolves varied up to 3-fold in North American studies where moose and/or caribou were the primary prey (Table 2). Therefore, even if wolves consume more caribou as caribou density increases, wolves could be killing the same or greater numbers of moose, i.e., the addition of more caribou in the system could have a neutral or detrimental effect on the moose population. Furthermore, an exodus of migratory caribou from a study area forces resident wolves to prey solely on moose, potentially at a rate higher than if caribou had not occurred in the area.

Wolves possibly have less effect on high-density prey populations because individual wolves apparently do not increase consumption rates as prey biomass increases (Fig. 2). However, this effect is partly offset because wolf density is highly correlated with prey density. We suggest the effect of wolf predation on lightly harvested predator and prey populations is unpredictable over a wide range of moose and caribou densities until weather or nutrition induce increased prey vulnerability. With increased vulnerability, the effect of predation on prey populations can increase dramatically, both because of numerical increases in wolves and because kill rates suddenly increase. The potential for adverse weather to change predator-prey relationships is important to recognize, but difficult to manage. Vulnerability of caribou and moose may differ under adverse weather but increased vulnerability of one prey species may be enough to trigger declines in both species through increased predation.

Naturally regulated predator-ungulate systems occur in less than half of Alaska today and in no cases have these ungulate populations (caribou or moose) increased to levels that occurred during prior predator reductions. This suggests that caribou and moose populations are limited at low densities by wolf and bear predation and probably the periodic stochastic effects of weather. Therefore, managers should not expect that increases in caribou populations will predictably allow moose to escape chronic low densities in lightly harvested systems. Fluctuations in prey populations are probably not predictable. Only with substantial reductions in predation can managers reliably expect to attain goals for increased prey and harvest in these systems, and favorable weather may be necessary to achieve such goals.

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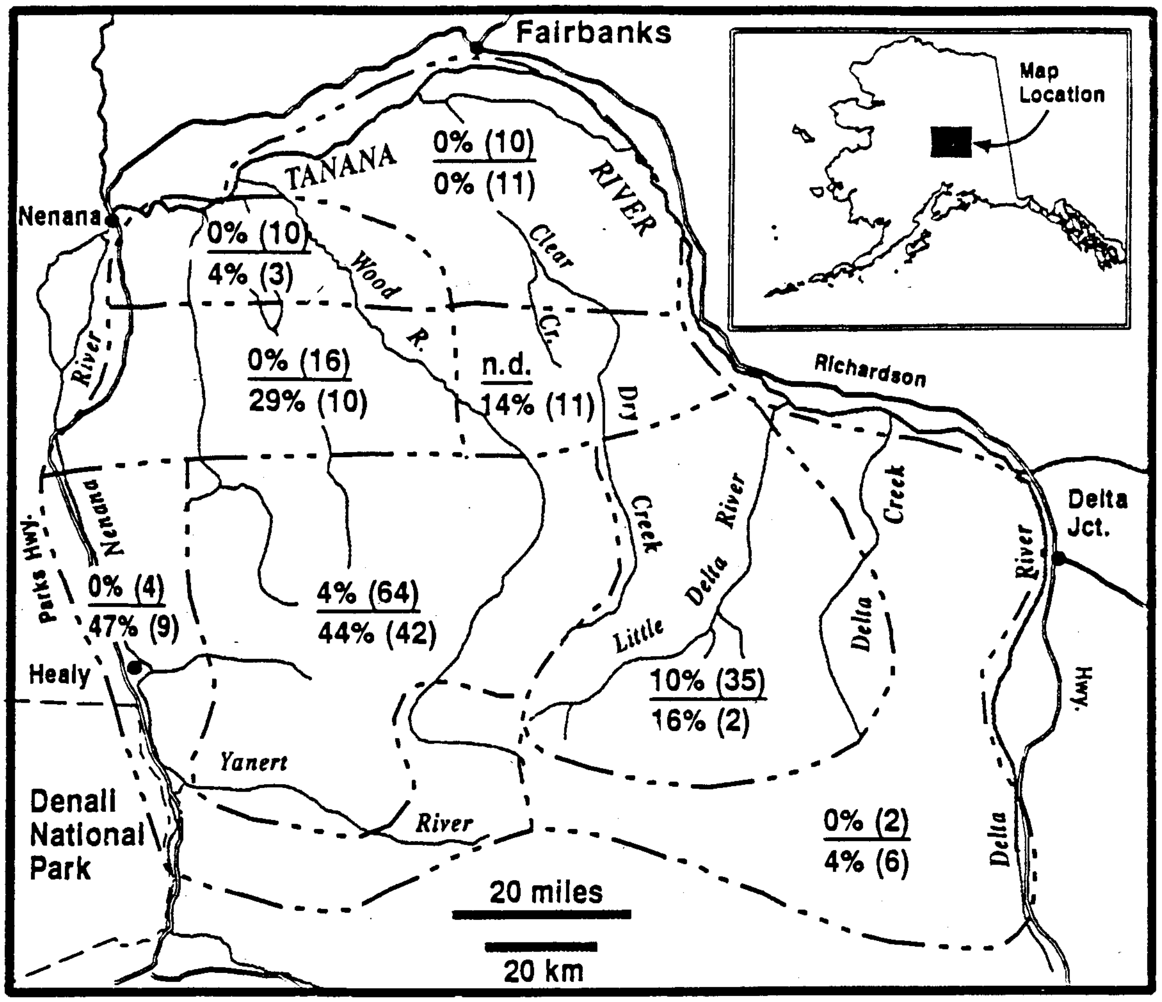

Fig. 1. Estimated percent caribou in the wolves' diets during 1976-79 (numerator) and 1986-90 (denominator) in the Delta Caribou Herd's range. Estimates were made using radiocesium assays of wolf and caribou muscle. Numbers of wolves sampled are in parentheses. Delineation of sub-areas is based on qualitative observations of caribou abundance. "n.d." signifies no data were available.

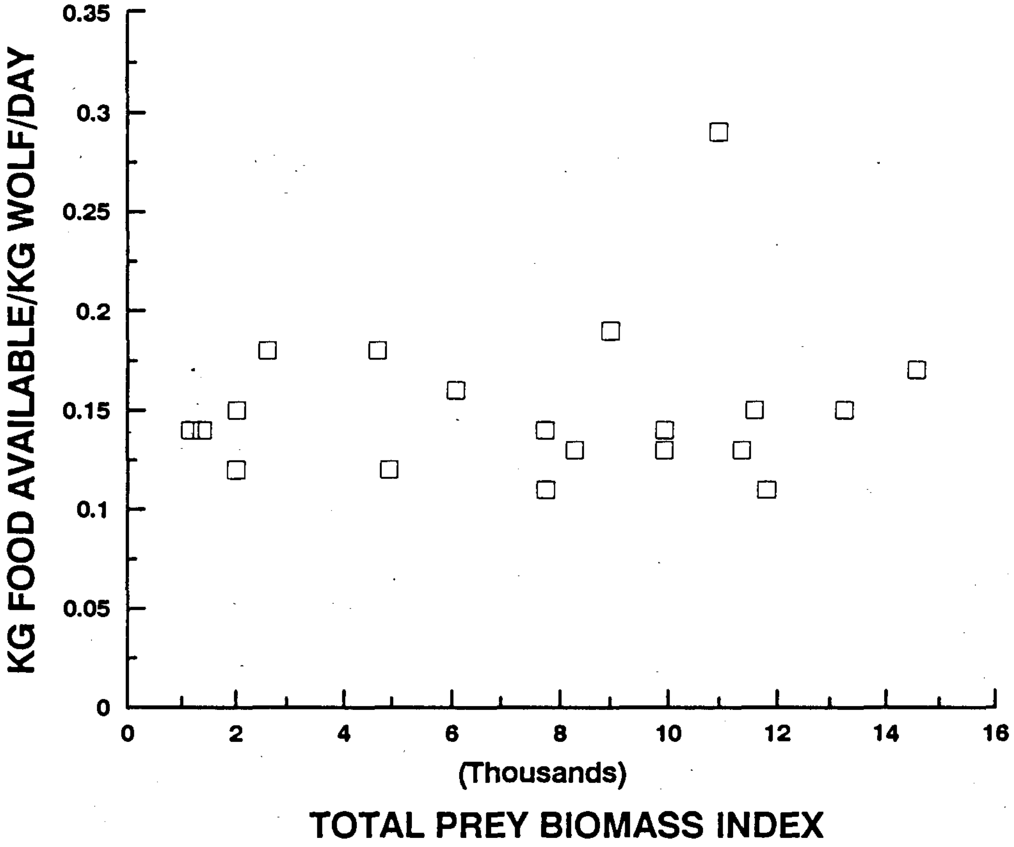

Fig. 2. Relationship between wolf consumption rates and total prey biomass index in 20 North American studies where moose and/or caribou were major prey and prey were not highly vulnerable. Total prey biomass index was calculated following Fuller (1989). Data are from Table 2.

Table 1. The percent Cs-137 in caribou muscle that was contributed by fallout from the explosion of the nuclear reactor at Chernobyl, U.S.S.R., on 26 April 1986.

	Herds						
Parameter	Western Arctic	Fortymile	Denali	Nelchina	Delta	Mentasta	Combined
Mean	10	16	16	20	22	20	17
n	6	9	9	6	9	4	43
SD	2	5	7	2	7	7	6
SE	0.9	1.5	2.3	0.7	2.2	3.4	0.9
Range	6	14	20	5	22	11	30

Table 2. Quantities of food available to wolves as observed in 26 study areas where moose and/or caribou were the major prey. All estimates of food availability at kill sites are based on edible portions of carcasses. If wolves killed well in excess of their needs, prey were classed as highly vulnerable versus normal vulnerability. Prey biomass index values were calculated following Fuller (1989) and Keith (1983).

Location	Major prey	Vulnerability N=normal H=high	Total biomass index/ $1,000km^2$	Biomass index/ wolf	kg/wolf /day	kg/kg of wolf /day	Wolf wt (kg)	Reference
Isle Royale, 1985	Moose	N	11,801	292	3.6	0.11	33	Peterson 1988, Peterson and Page 1987
Isle Royale, 1980	Moose	N	7,721	84	3.6	0.11	33	Peterson 1988, Peterson and Page 1987
Denali, 1970-71	Moose	N	2,002	334	4.5	0.12	39	Haber 1977
Kenai, 1977-79	Moose	N	4,826	345	4.8	0.12	39	Peterson et al. 1984
Isle Royale, 1979	Moose	N	8,272	105	4.2	0.13	33	Peterson 1988, Peterson and Page 1987
Isle Royale, 1986	Moose	N	11,360	309	4.2	0.13	33	Peterson 1988, Peterson and Page 1987
Isle Royale, 1983	Moose	N	9,926	208	4.2	0.13	33	Peterson 1988, Peterson and Page 1987
Isle Royale, 1959-60	Moose	N	7,720	193	4.6	0.14	33	Mech 1966; Peterson 1977, 1988
Isle Royale, 1978	Moose	N	9,926	135	4.6	0.14	33	Peterson 1988, Peterson and Page 1987
Coast Mtns. Yukon, 1984-87	Moose	N	1,160	187	5.3	0.14	38	Hayes et al. 1991
NE Alberta, 1977-78	Moose	N	1,384	231	5.5	0.14	38	Fuller and Keith 1980
Isle Royale, 1974	Moose	N	13,235	232	4.8	0.15	33	Peterson 1988, Peterson and Page 1987
Isle Royale, 1984	Moose	N	11,581	225	4.9	0.15	33	Peterson 1988, Peterson and Page 1987
Tetlin, 1987	Moose	N	2,020	348	6.0	0.15	39	Breeser et al. 1987

Table 2. Continued.

Location	Major prey	Vulnerability N=normal H=high	Total biomass index/ 1,000km^2	Biomass index/ wolf	kg/wolf /day	kg/kg of wolf /day	Wolf wt (kg)	Reference
Isle Royale, 1981	Moose	N	6,066	110	5.2	0.16	33	Peterson 1988, Peterson and Page 1987
Anderson-Inuvik, 1989	Caribou	N	--	--	5.4	0.16	34	Clarkson and Liepins 1991
Isle Royale, 1975	Moose	N	14,559	193	5.6	0.17	33	Peterson 1988, Peterson and Page 1987
Teslin, Yukon, 1984	Moose	N	2,580	143	6.8	0.18	38	Hayes and Baer 1986
Southcentral Alaska, 1979-80	Moose	N	4,612	659	7.1	0.18	39	Ballard et al. 1987
Isle Royale, 1977	Moose	N	8,934	143	6.2	0.19	33	Peterson 1988, Peterson and Page 1987
Ridge-Inuvik, 1989	Caribou	N	--	--	6.9	0.20	34	Clarkson and Liepins 1991
Isle Royale, 1982	Moose	N	10,919	424	9.6	0.29	33	Peterson 1988, Peterson and Page 1987
Isle Royale, 1976	Moose	H	11,029	136	4.4	0.13	33	Peterson 1988, Peterson and Page 1987
Isle Royale, 1973	Moose	H	15,331	348	7.7	0.23	33	Peterson 1988, Peterson and Page 1987
Isle Royale, 1972	Moose	H	12,132	287	7.9	0.24	33	Peterson 1988, Peterson and Page 1987
Isle Royale, 1971	Moose	H	12,463	339	9.1	0.28	33	Peterson 1988, Peterson and Page 1987

APPENDIX A. Alternative Prey Model

Purpose of the Model

This LOTUS 123 model helps evaluate how changing caribou, moose, and wolf abundance might affect wolf predation rates on moose and caribou populations. The primary output of the model is the percentage of the moose and caribou populations killed by wolves during a specified period of winter. The inputs can simulate real or hypothetical situations and can be varied to play "what if" games.

Inputs

The inputs are parameters relating to the diet and kill of wolves, duration of the winter period, prey and wolf densities, moose and caribou population composition, and whole body weights of moose and caribou.

The only cells in the spreadsheet that can be altered are the input parameter values and the comment section at the bottom of the model. All other cells are protected by the LOTUS 123 "protect" feature. If you want to modify formulas, make a copy of the file under a new name, and unprotect the cells in LOTUS 123.

Many formulas in the model use named-ranges instead of standard cell locations. The named-range method of writing formulas is easier to understand. Named-ranges are listed to the right of input values and some output values. The attached copy of the model shows all the names. To go to a named-range, press the F5 key, type the name, and press enter.

Comments on specific inputs are listed below:

1. Kg food available/wolf/day. Food available is the edible portion of prey that wolves kill or scavenge. Wolves may not eat all the food available to them; therefore, food available is not always equal to food consumed. The average food available to wolves was 0.15 kg/kg of wolf/day in North American studies where moose or caribou were the major prey. Wolves in Alaska averaged 39 kg; therefore, the average food available/wolf/day was 5.7 kg. Prior summaries of data are listed on this spreadsheet in the named-range AVAILABLE. To see these data press the F5 key, type AVAILABLE, and press enter. There is no correlation between food available to wolves and total prey biomass or prey biomass/wolf (view named graph FOOD3 and FOOD2). Therefore, the mean value can be used or you can use a value that is more appropriate for your simulation.

2. The proportion of caribou in the diet can be estimated from radiocesium (Cs-137) in wolves and caribou or some other data source. The model calculates the proportion of moose in the diet by subtracting the proportion of caribou and the