PREY SELECTIVITY OF WOLVES IN BANFF NATIONAL PARK

by

DAVID JOHN HUGGARD

B.Sc. (Hons.), The University of British Columbia, 1988

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

Department of Zoology

We accept this thesis as conforming

to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

June 1991

Department of *Zoology*

The University of British Columbia
Vancouver, Canada

Date *MAY 28, 1991*

Prey selectivity of wolves in Banff National Park

Abstract

The functional response of wolves to changes in the abundance of their prey must be understood to manage wolf-ungulate systems, but is difficult to measure directly. In this study, behavioral and environmental components of wolf predation were assessed and used to predict features of the dynamics of the wolf-large ungulate system in Banff National Park, Alberta. Elk were the most abundant ungulate, while white-tailed deer, mule deer, bighorn sheep, mountain goats, moose and several non-ungulate species provided a diverse prey base.

Two packs of wolves were followed using radio-telemetry and snow-tracking, and 652 scats and 130 animals killed by wolves were analyzed to determine wolf diet. Aerial total counts, ground classified counts, incidental sightings during field work and pellet group counts were used to estimate the numbers, composition and herd sizes of the ungulate prey species. Numerous animals killed on the road and railway provided information on the age structure and physical condition of the elk population.

Non-ungulate prey were used by one wolf pack, when ungulate prey were scarce. All available ungulate species were included in the diet of wolves. Bighorn sheep and mountain goats were underrepresented in the diet, due to their use of habitats segregated from the wolves. For social ungulates, the herd is the unit of available prey, and herd size and composition substantially influenced the selectivity of wolves. Abundance, habitat overlap and herd size determined encounter rates and were more important in determining diet than inherent preferences of the wolves, since all ungulate species were expected to be equally profitable upon encounter. How wolves encounter their prey determined the predicted functional response of wolves to different prey species.

Within elk, wolves preferred calves over adults and took adult males and females equally, but herd size and composition resulted in a slight overall selectivity for calves and adult males, and apparent avoidance of females. Adult elk killed by wolves were older than elk killed on the road or railway, but this may be due to a bias in obtaining the population age distribution from a mortality source, rather than due to selectivity by the wolves. Adult elk, but not calves, killed by wolves had lower reserves of marrow fat than road and rail kills.

Wolf kill rates increased with depth of snowpack and wolves killed primarily calf elk in moderately deep snow (51-58cm) and adults in deeper snow. Scavenging occurred more often in shallow snow and at low kill rates, because wolves travelled more and encountered more scavengeable carcasses under these conditions.

In an auxiliary study, the error associated with telemetry relocations in a mountainous environment and the effect of this error on assessment of habitat use were measured. Mean error distance in complex topography was greater than in simple topography (234m versus 156m). The error distance was correlated weakly with observer distance and size of the map error polygon, but neither was a good predictor of the error of a single relocation. Simulations showed that the habitat of a radio-collared animal would be assessed correctly 80% of the time for large habitat units, and would decline rapidly for units comprising less than 2% of the study area. Matrices were developed to correct for biases in habitat use information which is based on telemetry relocations.

Table of Contents

LIST OF TABLES

LIST OF FIGURES

Acknowledgments

Chapter 1. General Introduction

The response of predators to changes in the density of their prey species has been analyzed as two components since Solomon (1949) distinguished between the changes in the number of predators (the numerical response) and changes in the predation rate of each predator (the functional response). Holling (1959a, 1959b, 1965, 1966) described 4 basic forms that the functional response could assume, determined by the predator's search rate and efficiency, time to handle the prey, satiation and ability to switch to other prey types. The type I functional response is usually ascribed to simple foragers such as filter feeders, with predation rates proportional to prey density to an upper limit (satiation) after which predation rates remain constant. With a type II response, predation rates also increase with increasing densities of prey, but in a decelerating manner, approaching an asymptote at satiation. Type III responses are characterized by a convex upward curve at low prey densities, followed by a decelerating curve at higher densities. The type IV response features peak predation rates at intermediate prey densities followed by a decline at high densities.

Numerous subsequent studies have quantified the functional responses of various predators (e.g. studies reviewed in Hassell, 1978; Taylor, 1984), while others sought to determine the behavioural mechanisms responsible for the form of the response (Rogers, 1972; Real, 1979; McNair, 1980). In general, very simple animals were found to have simpler functional responses, but a variety of forms were found for most taxonomic groups. In particular, animals in complex environments attempting to optimize energy intake could have functional responses not fully described by Holling's (1959a) basic forms (e.g. Abrams, 1982; Wanink and Zwarts, 1985; Abrams, 1987; Mitchell and Brown, 1990). Additionally, several mechanisms could account for the same observed response. For example, a type III response could be produced by switching (Murdoch,

1969), use of refuges by prey (Taylor, 1984) or optimal allocation of foraging effort (Abrams, 1982).

The shape of the functional response has important implications for the behaviour and stability of predator-prey systems. Responses which include rapidly decreasing predation rates at low prey densities (i.e. Type III, Holling, 1959a) tend to produce more stable interactions in which the predator is less likely to drive the prey species to extinction (Armstrong, 1976; Emlen, 1984). Instability is more likely with simpler functional responses, though the numerical response of the predator and the prey recruitment characteristics also influence system behaviour (Levin, 1977). With complex combinations of functional and numerical responses and prey recruitment functions, the system may exhibit multiple stable equilibria (May, 1977), typically including a stable point with low numbers of predators and prey (the "predator pit"; c.f. Messier and Crete, 1985). Selective predation for certain age or sex classes within a species substantially influences the impact of the predators on the prey populations, particularly in determining whether predator mortality is compensatory or additive to other mortality sources. The form of the predator's functional response and the selectivity of the predator are therefore critical information for wildlife managers who wish to understand the dynamics of predator-prey systems and be able to predict their response to perturbation.

Unfortunately, the functional response is difficult to measure. In small-scale systems, prey abundance can be manipulated to a variety of levels and predation rates measured directly (e.g. many studies reviewed in Hassell, 1978). With larger-scale systems, the changes in predation rates with natural variation in prey numbers may be used (e.g. Peterson, 1977; Messier and Crete, 1985). For many large-mammal systems, of prime interest to managers, manipulation of prey numbers is infeasible and natural changes may occur on too long a time scale. Additionally, preventing the necessary large changes in prey numbers may itself be a management goal. In these cases, the functional

response must be predicted based on knowledge of the components which produce it - the density, distribution and behaviour of the predator and prey.

The prey selection models of optimal foraging theory (reviews in Pyke, 1984; Stephens and Krebs, 1986) provide a basis for predicting predator behaviour and predation rates. Indeed, the basic model of optimal prey selection may be derived from Holling's (1959a) disc equation for the functional response (Charnov and Orians, 1973). However, the prey selection model of foraging theory is concerned primarily with the decision of the predator whether or not to attack a prey type upon encounter. In complex field situations, several factors in addition to prey abundance may determine encounter rates with prey types, and these must also be included when using foraging behaviour to predict functional responses.

Wolves (Canis lupus) have recently recolonized the Bow Valley of Banff National Park, Alberta (Mickle et al., 1986). The prey base is abundant and diverse, comprised of elk (Cervus elaphus), mule deer (Odocoileus hemionus), white-tailed deer (Odocoileus virginianus), bighorn sheep (Ovis canadensis), mountain goat (Oreamnos americanus), moose (Alces alces) and numerous non-ungulate species. While fully protected by law in the Park, these species are affected substantially by human activities, primarily mortality on the highways and railways, hunting outside the park and some habitat loss due to development. Developing a model of the interactions of wolves and their prey and the effects of human perturbations is therefore a management priority in the park.

My work is part of a Parks study of wolf ecology initiated to determine the role of the wolf in the large mammal system in the Park. While collecting general information on wolf ecology in the Park, I focused on determining the prey selectivity of wolves, the causes of the observed selectivity and the implications for the functional response of wolves and wolf-prey dynamics. My objectives were:

1. To determine the diet of wolves in the Park, the available prey and the selectivity of wolves.

2. To determine the components of the behaviour and distribution of wolves and their prey, and the environmental factors which determine the observed selectivity.

3. To determine the implications of 1. and 2. for the dynamics of the wolf-prey system in Banff, and in other wolf-prey systems.

In chapter 2 of this thesis, I examine the selectivity of wolves for the different prey species in the Banff National Park system. My approach is to quantify the selectivity of wolves for different species, then examine the components that generate this selectivity, and combine these in a model to predict the functional responses of wolves to changes in the density of their major prey types. The time frame of this project is clearly too short to test these predicted functional responses rigorously, and they are only intended to provide a reasonable starting point for a model of the complete predator-prey system. The methods I use to analyze selectivity may also provide a framework for future studies of predators.

In chapter 3, I quantify the selectivity of wolves for different classes of elk, their major prey species. Rather than simply accepting traditional explanations for the observed selectivity, I again examine the components generating this selectivity. By understanding how selectivity is generated, I hope better to predict changes in selectivity with changes in composition and condition of the prey species.

Chapter 4 examines the impact of snow on wolf predation and feeding behaviour. Snow, particularly depth of snow pack, represents an extrinsic, abiotic factor which is not predictable, but can greatly influence wolf-prey systems (Nelson and Mech, 1986; Fuller, 1991). Incorporating this stochastic factor is essential for realistic models of wolf-prey

dynamics. In this chapter I also examine scavenging by wolves, to determine under what conditions wolves will scavenge and again consider implications for wolf-prey dynamics.

Radio-telemetry was used extensively in this study, in part to assess habitat use of wolves and their prey. In chapter 5, I evaluate the accuracy of radio-telemetry in a mountainous environment and how inaccuracy affects assessment of habitat use.

Chapter 2. Selectivity for prey species by wolves in Banff National Park

Introduction

The interaction of wolves (Canis lupus) and their prey has been studied in over 25 locations (see Carbyn, 1983b; Ballard et al., 1987 and references therein). Few of these studies involved more than one major prey species, and the dynamics of wolf - multiple prey systems remain poorly understood. A critical component of complex predator-prey systems is the functional response of the predator to each of its prey species (Taylor, 1984), which is central to predator-prey models and therefore to predicting and managing these systems. However, direct measurements of complex functional responses are rarely feasible for large mammalian predators, and a deductive approach must normally be used, in which functional responses are predicted based on the observed selectivity of wolves for different prey species. Long-term studies of wolf-multiple prey systems can then be used to examine predictions derived from observed behaviour.

Prey selectivity is the non-random representation of the available food in the observed diet (Chesson, 1978). In a complex environment, prey selectivity can be generated at several levels. Prey species may have different degrees of range overlap with the predators, and within their overall ranges, predators and prey may use the available habitats differently. Predators may search for particular prey types, particularly if certain prey occur in predictable patches . Additionally, if prey are encountered, and respond to predators as groups rather than individuals, the predator's effective encounter rate is reduced (Taylor, 1979). These spatial complexities may result in encounter rates for prey species which are not directly proportional to their densities.

Having encountered a particular prey species, selectivity can further be generated by the predator's decision to attack that prey or not. This is the basic decision variable in prey choice models of foraging theory (Stephens and Krebs, 1986). In addition, for

predators which hunt mobile prey, Nishimura and Abe (1988) have shown that the probability of capture success can be the critical determinant of prey use.

In this paper, I present initial results from an ongoing study of wolves in Banff National Park (BNP), Alberta and examine the prey selectivity of wolves in this complex prey system. By decomposing wolf hunting behaviour into the components that determine encounter rate and those that involve decisions to attack or success of attack upon encounter, I attempt to evaluate which processes are important in the wolf-prey interactions in BNP. I then integrate these components in a simple model which I use to examine how the diet of the predator should respond to changing prey densities, when prey species differ in how they are encountered by predators.

Study area and population

This work was part of a Parks Canada study of the ecology of wolves in Banff National Park (BNP). BNP is located 120km west of Calgary, Alberta, in the Front and Central Ranges of the Rocky Mountains. The main study area was the Bow Valley between Banff and Lake Louise, a broad (4-km wide) glacial-formed valley which runs northwest-southeast between high mountain ranges (Fig. 2.1). The valley bottom is at 1600m at the northwest end and descends to 1365m at Banff. Long, narrower valleys at higher elevations join the Bow Valley.

The climate is characterized by long winters with cold periods interspersed by warm dry weather caused by chinook winds, and short summers (Holland and Coen, 1982). Mean annual snowfall increases from 249cm at Banff to 418cm at Lake Louise, 55km to the northwest. Snow accumulation rarely exceeds 50cm at Banff and 75cm at Lake Louise, but is greater in the adjacent higher elevation valleys.

The vegetation of the 20km of the Bow Valley bottom west of Banff is montane, with lodgepole pine (Pinus contorta), Douglas fir (Pseudotsuga menziesii) and white spruce (Picea glauca) forest interspersed with aspen poplar (Populus tremuloides) groves,
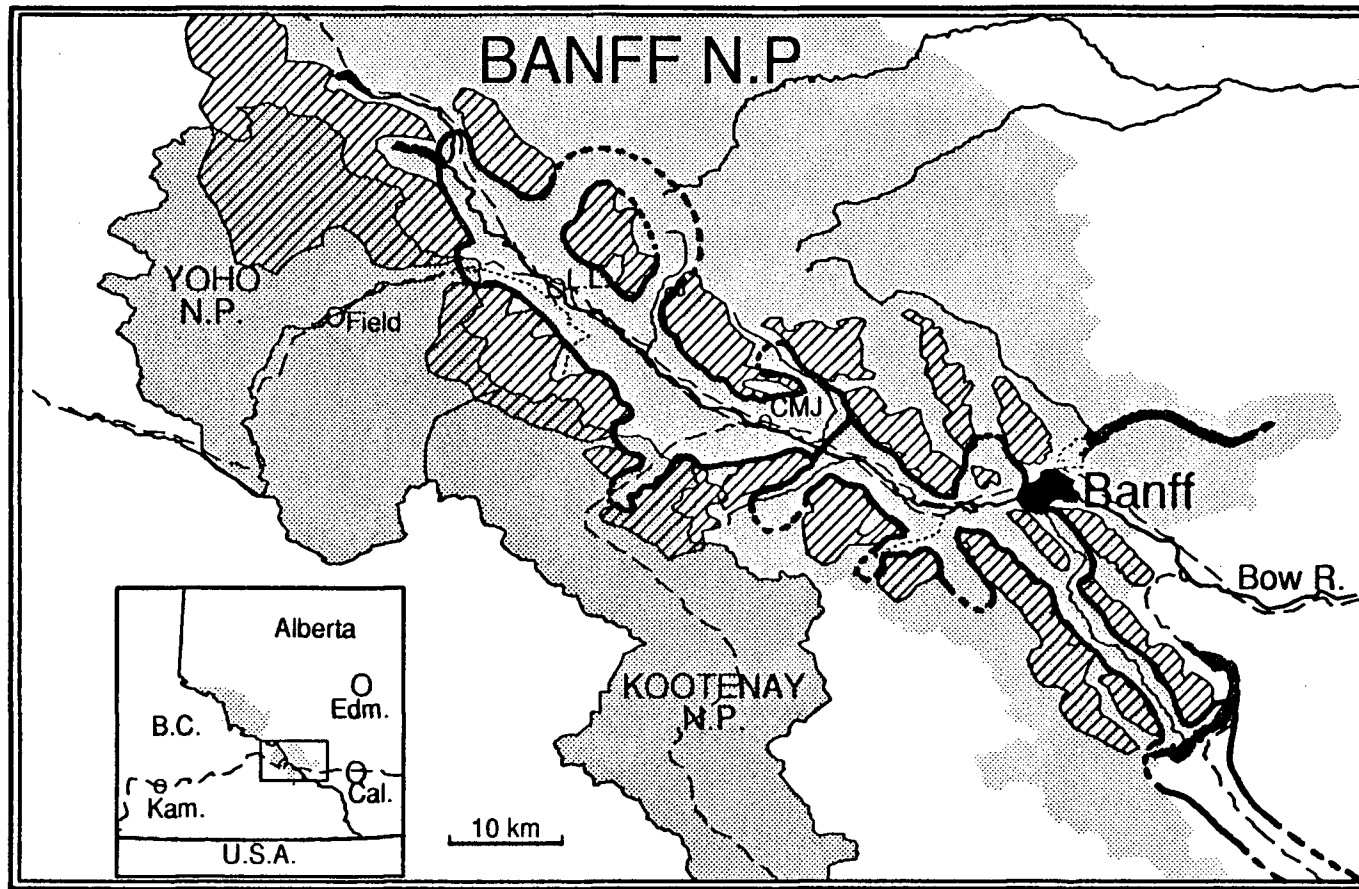
Fig. 2.1. Study area and home ranges of study wolves. Thick lines define the known home ranges of the two study packs, mainly oriented along the Bow Valley. The extent of the ranges in peripheral valleys is uncertain (thick dotted lines). Hatched areas are inaccessible mountains adjacent to the wolves' ranges. Thin dashed and dotted lines are main and secondary roads, respectively. L.L.=Lake Louise, CMJ=Castle Mountain Junction. Inset shows position of study area with respect to Edmonton, Calgary and Kamloops.

small open grasslands and wet shrub meadows. The northwestern two-thirds of the Bow

Valley bottom, the valley sides and the adjacent side valleys contain subalpine forest.

Engelmann spruce (Picea engelmanni) and subalpine fir (Abies lasiocarpa) forests are

mixed with successional lodgepole pine stands. South- and west-facing slopes in the

Bow Valley have a dry, open forest of Douglas fir and lodgepole pine. Several of the

adjacent valleys and ranges contain well-defined avalanche paths covered in grass or low

shrubs. The vegetation of the park has been fully described and mapped by Holland and

Coen (1982).

The southeastern half of the Bow Valley is an important wintering area for elk

(Cervus elaphus), mule deer (Odocoileus hemionus) and white-tailed deer (Odocoileus

virginianus). Smaller numbers of these species are found in the northern half of the

valley and in adjacent valleys in the winter. In the summer, roughly half the elk migrate

to higher elevation ranges; the rest remain in the Bow Valley bottom (Woods, 1991).

The deer species may follow the same pattern, though little is known of their seasonal

movements. Moose (Alces alces) are rare in the Bow Valley, though they are relatively

common to the north and south of the valley. Bighorn sheep (Ovis canadensis) are

abundant on certain slopes above the Bow Valley and in some of the adjacent valleys.

Mountain goats (Oreamnos americanus) are less common in these habitats.

The study area was defined as the ranges of the two wolf packs that use the Bow

Valley. The Spray pack uses the southern third of the Bow Valley and adjacent valleys

to the west and south, while the Baker pack uses the northern two thirds and adjacent

valleys. Radio telemetry (685 locations for members of the Spray pack, 199 for the

Baker pack) and ground tracking indicated the home ranges of the two study packs (Fig.

2.1). In a complex mosaic of useable and non-useable (e.g. cliffs, high mountains,

glaciers) habitat such as BNP, home range plots and areas produced by complex

analytical programs can bear little resemblance to the areas actually used by the animals

(Boulanger and White, 1990). Therefore, overall home ranges were plotted by hand,

based on the above information and the local topography. The edges of the packs' ranges were clearly bounded by high mountains. Where the two packs met in the central Bow Valley, a clear boundary was evident, with little overlap and no evidence of a buffer zone between territories (Mech, 1977). The extent to which territories extended up adjacent valleys was uncertain, but this is unimportant here as very few prey animals are found far up these valleys.

Both packs spent the majority of the winter in the Bow Valley with occasional trips to adjacent valleys. Ranges were larger in the summer with only occasional visits to the Bow Valley. The Spray pack ranged far to the south of BNP, where there are likely no established pack territories. Wolves are rare in the Bow Valley east of the town of Banff, despite abundant ungulates.

The Spray pack included 8 wolves until late summer, 1989, when pack fragmentation reduced the pack in BNP to 5 in the winter of 1989-90. The Baker pack included 8 or 9 wolves throughout the study.

Methods

Prey numbers and habitat use

Intensive helicopter surveys of elk wintering throughout the Bow Valley of BNP are conducted by the warden service in late winter (Kunelius, 1985b). The portion of the valley in the range of the wolves is surveyed in one day. The results of these surveys correspond well to mark-recapture estimates of the elk population based on 30-50 elk collared with highly visible radio-collars, resighted during systematic late winter ground surveys (Woods, 1991). Roughly 60% of the collared elk are resighted during these surveys. I used the aerial survey results, plus 10 per cent to correct for a suspected small number of missed animals, as the best estimate of numbers of elk available in winter.

All ungulate herds seen during field-work were recorded and these incidental sightings were used to determine average herd size for these species.

Pellet group transects were conducted to assess the relative numbers of elk, deer and moose and their habitat use. 130 1-km transects were conducted in the Bow Valley. Each 100m segment of a transect or each segment in a distinct vegetation type was recorded as a separate sample. The transect samples were stratified by position in the valley (5 areas, proportional allocation of sampling effort (Krebs, 1989)) and by vegetation type within each area (7 types, optimal allocation based on initial estimates of variance and sampling cost in each strata (Krebs, 1989)).

Transects were conducted in April and May, 1990, immediately after the snow had melted. All transects ran north-south, at 45 degrees to the main trend of the valley, and began at stratified random map co-ordinates. All pellet groups with centers within 1m of the transect line were recorded as elk, deer, moose or bighorn sheep. Pellet groups of the two deer species could not be distinguished reliably.

The mean densities of pellet groups of each species were calculated separately for each habitat type in each of the 5 areas. Because subtransects were of variable length, the density was calculated as the mean ratio of the number of pellets to the area of the subtransect (Krebs, 1989), and the appropriate variance of this ratio was calculated. A stratified mean for each habitat type was calculated using the means and variances for that habitat in each of the 5 areas. Overall stratified mean densities of pellet groups were then calculated for each species using the estimates for the 7 vegetation types. The area of each vegetation stratum was determined from biophysical maps of the park (Holland and Coen, 1983).

Defecation rates of ungulates and pellet group persistence times are not known in Banff; to convert pellet group densities to densities of individuals, the ratio of overall number of elk in the study area (based on the aerial survey and mark-recapture results) to

overall density of elk pellet groups was calculated. This ratio was applied to the pellet group densities for different habitats and different areas for both elk and deer to estimate number of each ungulate type in each habitat and area. Values for the more northerly strata were adjusted to compensate for the longer duration of the winter snowpack, and presumed longer persistence of the pellet groups. This procedure assumes that defecation rates and persistence times for the ungulate types in all habitats are similar. Several studies suggest rates of approximately 13 pellet groups/animal/day for elk and deer species in winter (Neff, 1968).

An additional 30 kms of pellet group transects were conducted in areas peripheral to the Bow Valley which are used by the wolves in winter.

To estimate the summer numbers of elk, the seasonal movements of 19 radio-collared elk (Woods, 1991) were used to indicate the proportion of wintering elk in each pack's range that remained through the summer, and the number of elk that migrated into the territories in the summer. Additional elk migrate into the northern part of the study area from the east of BNP (Morgantini and Hudson, 1988) and are included in summer estimates.

Deer summer numbers were estimated roughly based on suspected migration patterns, incidental sightings and information in Holroyd and Van Tighem (1983). Ratios of elk to deer mortalities on the highways are similar to the ratios of elk and deer population estimates by season and pack.

Helicopter surveys of bighorn sheep and mountain goats by the park wardens indicated the numbers and distribution of these species in the ranges of the two packs (Kunelius, 1985a; Bertch, 1988).

Observations during field work and a biophysical inventory of the park (Holroyd and Van Tighem, 1983) were used to estimate numbers and distribution of small mammal prey species.

Habitat use by wolves

Habitat use of wolves during the winter of 1989-90 was determined from telemetry relocations, when the wolves were in BNP. Aerial locations were used, and ground locations which the observer was confident were accurate. Tests of telemetry locations using collars in known locations indicate that ground locations were accurate within 190m, which is considerably less than the average dimension of the broadly-defined habitat blocks. Locations were weighted by half the number of days between the previous and subsequent locations; if locations were two days apart, each represented two wolf-days. The vegetation type at each location was determined from biophysical maps of the park to determine habitat use by the wolves. Habitat use data from 3 collared adults in the Spray pack were similar and were combined.

Wolf diet

Seasonal diets of the two packs were determined from analysis of 652 wolf scats. Scats were collected during snow tracking in the winter, during regular checks of roads and trails, at den and rendezvous sites in summer, and when encountered incidentally. Scats 30mm or larger in diameter or clearly associated with wolf tracks were classified as 'WOLF'; scats between 25 and 30mm not associated with tracks were classified as 'WOLF?' (Weaver and Fritts, 1979). Scats under 25mm were not collected unless associated with wolf tracks. Scats were autoclaved, washed and dried, and the percentages of bone, vegetation and hair types in each scat were estimated visually. Hair was identified to species based on size, colouration and microscopic features (Moore et al., 1974; Kennedy and Carbyn, 1981). Calf hair could be distinguished from adult hair in summer scats only and the two deer species could not be distinguished. The occurrence of elk, deer, moose, bighorn sheep and 'other' prey remains were compared between the two categories of scats ('WOLF' and 'WOLF?') using chi-square.

The distinction between elk and deer hair was sometimes uncertain. To assess repeatability of identification, 25 slides of hairs initially identified as elk and 25 identified as deer were chosen at random and were re-identified without reference to the initial identification. 47 of 50 were identified as the same species as initially. Two hairs initially identified as elk were reidentified as deer, and 1 initial deer as elk. This indicates good repeatability of identification, although an overall bias towards one species may still exist.

Fifty-two kills by the two packs found in winter 1989-90 give a second indication of wolf diet. All kills were examined on the ground. Evidence that an animal was killed by wolves included an obvious chase sequence in the snow or signs of a struggle before death (including broken vegetation, extensive patches of blood or canine slash marks on the animal).

Analysis of scats from known dates during this winter indicated an additional 19 missed kills. A missed kill was assumed when a series of scats contained hair of a species different from the known preceding kill. In most cases, kills were suspected in the area where the scats were collected, based on the movements of the wolves and the presence of scavengers, but could not be located. These missed kills occurred away from the railway and river where wolves occasionally scavenged carcasses.

The proportion of biomass provided by elk, deer and bighorn sheep was calculated from kills found during winter 1989-90 and compared to the estimates of diet from the same period derived from scat analysis. Two methods of converting percent occurrence in scats to biomass consumed were evaluated: 1) the regression of Floyd et al. (1978) extrapolated for prey larger than deer, 2) a direct proportionality of percent occurrence in scats and proportion of biomass, the most common method of interpreting scat data (Corbett, 1989). Method 2 was identical to the Floyd et al. method but the conversion factor for deer was applied to all animals the size of deer or larger. The

proportion of the diet comprised of deer, bighorn sheep and elk indicated by each method of scat analysis was compared to the proportion of each in the kills (including known missed kills) by correlation of arcsine square root transformed values.

Tracking

The tracks of prey species which crossed those of hunting wolves were used as an index of the prey encountered by wolves. Travelling wolves were considered to be hunting when they were known to have recently abandoned a well-used carcass, or when I was backtracking from a fresh kill. Peterson (1977) believes wolves are almost always hunting when they are travelling. The prey encounter rates on hunting tracks were compared to the number of prey tracks crossing 69 north-south transects of 500m randomly located in the Bow Valley bottom in areas used by the hunting wolves.

Habitat overlap

The habitat overlaps of wolves and their prey species were calculated using the percent overlap value (Krebs, 1989), based on the 7 broad habitat types. Bighorn sheep and mountain goats use areas at higher elevations than wolves. For these two species, overlap values with wolves accounted for both habitat and elevational separation.

Selectivity

Manly's (1974) index of selectivity was calculated for ungulate prey species, separately for each pack for summer and winter. The sample size for Manly's method is the number of individual prey items consumed. Scats collected on the same day often contain hair from the same kill and are not independent samples. Therefore the effective sample size of scats was taken as the number of days on which scats were collected. When two prey types occurred in the samples from one day, that day was considered as two samples. This effective sample size is likely to be conservative, which does not

affect the mean selectivity value for a prey type, but does increase the standard error of that value. For selectivity calculations using the scat data, the effective number of scats for each pack in each season was allocated to prey categories in proportion to the individual equivalent (Floyd et al., 1978 method estimate of biomass divided by mean prey weight) of each prey type found in the scats. For example, if a sample of scats collected on 80 days indicated that elk comprised 75% of the individual prey animals eaten, then the sample size for elk was 80 X 0.75 = 60.

Selectivity values were calculated using 3 sets of available prey :

1. Overall numbers in wolf ranges,

2. Overall numbers multiplied by percent habitat overlap (an index the prey as encountered on an individual basis),

3. Values from 2., divided by herd size (the prey encountered on a herd basis).

Results

Prey available

The best estimates of prey numbers and biomass in the ranges of the two packs are presented in Table 2.1. Biomass is highest in the territory of the Spray pack in winter, as this area contains the main wintering grounds of elk. In summer, most of these elk migrate out of this area. The Baker pack has greater biomass in summer than winter, as animals migrate into this area for the summer from the southern Bow Valley and from the Ya Ha Tinda area to the east of BNP (Morgantini and Hudson, 1988).

Table 2.1a. Best estimates of prey abundance in wolf territories - winter.

Type	Spray pack		Baker pack	
	Individuals	Biomass(kg)	Individuals	Biomass(kg)
Elk	258	58453	147	33100
Deer	85	5098	39	2309
Moose	14	3873	8	2485
BHS	145	11237	79	6123
MG	51	3570	30	2100
Subtotal: Ungulate	553	82231	303	46117
Beaver	90	1800	24	480
Porcupine	50	280	250	1400
SSHare	400	600	600	900
Squirrel	10000	1900	20000	380
Voles	50000	2500	80000	4000
Coyotes	75	1125	35	525
Bears	20	1500	30	2250
Subtotal: Non-ungulate	60635	9705	100939	9935
TOTAL	61188	91936	101242	56052

Table 2.1b. Best estimates of prey abundance in wolf territories - summer.

Type	Spray pack		Baker pack	
	Individuals	Biomass(kg)	Individuals	Biomass(kg)
Elk	123	21795	251	44689
Deer	77	3617	85	3982
Moose	12	3462	15	4229
BHS	145	10150	79	5530
MG	51	3570	30	2100
Subtotal: Ungulate	408	42594	460	60530
Beaver	90	1800	24	480
Porcupine	50	280	250	1400
SSHare	400	600	600	900
Squirrel	10000	1900	20000	3800
Voles	50000	2500	80000	4000
Coyotes	50	750	50	750
Bears	20	1500	30	2250
Subtotal: Non-ungulate	60610	9330	100954	13580
TOTAL	61018	51924	101414	74110

Table 2.2. Seasonal diet of wolves from biomass equivalent (kg) of prey remains in scats (Floyd et al., 1978 method). Number of items refers to hair or bone fragments which could be identified to species; some scats contained more than one identifiable prey type, others contained none.

	Spray pack		Baker pack	
	Summer	Winter	Summer	Winter
# OF SCATS	218	206	24	204
# OF ITEMS	231	194	24	194
Elk	448.3 (73.8%)	618.2 (85.0%)	86.9 (79.4%)	638.7 (75.7%)
Deer	37.6 (6.2%)	75.2 (10.3%)	5.0 (4.6%)	51.8 (6.1%)
Bighorn Sheep	6.5 (1.1%)	20.2 (2.8%)	2.2 (2.0%)	13.0 (1.5%)
Moose	49.0 (8.1%)	0.0 (0.0%)	15.2 (13.9%)	136.5 (16.2%)
Moutain Goat	13.0 (2.1%)	1.8 (0.2%)	0.0 (0.0%)	1.8 (0.2%)
Non-ungulate	52.8 (8.7%)	12.3 (1.7%)	0.1 (0.1%)	1.5 (0.2%)
TOTAL	607.2	727.7	109.4	843.3

Wolf diet

No difference was found between the contents (5 common classes of prey) of scats classified as 'WOLF' and scats classified as 'WOLF?' (chi-squared = 6.37, 4 D.F., p=0.17). Both groups were used in subsequent analyses to represent the wolf diet.

The biomass proportions of elk, sheep and deer in the diet calculated following Floyd et al. (1978) were more closely correlated to the kill data from the same time period than were the diet proportions from the percent occurrence method (Floyd et al.: r^2=0.999, n=3 prey species, p=0.02; percent occurrence: r^2=0.938, n=3, p=0.16). Additionally, the slope of the regression for the Floyd et al. method was almost exactly 1 (0.995), while for the percent occurrence method it was 0.751. The strong correlation, with a slope of 1, means that the Floyd et al. (1978) method of converting percent occurrence data from scats is a good indicator of the animals killed by wolves. Uncorrected percent occurrence data do not represent the diet well. The Floyd et al. (1978) method was therefore used for subsequent analyses.

The seasonal diets of the two packs are presented in Table 2.2. The diets are dominated by elk, though all ungulate species within the range of the wolves are used. Non-ungulate prey are only important for the Spray pack in the summer (Fig. 2.2), and include beaver (Castor canadensis), canids (Canis sp.), bears (Ursus sp.) and porcupines (Erithezon dorsatum).

Kills of ungulates could generally be found only in winter, and are summarized in Table 2.3.

Habitat use of wolves and prey species

Habitat use by elk, deer and moose from pellet groups and the percent overlap with wolves are summarized in Table 2.4. Elk and deer in both territories show similar habitat use and overlap highly with wolves, while moose have more specific habitat preferences and a lower overlap. These species occupy the same elevational range as

a.

Available biomass (kg)

80000
40000
0

NON-UNGULATES	NON-UNGULATES	NON-UNGULATES	
OTHER UNGULATES	OTHER UNGULATES	OTHER UNGULATES	NON-UNGULATES
ELK	ELK	ELK	OTHER UNGULATES
			ELK

Spray summer   Baker summer   Spray winter   Baker winter

b.

Proportion of diet by weight

0.8
0.4
0.0

NON-UNGULATES	OTHER UNGULATES	OTHER UNGULATES	OTHER UNGULATES
OTHER UNGULATES			
ELK	ELK	ELK	ELK

Spray summer   Baker summer   Spray winter   Baker winter

Fig. 2.2 a. The total biomass available in the territories of each pack, by season. b. The seasonal diet of each pack based on the biomass equivalent of prey remains in scats (Floyd et al., 1978 method).

Table 2.3. Kills by species found in winter of 1989-90. Numbers in parentheses are total known kills, including kills determined from analysis of scats from known dates (see text for explanation). Biomass is based on total known kills.

	Spray pack		Baker pack	
	Kills	Biomass (kg)	Kills	Biomass (kg)
Elk	24 (29)	6450 (82.5%)	10 (11)	2446 (61.5%)
Deer[*]	7 (12)	742 (9.5%)	2 (7)	433 (10.9%)
Bighorn Sheep	2 (4)	280 (3.6%)	4	340 (8.6%)
Moose	1	343 (4.4%)	1 (2)	685 (17.2%)
Mountain Goat	0	0	1	70 (1.8%)
TOTAL	34 (46)	7815	18 (25)	3974

[*] Known deer kills for the Spray pack included 5 mule deer, 2 white-tailed deer; for the Baker pack, 2 mule deer. Missed deer kills determined through scat analysis could not be identified to species.

Table 2.4. Winter habitat use of elk, deer and moose from pellet group counts, and wolves from winter telemetry locations, and per cent overlap of habitat use with wolves. The number of pellet groups or telemetry locations is given beside the species' name.

Spray territory

| Habitat | Proportion of pellet groups | | | Proportion of locations |
	Elk (1902)	Deer (624)	Moose (63)	Wolf (520)
Pine	0.34	0.46	0.00	0.25
Variable	0.08	0.10	0.09	0.13
Spruce	0.25	0.24	0.87	0.42
Wet	0.10	0.10	0.04	0.10
Dry	0.03	0.01	0.00	0.03
Aspen	0.12	0.05	0.00	0.05
Grass	0.08	0.04	0.00	0.01
Overlap with wolves	77.2%	75.7%	57.3%	

Baker territory

| Habitat | Proportion of pellet groups | | | Proportion of locations |
	Elk (989)	Deer (260)	Moose (54)	Wolf (165)
Pine	0.45	0.48	0.22	0.42
Variable	0.24	0.33	0.62	0.32
Spruce	0.04	0.06	0.00	0.22
Wet	0.12	0.00	0.16	0.04
Dry	0.14	0.12	0.00	0.03
Aspen	0.00	0.00	0.00	0.00
Grass	0.01	0.01	0.00	0.01
Overlap with wolves	77.9%	84.3%	57.3%	

wolves, mainly the valley bottom. Bighorn sheep and mountain goats typically occupy higher elevation areas which wolves rarely visit. These habitat results derive from winter work; comparable information is not available for the summer.

Selectivity of wolves

There is no difference between the encounter rate of elk and deer tracks along hunting tracks of wolves and the encounter rate on random snow transects (Table 2.5) for the intensively studied Spray pack. Local areas where predictable high prey concentrations occurred were excluded from both tracking and random transect results (discussed below). These results indicate that when travelling in their preferred hunting areas, wolves do not generally choose areas of particularly high density of certain prey species, and relative densities of prey types, corrected for habitat overlap, are therefore good indicators of the encounter rates. For the Baker pack, encounter rates (tracks/km) are higher during hunting than on random transects, because this pack often hunted in the south end of their range where prey densities were higher, and both wolves and prey used particular travel corridors such as rivers and ridge tops in the deeper snow. The ratio of elk to deer encounters is similar on hunting tracks and random transects.

The relative abundance of each prey species is presented in Table 2.6 (column 1), based on numbers through the entire home range. In Table 2.6 (column 3), the number of each prey species has been multiplied by the percent overlap of that species with the wolves, and expressed as a proportion of the total of these values. This gives a more accurate index of the relative numbers of each species encountered by the wolves. This index of encounter rate is only calculated for the winter, as no summer habitat use information is available.

The above analysis considers encounters with individual prey animals. However, ungulates, especially wintering elk, typically occur in herds ranging from 2 to over 100 animals (Table 2.7). The area occupied by a herd is small relative to the area between

Table 2.5. Comparison of encounter rates of prey on tracks of hunting wolves and on random transects. Encounter rates are indexed by the number of tracks of prey species crossing the wolf tracks or transect per km-day.

	n	Km-Days	Elk/km-day	Deer/km-day
Spray				
transects	20	25.2	5.41(SE=1.82)	1.43(SE=0.58)
tracking	26	106.7	5.76(SE=0.87)	1.35(SE=0.38)
Baker				
transects	49	60.0	3.17(SE=0.57)	0.81(SE=0.19)
tracking	17	110.4	4.41(SE=1.11)	1.52(SE=0.47)

Encounter rates are higher on hunting tracks of the Baker pack than on random transects (Elk: $t=2.23$, 61 D.F., $p=0.03$; Deer: $t=9.60$, 61D.F., $p<0.001$). There is no difference for the Spray pack.

Table 2.6. Relative abundances of ungulate prey species at the different levels at which selectivity may be calculated. Habitat use and overlap information is presented in Table 2.4; herd sizes are presented in Table 2.7. Explanations of the different levels may be found in text.

	Overall	Habitat overlap	Individual encounter	Herd size	Herd encounter
WINTER					
<u>Spray pack</u>					
Elk	0.47	HIGH	0.69	LARGE	0.38
Deer	0.15	HIGH	0.22	SMALL	0.50
Moose	0.03		0.03	SMALL	0.08
BHS	0.26	LOW	0.05		0.03
MG	0.09	LOW	<0.01		<0.01
<u>Baker pack</u>					
Elk	0.49	HIGH	0.71	LARGE	0.40
Deer	0.13	HIGH	0.20	SMALL	0.48
Moose	0.03		0.03	SMALL	0.08
BHS	0.26	LOW	0.05		0.03
MG	0.10	LOW	<0.01		<0.01
SUMMER					
<u>Spray pack</u>					
Elk	0.30				
Deer	0.19		Habitat use information		
Moose	0.03		not available		
BHS	0.36				
MG	0.13				
<u>Baker pack</u>					
Elk	0.55				
Deer	0.18		Habitat use information		
Moose	0.03		not available		
BHS	0.17				
MG	0.07				

herds and all members of a herd can see and hear most other herd members. This suggests that herds respond to predators as a unit and, therefore, that predators encounter herds as a unit. Haber (1977) also treated caribou and sheep herds as the unit of encounter. Field observations confirm that herds flee together from a threat and are more prone to fleeing when a kill has been made from the herd (Chap. 3). Probably because of this increased wariness, consecutive kills are rarely made from the same herd. The effective encounter rate is, therefore, proportional to the number of herds rather than individuals. Table 2.6 (column 5) presents the relative encounter rates for ungulate species based on the herd as the unit of encounter. These values were calculated by dividing the proportions in column 3 by the mean herd size for that species, and expressing the results as a proportion of the total.

Telemetry and snow-tracking data show that when wolves in Banff are hunting, they typically move quickly, and relatively directly, towards one of a small number of locations where prey herds are predictably found. Wolves tend to remain near these herds and probably test the herds several times before making a kill or leaving the area. Two types of kills result - those resulting from "random" encounters with prey animals while travelling between predictable patches, and those resulting from "intentional" encounters with predictable herds. Large herds of elk closely associated with grasslands or avalanche slopes, and herds of bighorn sheep associated with avalanche slopes represent predictable patches for the Spray and Baker packs, respectively. In contrast to white-tailed deer in eastern North America (Fuller, 1990), deer do not congregate in obvious wintering herds or "yards" in Banff and it is likely that they are only encountered randomly. Some mule deer occur with bighorn sheep on avalanche slopes and may be an exception.

Wolf kills from the winter of 1989-90 were classified as either "random" or "intentional" based on the movement patterns of the wolves preceding the kill (Table 2.8a). Intentional kills were preceded by a fairly direct movement to a predictable prey

Table 2.7. Sizes of herds of ungulates observed in Banff National Park.

	Herd size (SE)	n
Elk	10.3 (1.4)	108
White-tailed deer	2.2 (0.2)	49
Mule deer	3.0 (0.4)	25
Deer combined	2.5 (0.4)	74
Moose	2 - estimate, rarely seen	
Bighorn sheep	8.3 (0.8)	28
Mountain goat	5 - estimate, rarely seen	

Table 2.8 a. Summary of 'random' and 'intentional' kills by wolves in the Spray pack, winter 1989-90.

	Random	Intentional
Elk	12	10
Deer	10	1[*]
Bighorn sheep	2	2

[*]The one deer kill classified as intentional was a mule deer which was part of a mixed herd of mule deer, bighorn sheep and mountain goats, on a mountain col at 2200m.

b. Relative numbers of elk and deer herds, not including predictable herds of elk.

	Individuals	Herd Size	Proportion of 'Random' Herds
Elk	121	6.08	0.365
Deer	85	2.46	0.635

patch and local searching in that area. Random kills occurred between predictable patches and the encounter was typically preceded by fairly direct travel. The distinction is not clear-cut and requires my subjective opinion of predictable patches. Thirty-seven of 46 kills for the Spray pack could be classified and show that elk dominate the intentional kills, while similar numbers of elk and deer occur in random kills. All bighorn sheep kills and the single mountain goat kill by the Baker pack were the result of direct movements to isolated avalanche slopes with herds of these species. Less intensive tracking and the possible influence of a bait station on the movements of the wolves made it difficult to classify most of the kills of the Baker pack. The relative encounter rates for elk and deer herds for the Spray pack travelling between predictable elk herds are presented in Table 2.8b. These were calculated based on the number and mean herd size of deer and elk excluding the predictable herds used to classify the kills in Table 2.8a.

The overall selectivity of wolves is presented by season and pack in Fig. 2.3, based on the proportional abundances of species in Table 2.6 (column 1). A general preference for elk and deer, avoidance of bighorn sheep and mountain goats and variable selectivity for moose are seen.

Calculating selectivity (Fig. 2.4a) based on encounters of individuals by correcting for different habitat overlaps (Table 2.6, column 3) shows no evidence of strong selectivity or avoidance for any ungulate species. The initial appearance of preference for elk and deer over bighorn sheep and mountain goats is based on higher encounter rates for the first two species, and not on any inherent preferences for any other species.

The selectivity values for the ungulate species based on relative numbers of herds encountered are presented in Fig. 2.4b. Because elk occur in larger herds, they are encountered proportionally less often than deer and the same proportion in the diet indicates a greater selectivity upon encounter. The increased selectivity for elk may be
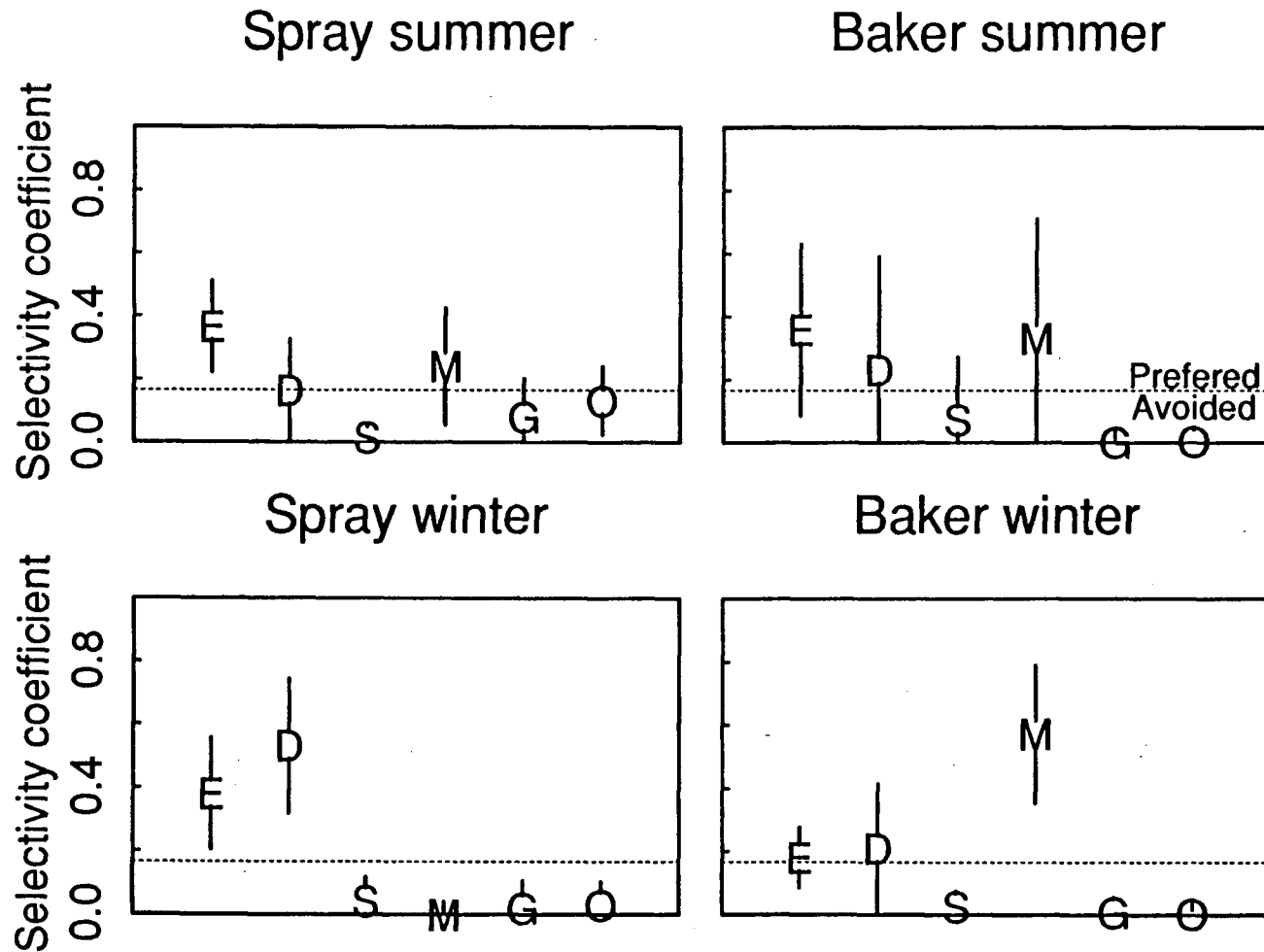
Fig. 2.3. The overall selectivity (Manly's index) of wolves for prey types by pack and season, not corrected for different encounter rates due to habitat overlap or effects of herd size. Values above the dotted line indicate preference; values below indicate avoidance of the prey type. Error bars represent 95% confidence intervals. E=elk, D=deer, S=bighorn sheep, M=moose, G=mountain goat, O=other (non-ungulate).
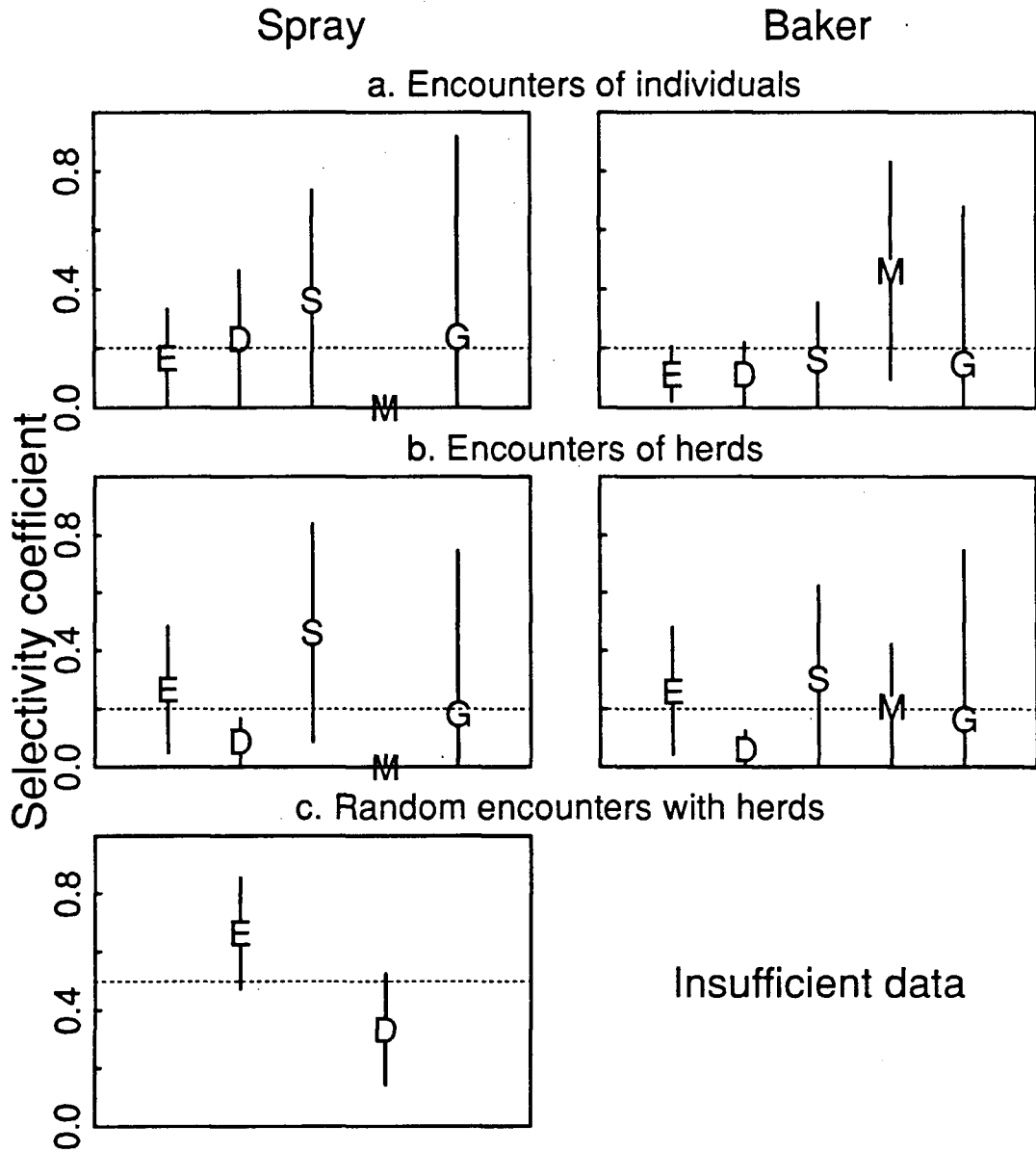
Fig. 2.4. Selectivity of the two packs in winter, accounting for the different habitat overlap of the species with wolves (a.), the different herd sizes of the prey types (b.), and the effect of elk herds predictably associated with certain areas. See text for full explanation. Values above the dotted line indicate preference; values below indicate avoidance of the prey type. Error bars represent 95% confidence intervals. E=elk, D=deer, S=bighorn sheep, M=moose, G=mountain goat.

partially due to some elk occurring in predictable herds, and therefore being killed both "randomly" and "intentionally", while deer are only killed "randomly", when wolves are travelling between predictable elk herds. However, when selectivity is calculated based on the relative numbers of deer and elk encountered randomly between predictable elk herds (Table 2.8b), a significant selectivity for elk is still apparent (Fig. 2.4c).

Discussion

The importance of non-ungulate prey to wolves

The simple prey selection model of foraging theory predicts that diet diversity will decrease as available biomass increases (Stephens and Krebs, 1986), as less profitable prey are dropped from the diet. In BNP, non-ungulate prey are the only types that are included in the diet when prey are scarce (Spray summer), but are dropped almost entirely when prey are more abundant. This pattern occurred in both summers for which scats are available for the Spray pack, and suggests that non-ungulates are less profitable prey. However, this conclusion is confounded by increased availability of most non-ungulate species in the summer. Wolves also change to central-place foraging (Orians and Pearson, 1979) in the summer, with hunting forays centered around the densite.

Several studies have reported high percent occurrence of non-ungulate prey in the diet of wolves (e.g. Pimlott et al., 1969; Peterson, 1977). However, one occurrence of moose in scats represents almost 10 times as much biomass as one occurrence of beaver (from Floyd et al., 1978), and one deer occurrence 3 times as much. The biomass of non-ungulates eaten is therefore much less in these studies than the raw data on percent occurrence indicate. In general, non-ungulate prey typically provide only a small percentage of the biomass in wolves' diets (Ballard et al., 1981; Fritts and Mech, 1981; Peterson et al., 1984; Ballard et al., 1987), except in 3 circumstances:

1. Ungulate prey have declined (Voigt et al., 1976; Mech and Karns, 1977), are relatively uncommon (Ballard et al., 1981; "area M" of Messier and Crete, 1985) or seasonally scarce (Bibikov, 1979; this study).

2. Non-ungulates occur in abundance near the densite (Theberge and Cottrell, 1975; Theberge et al., 1978)).

3. Non-ungulates are very abundant and ungulate prey (moose) are difficult to catch (Shelton and Peterson, 1983).

Circumstance 1 suggests non-ungulates are a lower ranked prey than ungulates (prey model (Stephens and Krebs, 1986)). However, Boutin and Cluff (1989) point out that diet proportions from scat analysis may show the same qualitative changes with changing prey density, whether one prey type is preferred or not. Peterson's (1977) observations that wolves do not spend much time intentionally hunting or stalking beaver, and do not chase snowshoe hares they have flushed support the view that non-ungulates are a less preferred prey type. Circumstance 2 indicates that non-ungulates provide a smaller energetic return than ungulates. Central place foraging models predict low-energy prey types (non-ungulates) will only be pursued if they are found near the central place (den) (Stephens and Krebs, 1986). In contrast, circumstance 3 suggests that non-ungulates, primarily beaver, may be more desirable than moose in some circumstances, due in part to the danger of capturing moose. This is particularly true when wolves are hunting alone or in small groups to provision pups in the summer.

Peterson (1977) reports that high beaver populations may have helped one pack's growth when moose were rare, but Ballard et al. (1981) found that 3 packs forced to rely on small mammals suffered greater nutritional deficiencies than other packs. Though they may provide a buffer food source, non-ungulates are unlikely to play a major role in wolf-prey dynamics in BNP, where ungulates are abundant, and beaver, the main non-ungulate prey, are uncommon and located far from the wolves' dens.

The preference of wolves for different ungulate species

Determining which ungulate species are preferred in complex prey systems is less clear. Comparing the proportion in the diet to the proportion in the overall range of the wolves, Cowan (1947) and Carbyn (1974) concluded that mule deer and elk were preferred over other ungulate species and deer were preferred over elk in Jasper National Park. In Riding Mountain National Park, Manitoba, Carbyn (1983a) also concluded that mule deer were the "optimal" prey species, followed by elk and moose. However, in the current study elk and deer were selected equally on a per individual basis and elk were apparently preferred on a per encounter (herd) basis (Fig. 2.4). Deciding that a species is inherently optimal or preferred based on a comparison of consumption and availability may be misleading, because this implies that if all prey types become more abundant, the optimal type will sustain a greater proportion of the predation while other types will become less important in the diet (a prediction of foraging theory (Stephens and Krebs, 1986)). I will show below that this is unlikely to be the case.

Profitability of ungulate prey types

Using the common currency of foraging theory, the ratio of net energy gain to handling time (e/h), we can show that no ungulates should be greatly preferred over any other. Handling time of wolves feeding on ungulates can be considered in 4 components: chase time, time to kill the animal once caught, time to eat the meat and time to digest. Observed chases of elk, deer and sheep in winter in Banff were short (5-1000m, with 28 of 31 discernable chases less than 300m) and there was little evidence of prolonged struggle. Cowan (1947) and Carbyn (1974), working in the same area, also observed short chases and quick kills. The complex topography in the mountains allows either a quick kill by wolves or a quick escape by prey (Cowan, 1947; Bibikov, 1979). Therefore, the first two components of handling time are small, usually well under 20 minutes.

Prey the size of deer or larger represent at least one full meal (about 8 kg, Mech, 1970) for each wolf in a pack. The time to consume a full meal and the time to digest it are similar for different ungulate prey types, roughly 6-10 hours, and are much longer than the chase and kill components of handling time. Because wolves do not hunt or consume more food while they are digesting, digestion time is an additive component of handling time (e.g. Temeles, 1989), unlike some foragers in which digestion and foraging are simultaneous constraints (e.g. ungulates; Belovsky, 1978).

The energy or protein gained from one meal is fairly constant, at least in the initial stages of carcass use (i.e. meat from any species is of the same quality). Large prey such as elk provide several meals, while deer may provide only one; however, because both energy gained (e) and digestion time, the main component of handling time (h), are proportional to the number of meals, the ratio of e/h will differ little between ungulate species. From the perspective of energetic profitability, all ungulate species are equal, all (or none) should be attacked or tested upon encounter (1/0 rule, Stephens and Krebs, 1986) and no ungulate species is inherently preferred or "optimal".

Risk of injury and probability of successful capture

The decision whether to attack an animal or not may be mediated by the risk of injury to wolves posed by the prey animal. With similar e/h ratios, predators may make foraging decisions based on the ratio of energy gain to injury risk, minimizing the long-term chance of serious injury from prey. Comparable quantitative data are not available on injury risk to wolves from different prey types, though even deer are known to have killed wolves (Nelson and Mech, 1985). However, known prey defensive behaviour suggests that moose are the only species in the BNP system which pose a substantial danger. Moose often defend themselves against wolves using foreleg kicks. Elk rarely defend themselves actively (Carbyn, 1974), but frequently seek refuge in deep water, while sheep and goats escape onto difficult terrain. Neither defense is a risk to wolves.

Therefore, with the possible exception of moose, risk of injury should not influence attack decisions by wolves in BNP.

The probability of success upon attack will affect observed selectivity if success rates differ for different prey types (Nishimura and Abe, 1988). Success rates are low for moose (Haber, 1977; Peterson 1977), and higher for smaller species (Kolenosky, 1972; Haber, 1977). When chase times are short compared to search times, wolves should still attack species with low success probabilities. The small time and effort lost in an unsuccessful chase is negligible, even if multiplied by several unsuccessful chases, compared to the expected time until the next encounter of another species. Success probability therefore determines what proportion of the attacked prey becomes part of the diet, but should not influence whether an animal is attacked upon encounter.

Selectivity based on encounters of herds

The above discussion suggests that all ungulates should be tested by wolves upon encounter. This is consistent with the observed lack of selectivity calculated on a per encounter basis (Fig. 2.4a) Anomalous values for moose are likely the result of very small sample size as moose are rare in both the prey base and the diet in Banff.

However, when selectivity is calculated on the basis of encounter rates with herds of prey, which is more realistic biologically, deer are underrepresented in the diet (Fig. 2.4b). This is partially due to some elk being associated with predictable herds, but the selectivity for elk persists when predictable elk herds and kills associated with them are not included and selectivity is calculated based on the remaining, randomly encountered elk and deer, and random kills (Fig. 2.4c).

This apparent selectivity may be an artefact of the difficulty of finding deer carcasses. Of the missed kills identified through scat analysis, 10 were deer, while only 6 were elk, despite the majority of known kills being elk. Scat analysis would not have identified all missed kills, producing a bias against deer in the diet data.

Several factors could generate a real selectivity for elk. Elk may be more detectable than deer, being larger, in large herds and more often in open areas. Deer are often captured after being flushed by wolves, which may travel beside each other in deer habitat (Stenlund, 1955; Kolenosky, 1972; Carbyn, 1974), suggesting deer are not easily detected at a distance by wolves. Wolves in BNP rarely exhibit this deer-flushing behaviour and may therefore be less adept at detecting deer than elk.

Wolves may also be more persistent in their attacks when they encounter a large herd of elk, which would mitigate the effect of herding on lowering encounter rates. Haber (1977) records wolves individually testing every moose in a small herd. However, moose do not always flee from wolves as elk do, and the opportunity to test more than one elk per herd likely does not occur. Wolves may be more successful when they encounter a larger herd of elk, because larger herds are more likely to contain a weak or vulnerable animal (discussed in next chapter).

A model of wolf-prey encounters and functional responses of wolves

If probability of capture success is assumed to change little with prey density and there are no inherent preferences for certain prey species, then changes in encounter rates of prey with changes in density are the most important influence on wolf diet. The three main prey types in BNP, deer, elk and bighorn sheep, are probably encountered by wolves in different ways. A simple model of wolf foraging was therefore developed to examine how changes in densities of these prey could affect wolf diet, without any "optimal" foraging decisions, preference or switching (Murdoch, 1969) by the predator.

In BNP and in the model, part of the elk population occurs in herds which are predictably associated with good habitat patches, while the rest are encountered randomly. Wolves travel from one predictable herd to another and hunt intensively in these areas. However, they also hunt while travelling and will attack animals encountered randomly during this time. Deer are only encountered randomly, during

travel periods. Search time is therefore a function of the density of animals between predictable herds, but has a maximum limit - the time wolves require to travel between two predictable herds - which is a function of the number of predictable herds. Because elk are encountered as herds, changes in herd composition could mediate effects of changes in density. If herd size increases with density, the number of herds of elk and the encounter rate by wolves will not increase as rapidly as the elk density (c.f. Taylor, 1981). However, increases in herd sizes could result in more large, predictable herds towards which wolves could direct their searches, resulting in an increased proportion of elk in the diet.

Bighorn sheep (and mountain goats to a lesser degree) are encountered by wolves under two circumstances: 1. The ungulates are using low elevation ranges near the usual valley bottom ranges of the wolves, or are visiting valley bottom salt licks (summer); or, 2. The ungulates are predictably associated with small areas such as avalanche slopes and the wolves make intentional excursions to these areas. In BNP, the Spray pack encounters sheep and goats under the first circumstance, while the Baker pack encounters them primarily on specific trips to avalanche slopes. With increasing bighorn sheep or goat densities, inclusion in the wolf diet would increase more than proportionally, as: 1. Sheep are forced (by intraspecific competition) into less preferred habitat nearer to valley bottoms, where random encounters with wolves are more likely; and, 2. Numbers in predictable herds on avalanche slopes are enough to merit more frequent intentional trips by wolves.

When numbers of each of the three species in the model are varied singly, wolves are predicted to have different functional responses for each. With deer, which are encountered randomly, a standard type II functional response (Holling, 1959a) is predicted (Fig. 2.5c). (The quantitative results of the model are approximations based on estimates of several parameters and simplifying assumptions. The qualitative differences are the important point.)
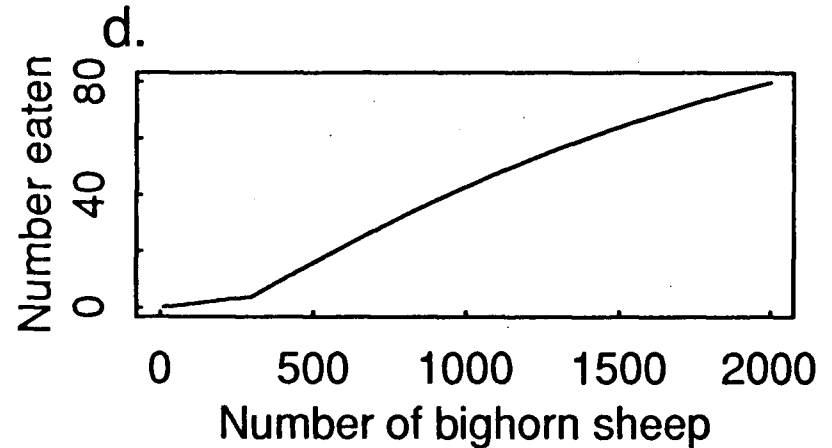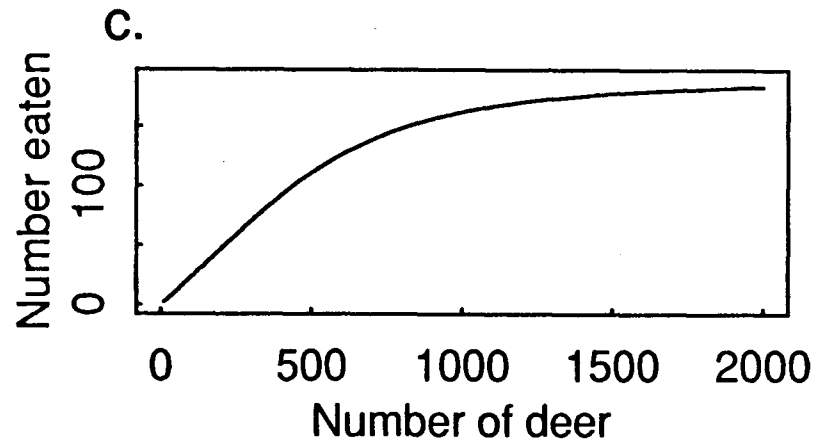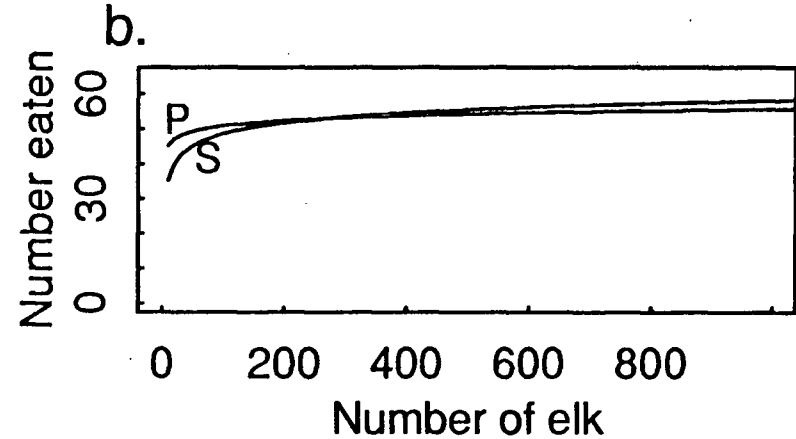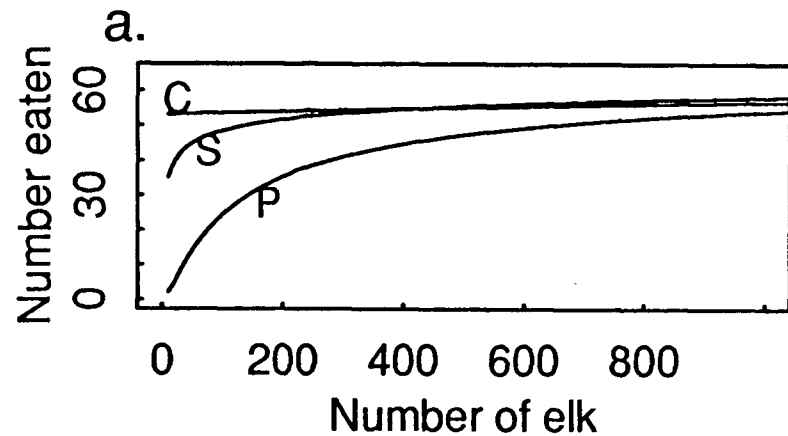
Fig. 2.5. Functional responses predicted by a simple model of encounters with three prey types. In a., curve C is based on the assumption of a constant number of predictable elk herds; S is based on numbers of predictable elk herds increasing with the square root of elk numbers; and P is based on the number of predictable herds increasing in proportion to elk numbers. In b., curve P is generated when the size of random herds is proportional to elk numbers; S is generated when the size of random herds increases as the square root of elk numbers. The details of the model are outlined in the text.

For elk, which are encountered both randomly and intentionally in predictable herds, wolves show a functional response which rises towards an asymptote very quickly (Figs. 2.5a and 2.5b), particularly if herd size increases with density. Predation rates remain high as numbers decline, because the predictable herds, though fewer and further apart, can still be encountered relatively quickly and the total number of herds which can be encountered does not decline as quickly as elk numbers. This is equivalent to the predator having an increased effectiveness of search at low densities. Such a sharply-curved functional response is more likely to create an unstable predator-prey system in which elk numbers could vary widely and predation would have little regulatory effect (Taylor, 1984). The 'sharpness' of the functional response curve and the associated instability of the predator-prey system increase the more directly herd **size** is proportional to elk numbers (i.e. the more constant the number of herds).

Bighorn sheep in the model use suboptimal habitats, where wolves hunt, only at high densities. This is equivalent to using a refuge at low densities (McMurtrie, 1978). The same effect would occur if wolves started using high elevation habitats when sheep reached a high density. The result is a functional response which is shaped like a type III curve (Holling, 1959a) (Fig. 2.5d). This type of functional response is more likely to generate a stable predator-prey system in which predators can regulate prey numbers, except at very high prey densities (Taylor, 1984).

These responses, which generate different predicted stability properties in the predator-prey systems, differ only because the predator is encountering the prey types in different ways. The predators in the model have no inherent preferences for any species, nor is the search constant (a; Holling, 1959b) or probability of successful capture different for any species, and predators do not switch prey types with changing density. These could all add complexity to the predicted responses, as could variable or optimal allocation of foraging effort (Abrams, 1982), or variable carcass use. Hunting effort and carcass use are both known to change with changing prey availability (Mech et al., 1971).
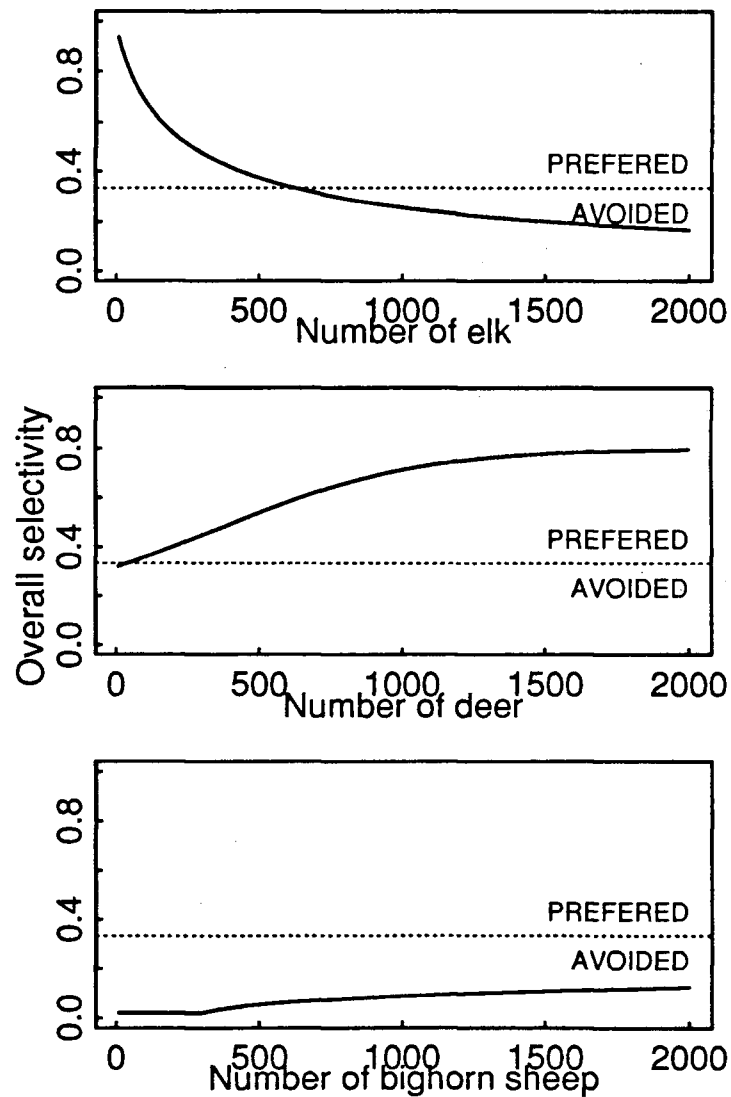
Fig. 2.6. Changes in the overall selectivity for different prey types
as their numbers change in the simple model of wolf-prey encounters,
demonstrating that selectivity can occur without preference, and can
change with relative abundances of prey types.

This deliberately simple model ignores these to demonstrate the importance of how the predator encounters its prey and how this changes with prey density.

The model secondarily illustrates how designating a species "optimal" or "preferred" based on observed selectivity can be misleading. No species is optimal or preferred in the model, yet under most combinations of prey numbers, one species appears to be selected for and others avoided (Fig. 2.6). Furthermore, a species can change from being selected to being avoided, or vice versa, as its abundance changes (Fig. 2.6). Understanding how and where in the system selectivity is generated is critical to interpreting selectivity and predicting diets under different prey conditions.

Chapter 3. Selective predation by wolves on elk in Banff National Park

Introduction

Most studies of wolf (Canis lupus) predation have found that the animals killed by wolves are not a random sample of the available prey population with respect to age, sex and body condition. However, the selectivity shown by wolves differs in different areas and with different prey types, as a result of inherent vulnerabilities of prey types, environmental conditions such as snow depth (Mech and Frenzel, 1971; Peterson, 1977; Carbyn, 1983a; Fuller, 1991) or the spatial distribution of prey (Kolenosky, 1972). Selectivity for prey types within the principal prey species influences how wolves affect the population dynamics of their prey (Mech, 1970; Mech and Karns, 1977; Peterson, 1977).

Wolf predation on moose (Alces alces) and white-tailed deer (Odocoileus virginianus) is well documented in North America. In contrast, few studies have examined wolf predation on elk (Cervus elaphus) (Carbyn, 1983a). Cowan (1947) first studied wolf-elk interactions in Jasper National Park, Alberta and to a lesser extent in Banff National Park. Elk were the main prey, with some selectivity demonstrated by wolves for calves and "senile" animals, though substantial quantitative data were not presented and no comparison was made with the live population. Carbyn (1974) studied a pack of wolves in Jasper and found no clear evidence of selection for young or old animals with a small sample of elk kills. Cowan (1947) and Carbyn (1974) studied the wolves primarily away from the wintering grounds of the elk where the wolves were dependent on mule deer and other ungulates. Carbyn (1983a) reported a more intensive study of wolf predation on elk, in Riding Mountain National Park, Manitoba, and found strong selectivity for calves and old adults compared to hunter kills on the park edge. The fat content of femurs in kills was extremely high suggesting the prey were in good

condition. Carbyn (1983a) also noted seasonal changes in selectivity from calves in early winter to cows in late winter, probably related to snow depth. Elk are a minor component of wolf diets in northern Alberta (Bjorge and Gunson, 1989) and Vancouver Island (Scott and Shackleton, 1980) and no substantial data are available on selectivity in these areas.

Studies of predation on elk provide insights into selectivity by wolves because elk are one of the most sexually dimorphic prey species in size, social groupings, longevity and reproductive effort (Clutton-Brock et al., 1982). Elk are intermediate in size between white-tailed deer and moose and probably intermediate in difficulty of capture (Mech, 1970; Carbyn, 1974). Additionally, elk occur in herds which are intermediate between the small family units of moose and the large aggregations of wintering deer (Nelson and Mech, 1981; Fuller, 1990) or herds of caribou (e.g. Stephenson and James, 1979). Sexual dimorphism, difficulty of capture and social grouping may all affect selectivity of predators.

In Banff National Park, Alberta, elk are the most abundant ungulate in a diverse prey base, and contribute over 80% of the biomass consumed by wolves. In this paper, I describe wolf predation on elk in this system, and examine the mechanisms causing selectivity for age, sex and body condition.

Study area

The study area is described in chapter 2, and in more detail in Coen and Holland (1982). The elk population is described fully in Woods (1991).

Methods

Kills

Elk that had been killed by wolves were located in the winter during helicopter radio-telemetry surveys, while tracking wolves in the snow or by investigating areas

which had recently been used intensively by wolves. All kills were examined on the ground. Evidence that an animal was killed by wolves included an obvious chase sequence in the snow or evidence of a struggle before death (including damaged vegetation, extensive blood on the snow or canine slash marks on the animal; Haber, 1977). Few kills were found during the summer and these were not included in this analysis.

Composition of the elk population

Semiannual classified counts of elk in the main Bow Valley study area indicated the ratios of calves, yearling males, adult males 2 years or older, and adult females 1 year or older (Woods, 1991). Counts were conducted along the extensive road network in the valley which allowed a close approach to the elk for age and sex classification. Approximately 60% of the elk population was classified in each count (Woods, 1991), as determined by resightings of a known number of collared elk.

The sizes of elk herds and their composition by sex and age class (calf, adult female, adult male) were determined from all herds seen incidentally during field work in winter. Each recognizable herd was recorded only once per day. Herds of mixed age class or sex composition were counted as one herd and were allocated to each sex and age class in proportion to the numbers of individuals in the herd. For example, a herd of 6 cows and 4 calves would have been counted as 0.6 cow herds and 0.4 calf herds. The mean herd size for each class was calculated using the number of animals of that class in the herd (i.e. 6 cows and 4 calves in the above example). The rationale for this is to test a null model of no selectivity by wolves upon encounter with a herd (discussed below under "Selectivity for age and sex class"). Incidental sightings may be biased if one class is more visible than the others. To test for this, I compared the total number of elk in each class in the incidental sightings to the expected number based on the population composition from the systematic classified counts.

Population age structure and body condition

Elk killed along roads and the railway in the park were used to indicate the age structure and condition of the elk population. Compared to results of classified counts, a disproportionate number of calves and yearling male elk are killed on the roads and railway, but the sample is considered representative of body condition of each age class in the population and the age structure of the adult (2 years or older) population (Woods, 1991). I will argue below that this sample may only represent the part of the elk population living near the road and railway.

Ages of elk were determined by tooth eruption and replacement for animals 2 years of age or younger (Taber, 1971) and by cementum analysis for older animals (Fancy, 1980). Lower jaw length, measured from the posterior edge of the lower canine socket to the posterior point of the jaw angulus, was used as an index of body size. Antler weight, total beam length and length of brow tine were measured for all bulls with antlers out of velvet. Left-right asymmetry was calculated for each of these measurements, using the formula $|R-L|/((R+L)/2)$, where R and L refer to the measurements for the right and left antlers (Palmer and Strobeck, 1986).

Percent fat content of the femur marrow was measured following the method of Verme and Holland (1973). For some kills collected earlier in the study, the appearance of the femur marrow was only described qualitatively. Quantitative and qualitative estimates of fat content were combined by classifying marrow fat into 4 groups :

1. Good. Fat content over 75%, or descriptions such as "white", "solid", "hard" or "light pink".

2. Fair. Fat content between 50% and 75% or descriptions such as "soft pink" or "some red".

3. Poor. Fat content between 25% and 50% or descriptions such as "pink jelly" or "very soft red".

4. Near starvation. Fat content less than 25% or descriptions such as "red liquid" or "bloody".

Categories 1 and 2 correspond to Peterson's (1977) categories 1 and 2, while 3 and 4 are a finer resolution of his category 3.

Wariness of herds and resource depression

Researchers in Banff National Park have observed that elk in proximity to wolves appear to be more wary, vigilant or 'flighty' (Woods, pers. comm.; Kunelius, pers. comm.). To quantify this effect, I approached herds of elk at a rapid walk near recent wolf kills or in areas where wolves had been hunting. I recorded the distance from me to the nearest herd member when the elk first noticed me, when they began to move away and when they turned and fled. In many cases, the elk had noticed me before I had seen them and I could not take the first measurement. For each herd which I tested in this way, I found a herd of similar size and composition and in similar habitat, but in an area with no known recent wolf activity, and repeated the procedure. This provided paired samples of an index of the wariness of elk with and without wolves nearby.

Habitat overlap of elk and wolves

Telemetry locations of radio-collared elk and wolves were assigned to one of seven broad habitat types based on ecosite classification maps of the park (Holland and Coen, 1982). Aerial relocations and ground locations considered accurate by the observer were used. In 83 relocations of fixed collars, using the same ground techniques and comparable effort, the mean Euclidean error distance (Saltz and White, 1990) was 190m, considerably less than the dimensions of the broad habitat units. No calves were collared in the study area and habitat use by calves and cows was assumed to be the same. Habitat overlap of wolves with the classes of elk was assessed with the percent overlap measure (Krebs, 1989).

Selectivity for age and sex classes

Manly's (1974) index of selectivity was calculated for calf, adult male and adult female elk, based on the number of kills found of each class and the proportions in the population estimated from classified counts. This overall selectivity value includes two broad components - the probability of encounter of a prey class and the probability of kill upon encounter. The proportions of each elk class in the population were multiplied by their percent overlap with wolves to provide an index of the encounter rate of wolves with each elk class. Selectivity upon encounter was calculated using these values as an index of available prey. For example, if prey types A and B were equally abundant, but A had 50% overlap with wolves and B 100% overlap, B would be encountered twice as often as A. Equal numbers of kills of A and B would then indicate strong selectivity for A upon encounter. Selectivity values were also calculated using herds as the unit of available prey. The number of herds of each class seen incidentally was used as an index of the relative abundance of herds. As with the number of individuals, the numbers of herds were also multiplied by percent overlap of habitat use to indicate relative numbers of herds of each class encountered by wolves.

Selectivity for age and body condition

The age and body condition measurements of wolf kills were determined as for the road and rail kills above, when possible. Ages of adult elk killed by wolves and road and rail kills were compared using chi-square. Ages of males were combined into 4 categories: yearlings, 2-5 years (young), 6-8 years (prime rutting age), 9 or over (old); those of females were combined into 3 classes: 1-5 years, 6-10 years and 11 or older. The proportion of the population in each age class was determined from ages of road- and rail-kills, except for yearling males, the proportion of which was estimated directly from classified counts.

The length of the jaw of elk increases until 4 years of age, when full adult size is attained. Ages of kills under 4 years were calculated to the nearest month, based on a standard birth date of May 1. For example, a 1 year old animal killed in October would be 1 year + 5 months = 17 months old. For the population, three month running averages of log-transformed jaw lengths were calculated. Then for each wolf kill, the difference between the running average population value at the appropriate monthly age and the log-transformed length of the jaw of the wolf kill was calculated. These differences, positive or negative, were summed for all the wolf kills. If there was no difference between wolf kills and the population, some jaws of wolf kills would be longer than the population mean, some would be shorter, but the expected sum of the differences would be 0. To calculate confidence intervals on the observed difference, 1000 bias-adjusted bootstrapped estimates of this value were calculated (following Krebs, 1989). Both the jaw lengths of wolf kills and those of the population were subjected to resampling for these estimates. This test was performed separately for all kills under 4 years of age and for calves only. For elk over 4 years killed by wolves, jaw lengths were compared to the population jaw lengths directly, using the T-test. Males and females were compared separately.

A similar technique was used to compare antler weight, total length and brow tyne length of wolf kills and the population. Since antler size increases with age, mean antler values in the population were calculated for each yearly age, and the difference between antler values for each wolf kill and the population mean at that age was calculated and summed. Confidence intervals were established on the total difference using 1000 bootstrapped estimates, in which both the population values and the wolf kill values were resampled. Antler asymmetry did not show any trends with age, after the first year. Antler asymmetry values for wolf kills and for the population 2 years of age or older were compared directly using the Mann-Whitney U-test.

Body condition as indicated by femur marrow fat tends to decline through the winter, and most kills were found in later winter. A direct comparison of road/rail kills with wolf kills would therefore indicate lower fat levels in wolf kills, because of the different seasonal distributions of the samples. To avoid this bias (c.f. Ballard et al., 1981), femur fat classes of wolf kills and the population were compared on a monthly basis. The mean fat class of the population was calculated for each month. The difference between the fat class of each wolf kill and the population for the appropriate month was calculated and summed for all wolf kills. Again, confidence intervals on this estimate were established using 1000 bootstrapped estimates in which both the population values and kills were subjected to resampling. The analysis was done separately for calves, adult males and adult females.

Results

Population composition and herds

The results of classified counts of elk are presented by Woods (1991), and are summarized in Table 3.1. The ratios of calves to cows and bulls to cows decline from autumn through spring, and an average value is used. The number of herds seen incidentally during field work and the average size are included in Table 3.1. The number of elk of each class seen incidentally did not differ significantly from the expected numbers based on the classified count results (chi-square=2.07, 2 D.F., p=0.36). This indicates that there is no sightability bias for a particular class of elk, and the incidental herd observations are a good index of relative herd numbers.

The responses of bull and cow/calf herds to my approach are summarized in Fig. 3.1. The results show a significantly greater (t=3.33, 1 D.F., p=0.005) flight threshold distance when wolves have been in the area or have made a kill. The same pattern occurred with the distance at which herds first began to move. This increased wariness

Table 3.1. The composition of the elk population, the relative numbers of herds of each class and their average size. Composition data are summarized from Woods (1991). Calculation of number of herds and herd size are explained in text.

Sex/age class	Number per 100 cows	Proportion	Herds # seen	Size
Males 2+	20	0.12		
Males 1	8	0.05		
Males 1+	28	0.17	49.2	4.5
Females 1+	100	0.65	48.7	16.6
All calves	30	0.18	9.6	7.9

N.B. Elk which could not be classified during incidental sightings comprised 1.5 herd equivalents.
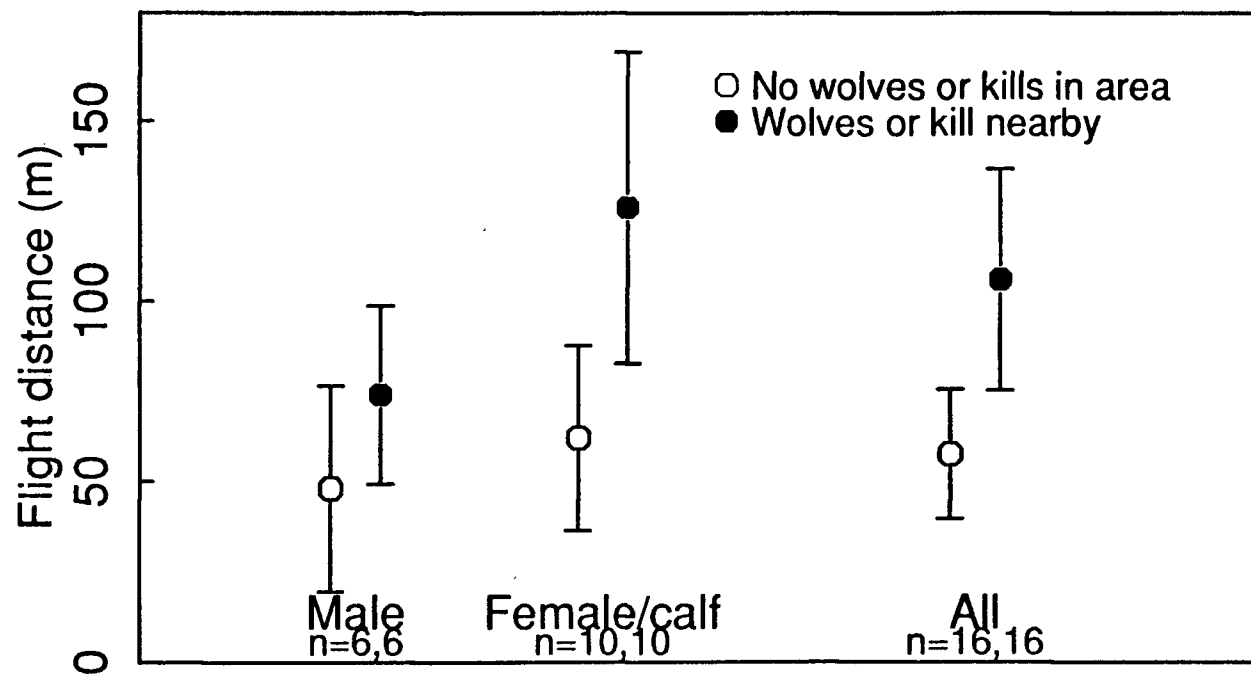
Fig. 3.1. The distances at which herds of elk flee from an approaching human with or without wolves in the area. Error bars are 95% confidence intervals.

or willingness to flee may make it difficult for wolves to make two successive kills from a herd. Consecutive kills are rarely if ever made from the same herd, though uncertainty about herd movements makes this pattern difficult to quantify.

Female elk had a higher habitat overlap with wolves than males (Table 3.2). Strong segregation by elevation did not occur, though outside the study area, some male elk are found at high elevation ranges during the winter (Cowan, 1950; Woods, 1991).

Selectivity for elk classes

Elk kills found during this study are summarized in Table 3.3. The resulting selectivity values based on the overall proportion of individuals of each class are shown in Fig. 3.2a. On an individual basis, adult male elk and calves are slightly, but significantly selected for while adult females are strongly avoided. Because males show less habitat overlap with wolves, they are encountered proportionately less and the observed kills, therefore, represent a slightly higher selectivity for males upon encounter (Fig. 3.2b). On a herd basis, however, both adult classes are avoided and calves are strongly preferred (Fig. 3.2c). There are fewer males than females in the population, but because females are in larger herds, there are almost equal numbers of male and female herds. Calves occur in far fewer herd equivalents, because they make up a small proportion of the cow/calf herds in which they are found. The result is fewer expected encounters with herds containing calves, and the number of calf kills represents a strong selectivity for calves upon encounter with herds.

Selectivity for age and body condition

The age distribution of adult elk killed by wolves differs significantly from the age distribution of the road and rail kills for both males (chi-square = 14.4, 3 D.F., p < 0.005) and females (chi-square = 18.8, 2 D.F., p < 0.001). For both sexes, old animals are overrepresented and young adults are underrepresented in kills (Fig. 3.3).

Table 3.2. Habitat use by collared elk in the Bow Valley, Spray pack territory, and habitat overlap with wolves.

Habitat type	Proportional use of habitat by:		
	Male elk	Female elk	Wolves
Pine	.49	.33	.25
Heterogeneous	.18	.15	.13
Spruce	.21	.36	.42
Wet meadows	.07	.10	.10
Dry woods	.01	.02	.03
Aspen	.04	.04	.05
Grassland	.00	.00	.01
Overlap with wolves	70.3%	88.8%	

Table 3.3. Summary of elk kills found in Banff National Park, Sept. 1985 - May, 1990.

Spray pack

	Adult		Yearling			Calf			Total
	M	F	M	F	U	M	F	U	
85-86	3	4	1				1	3	12
86-87	4						1	2	7
87-88	9	1					1	7	18
88-89	2	4	3		1		1	4	15
89-90	4	5			1	6	4	4	24
Total	22	14	4		2	6	8	20	76

Baker pack

	Adult		Yearling			Calf			Total
	M	F	M	F	U	M	F	U	
86-87	1	1	2						4
87-88	2	1						2	5
89-90	2	3	1					4	10
Total	5	5	3					6	19

Combined

	Adult		Yearling			Calf			Total
	M	F	M	F	U	M	F	U	
Total	27	19	7		2	6	8	26	95
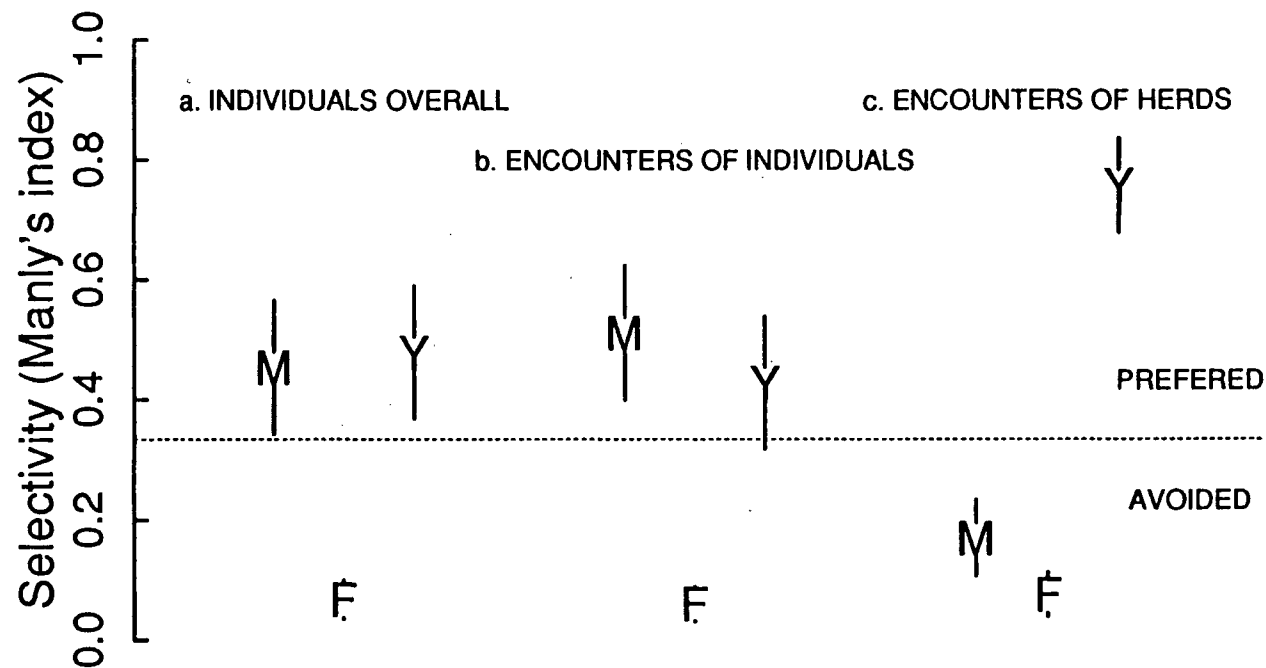
Fig. 3.2. Selectivity for elk classes by wolves, based on overall numbers of individuals (a.), numbers of individuals corrected for habitat overlap (b.), and numbers of herds,also corrected for habitat overlap (c.). M=adult male, F=adult female, Y=young of year (calf). Error bars are 95% confidence intervals.
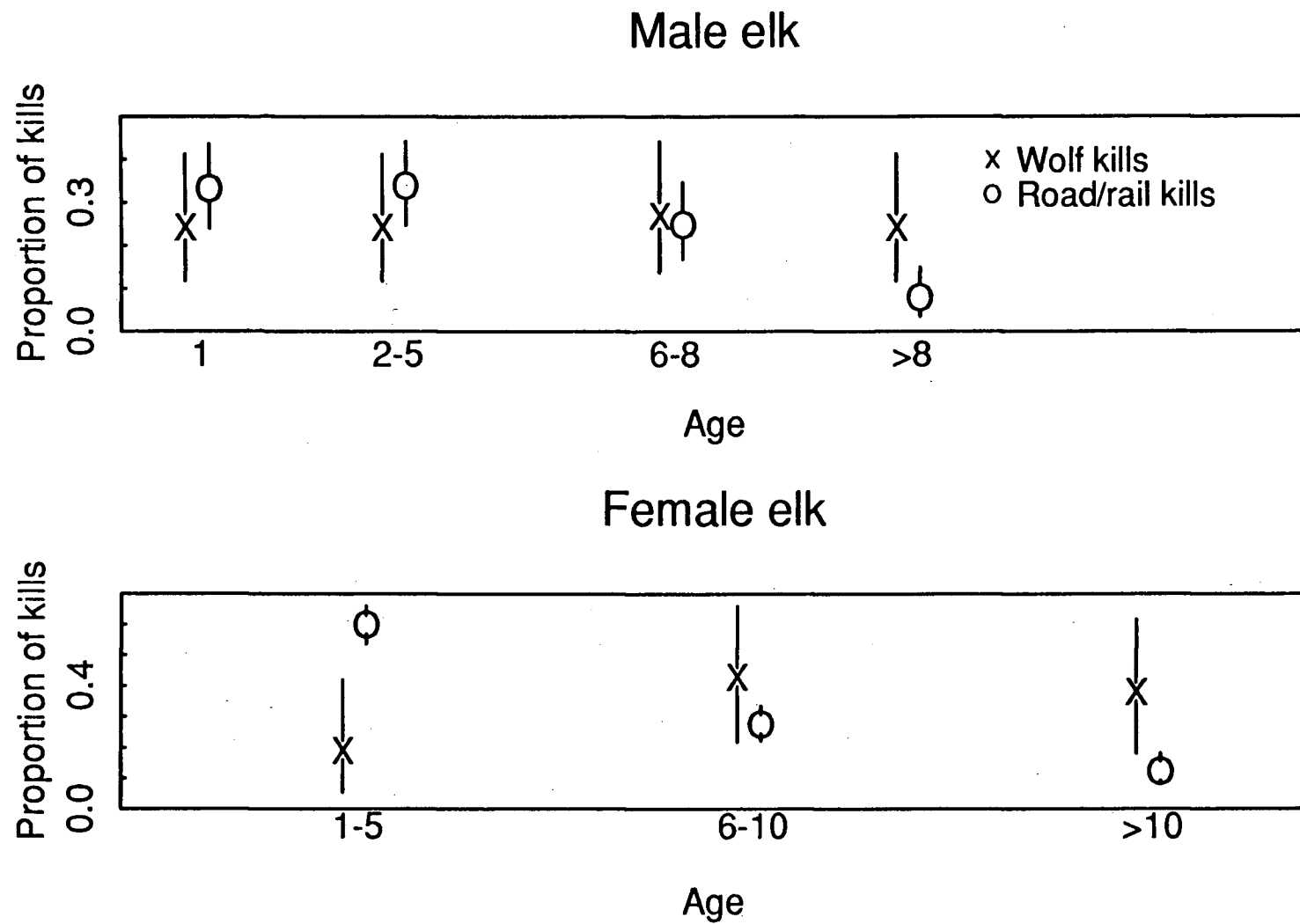
Fig. 3.3. Ages of elk killed by wolves compared to elk killed on the road or railway. 'Error bars are binomial 95% confidence intervals.

Among yearlings, more males than females were killed (7 vs 0, chi-square = 7.0, 1 D.F., p < 0.01; 2 kills not sexed). Only 14 of 38 calves killed by wolves could be sexed and these did not indicate selection for either sex (6 males, 8 females, chi-square = 0.3, 1 D.F., p = 0.59).

Jaw lengths of elk killed by wolves were not different from those of road and rail kills (Table 3.4).

Antler measurements of wolf kills were also not significantly different from the road and rail kills. For all 3 measurements, however, the antlers of elk killed by wolves tended to be larger than those of the population (Table 3.5). Left-right asymmetry of the three characteristics did not differ between wolf kills and the population (weight: U=502, n=62, p=0.18; length: U=517, n=67, p=0.29; brow length: U=474, n=65, p=0.43).

Adult male and adult female elk killed by wolves were in significantly poorer condition than road and rail kills, based on femur fat (Table 3.6). The femur fat levels of calf elk kills were not significantly different from those of calves killed on the road and railway.

Discussion

Selection for classes of elk

Many studies of predation on moose have demonstrated a selection for calves (Stephenson and Johnson, 1973; Rausch et al. 1974; Haber, 1977; Peterson, 1977; Fuller and Keith, 1980; Peterson et al., 1984) while in other studies calves were taken in proportion to their abundance (Messier and Crete, 1985; Bjorge and Gunson, 1989), or selectivity changed seasonally (Ballard et al., 1984; Ballard et al., 1987). A similar selectivity for calves and for old animals has been found in most studies of predation on white-tailed deer (Pimlott et al., 1969; Mech and Frenzel, 1971; Mech and Karns, 1977; Fritts and Mech, 1981), though selectivity is not always apparent (Stenlund, 1955;

Table 3.4. Comparison of jaw lengths of elk killed by wolves and population samples from road and rail kills. See text for the calculation of the mean difference for elk under 4 years of age; a mean difference of 0 is expected if the kills do not differ from the population. The 2.5% and 97.5% quantiles (in parentheses) are derived from 1000 bootstrapped estimates and are similar to 95% confidence intervals on the mean difference.

All elk less than 4 years of age

Mean difference (mm, kill-population) = 0.70 (-4.08 - +5.83)

Young-of-year (calf) elk only

Mean difference (mm, kill-population) = 1.28 (-3.41 - +6.27)

Adults > 4 years of age

Sex	Population		Kills		Difference
	n	Length (mm)	n	Length (mm)	
Male	30	348.03 (SE=1.96)	18	348.06 (SE=2.58)	t=0.01, p>0.5
Female	81	331.85 (SE=0.97)	15	334.73 (SE=2.92)	t=1.14, p>0.2

Table 3.5. Comparison of antler measurements of elk killed by wolves and the population. The calculation of the mean difference is explained in the test. A difference of 0 is expected if kills do not differ from the population; positive differences indicate antlers of wolf kills are larger than the population.

Measurement	Difference (Wolf - road/rail) (2.5% - 97.5% quantiles)	Per cent Difference
Weight (g)	+25 (-244 - +287)	+1.08%
Total length (cm)	+1.9 (-2.6 - +6.2)	+1.97%
Brow tine length (cm)	+1.7 (-0.2 - +3.6)	+5.49%

Table 3.6. Comparison of femur fat of wolf kills (W) and the population (P). Calculation of mean difference explained in text. A mean of 0 is expected if there is no difference between the two samples; a positive difference indicates kills are in higher numbered fat classes and therefore are in poorer condition. Numbers in parentheses are 2.5% and 97.5% quantiles of 1000 bootstrapped estimates, approximating 95% confidence intervals.

Adult males:

		Number of kills in each class											
Class		Ja	Fe	Ma	Ap	Ma	Jn	Jl	Au	Se	Oc	No	De
1	P:	4	5	5	1	0	0	2	4	4	7	3	3
	W:	1	4	1								1	1
2	P:	2	4	1	1	1	0	0	0	0	0	0	0
	W:	1	4	1									1
3	P:	0	0	0	0	1	2	0	0	0	0	0	0
	W:												
4	P:	0	0	0	0	3	0	0	1	0	0	0	0
	W:	2											

Mean difference = 0.52 classes (0.31 - 0.72)

Adult females:

		Number of kills in each class											
Class		Ja	Fe	Ma	Ap	Ma	Jn	Jl	Au	Se	Oc	No	De
1	P:	11	6	5	5	1	3	3	4	6	2	3	6
	W:	2	1						1			1	
2	P:	3	0	1	1	1	2	0	0	0	0	0	1
	W:	1				1							
3	P:	0	0	2	0	0	0	0	0	0	0	0	0
	W:												
4	P:	0	0	2	0	1	1	0	0	0	0	0	0
	W:	2											

Mean difference = 0.58 classes (0.41 - 0.77)

Calves:

		Number of kills in each class											
Class		Ja	Fe	Ma	Ap	Ma	Jn	Jl	Au	Se	Oc	No	De
1	P:	4	2	0	0	0	0	1	1	2	0	2	7
	W:	2	1								1	3	2
2	P:	1	1	2	0	0	0	0	1	0	0	1	0
	W:	2	4	1									
3	P:	1	2	3	0	0	3	0	2	1	0	0	1
	W:		4										
4	P:	0	0	2	4	0	0	0	2	1	2	0	1
	W:	2	1					1					

Mean difference = 0.12 classes (-0.26 - 0.49)

Kolenosky, 1972). Selectivity for caribou calves was reported by Murie (1944), but not by Haber (1977) or Ballard et al. (1981), due perhaps to segregation of wolves and caribou calving grounds.

Preference for calves, when they are available, is expected as they are generally slower, less dangerous, and inexperienced with predators. The lack of strong selectivity for calves, considered on an individual basis (Fig. 3.2a and 3.2b) is therefore surprising. I will argue below that calves are highly preferred by wolves, but are not highly selected overall because of the social organization of elk.

Wolves show a similar, weak overall selectivity for adult male elk, calculated on an individual basis. Females are highly avoided overall. With moose, adult males are favoured over adult females in some systems (Fuller and Keith, 1980; Bjorge and Gunson, 1989), while females are selected in others (Ballard et al., 1981; Peterson et al., 1984). No selectivity is found in other areas (Stephenson and Johnson, 1973; Messier and Crete, 1985; Ballard et al., 1987), or the selected sex may change seasonally (Peterson, 1977). Adult males are preferred over females in white-tailed deer (Stenlund, 1955; Pimlott et al., 1969; Kolenosky, 1972; Mech and Karns, 1977), or no selectivity is found among adults (Mech and Frenzel, 1971; Fritts and Mech, 1981).

Selectivity for adult males is often credited to males being in poorer condition than females in the winter due to depletion of fat reserves during the autumn rut (e.g. Flook, 1970; Bibikov, 1979). However, in Banff National Park, adult female and adult male elk in the population in winter have the same femur fat levels (females average 0.07 of a fat class lower; bootstrapped 95% confidence interval approximations are 0.57 of a class lower to 0.46 of a class higher). Poorer body condition cannot explain selectivity for adult males.

The effect of herds

The spatial distribution of male and female white-tailed deer has been considered as a factor generating increased predation on males, which tend to occur on the periphery of wintering areas where they are more likely to be encountered by wolves (Kolenosky, 1972). A similar effect may explain the bias towards male yearling elk in wolf kills in Banff. Male elk calves remain with their mothers until the rut in the autumn of their second (yearling) year, at which time the harem-holding male chases the yearling males to the periphery of his territory, while female yearlings remain in the harem herd (Altmann, 1960). Yearling males generally remain at the edges of larger herds through the winter. Peripheral individuals are the first to be encountered when wolves attack an elk herd, and naive male yearlings are likely to be particularly vulnerable in these encounters.

During the winter, elk are usually found in small bull herds or larger cow/calf herds. Animals in herds can see and hear others in the herd and react to danger together. All animals in a herd detect an approaching human, start to move and flee at roughly the same time. Though elk may respond to a human differently from an approaching wolf, the increased flight threshold to my approach when wolves were in the area or had recently made a kill nearby demonstrates that the presence of wolves makes elk more prone to flight. This increased wariness probably makes elk less vulnerable to subsequent attacks by wolves, an example of resource depression (Charnov et al., 1976). It is uncertain how long this effect persists, but the decreased vulnerability may explain why consecutive kills are rarely made from the same herd. Carbyn (1974) has suggested that increased alertness of elk following an attack by wolves causes the wolves to move to another area. Wolves preying on bison occasionally follow the herd they attacked previously, but these herds are more alert (Oosenbrug and Carbyn, 1985), and the long average distance between kills (57.5 km) in that study suggests wolves must frequently travel to other herds to make kills. Wolves move throughout their territory and do not

remain in areas of high prey density (Carbyn, 1983a), and kills are distributed more uniformly than the prey (Fritts and Mech, 1981). These patterns indicate that kills cannot be made repeatedly from one herd.

The relatively small size of herds compared to the distances between herds, the coordinated response of herds, their increased wariness following an attack by wolves and the movement of wolves from herd to herd all imply that the herd should be considered the unit encountered by wolves (as Haber (1977) did for caribou and Dall sheep). Available prey should then be expressed as the number of herds of a given prey type rather than the number of individuals. If wolves had no preferences, the number of kills of a prey type would be proportional to the number of herds.

When selectivity is calculated based on the number of herds available, a very strong selectivity for calves is apparent, and a strong avoidance of both male and female adults. Adult males are slightly selected over adult females. The relatively high number of males in the kill sample is offset by the smaller size of male herds, which are therefore as abundant as female herds and as likely to be encountered by wolves. Females may be underrepresented compared to males because females usually occur in herds with calves which are strongly preferred by wolves in this analysis. When wolves encounter a cow/calf herd, they are likely to attack a calf, and the alerted females become less vulnerable to predation. Males generally do not have the benefit of calves to divert predation.

With this herd view, males are not necessarily more vulnerable or preferred than females. They are encountered proportionately more by wolves because they are in small, and therefore relatively more numerous herds, and they do not benefit by associating with preferred calves. Calves, though more preferred, are not highly selected overall because they occur in fewer herds.

Selection for age

Among adult elk, older animals are overrepresented in kills and younger ones avoided, compared to road and rail kills. Selection for old animals is a common finding in studies of wolf predation on moose (Haber, 1977; Peterson, 1977; Fuller and Keith, 1980; Peterson et al., 1984; Messier and Crete, 1985; Bjorge and Gunson, 1989), and in most studies of predation on white-tailed deer (Pimlott et al., 1969; Mech and Frenzel, 1971; Mech and Karns, 1977; Fritts and Mech, 1981), though not in all studies (Stenlund, 1955; Stephenson and Johnson, 1973; Rausch et al., 1974). Selectivity for old animals is generally attributed to increasingly debilitating pathologies developing with age (Peterson et al., 1984), though effects of environmental stress during development may make younger animals vulnerable (Peterson, 1977). Obvious abnormalities such as healed fractures occurred rarely in elk in Banff, and were found both in wolf kills and accidental kills. Subtler pathologies were not noted. Flook (1970) reports a drop in perinephric fat for male elk over 7 years of age, but no decrease for old females. Liver flukes are a common and occasionally fatal parasite in Banff (Woods, 1991) and may render older animals more susceptible to predation.

An alternative explanation is that the road and rail kills are biased towards younger animals. Because elk in Banff show high fidelity to their home ranges (Woods, 1991), animals whose ranges overlap the road or railway are less likely to survive to old age than animals away from these mortality sources, but both groups, near and away from roads, are vulnerable to predation. The predator sample could, therefore, contain more older animals, even without any selection. The same effect could occur when the population sample comes from hunter kills, with the more hunter-wary or remote animals living longer and not occurring in the population sample, but still being vulnerable to predation.

To explore the extent of this bias, I created a model with 2 simple age-structured subpopulations of prey. Only one subpopulation is subject to highway (or hunter)

mortality, which provides the sample of the population age structure. Both subpopulations are preyed on by wolves. Neither the vehicles (or hunters) nor the wolves are selective for ages; all age classes in a subpopulation have the same mortality rate. A constant number of animals enters the youngest age class each year and a stable age distribution is set up. Some dispersal between subpopulations can occur with animals of all ages equally likely to disperse. The proportion of wolf kills and highway kills are calculated in four age classes (1-4, 5-8, 9-12, 13+). I then calculate the number of kills that would be needed for these two age distributions to be significantly different, using chi-squared.

The simulations show that an apparent selectivity for old animals can occur due simply to the segregation of the prey into two subpopulations, one vulnerable to highway mortality and one not (Fig. 3.4a). The highway mortality rate of 0.1 in Fig. 3.4a only applies to the 50% of the population vulnerable to highway mortality; the overall highway mortality rate is therefore 0.05. A fairly low interchange between the two subpopulations (10% of the animals per year) can eliminate the effect (Fig. 3.4b). However, if highway mortality is high compared to wolf mortality (Fig. 3.4c) or only a small part of the population is vulnerable to the highway (Fig. 3.4d), then the apparent selectivity is more pronounced. Low rates of dispersal do not eliminate this bias under these conditions. Increased mortality rates (i.e short prey lifespans) increase the apparent selectivity.

Elk killed by wolves more than 1km from the highway and railway in Banff tend to be older than animals preyed upon near these mortality sources (Table 3.7). This provides indirect support for the idea of two sub-populations, with more old animals occurring away from the mortality sources. As shown by the model above, this may generate an apparent selectivity by wolves for old animals, where none exists.

Many wolf studies use hunter kills to indicate the population age structure (e.g. Mech and Frenzel, 1971; Kolenosky, 1972; Bibikov, 1979; Fritts and Mech, 1981;

a. Wolf mortality=0.1
Highway mortality=0.1
No dispersal

58 kills needed

b. Wolf mortality=0.1
Highway mortality=0.1
Dispersal=0.1

785 kills needed

c. Wolf mortality=0.05
Highway mortality=0.15
No dispersal

16 kills needed

d. Wolf mortality=0.1
Highway mortality=0.1
No dispersal
20% affected by highway

31 kills needed

Proportion of kills

0.5

0

1-4   5-8   9-12   13+

Age class
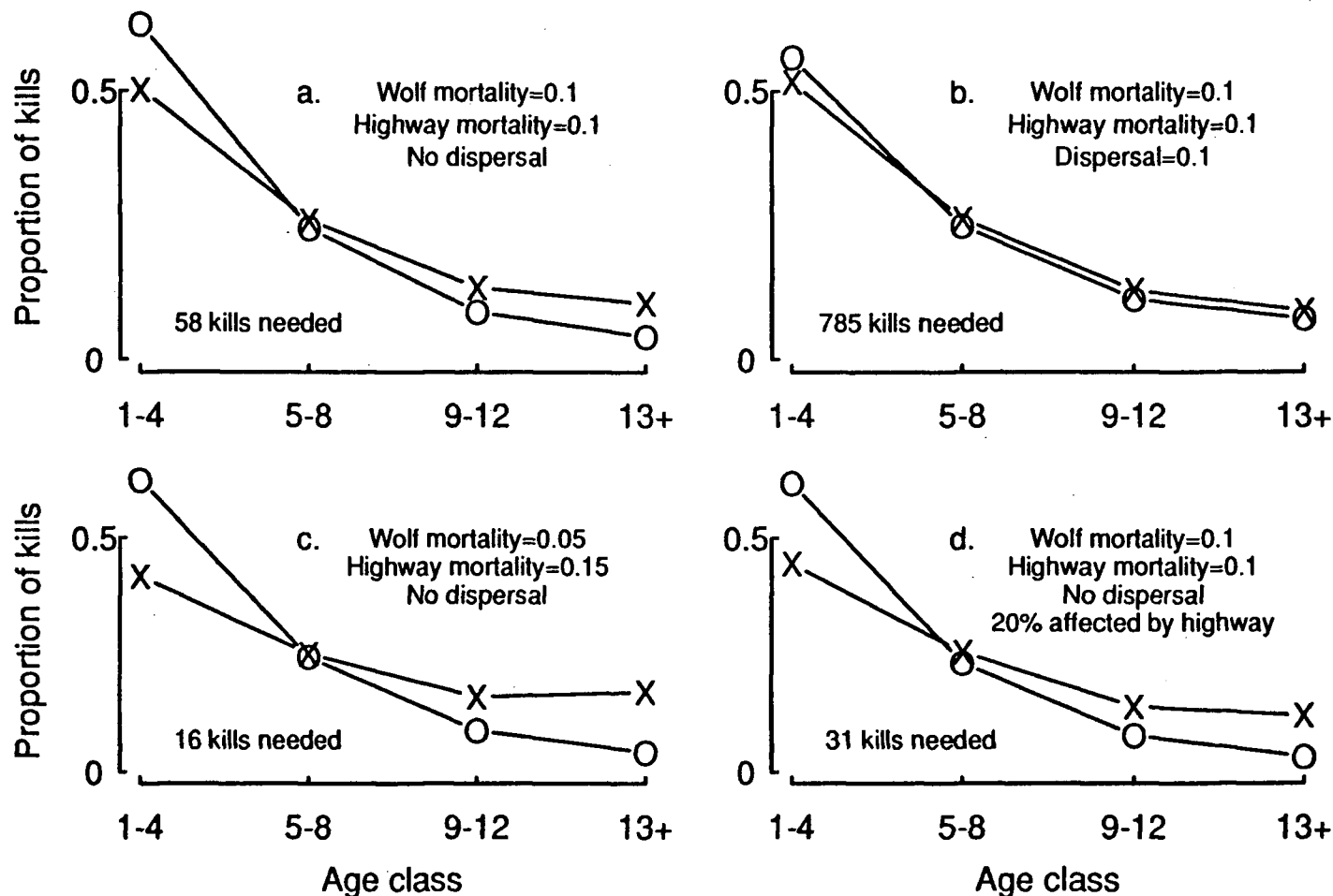
Fig. 3.4. Sample results of a simulation of predation on an age-structured population subject to highway mortality. O=highway kills, taken to represent the age structure of the population; X=wolf kills. The number of wolf kills which would have to be found to create a significant (chi-square) difference between the age distributions of the wolf kills and the highway kills is recorded with each graph.

Table 3.7. Ages of elk killed by wolves close to and far from the major human mortality sources (Trans-Canada Highway TCH and railway RR). Because the TCH and RR are often close together, these are not independent comparisons.

	<1000m from TCH	>=1000m from TCH	
Adult males	4.40 (SE=0.98) n=15	6.29 (SE=3.16) n=17	U=169,p=0.06
Adult females	7.30 (SE=1.29) n=10	11.78 (SE=2.14) n=9	U=68,p=0.03
All adults	5.56 (SE=0.81) n=25	8.19 (SE=1.00) n=26	U=438,p=0.03
	<1000m from RR	>=1000m from RR	
Adult males	4.96 (SE=0.77) n=23	6.56 (SE=1.06) n=9	U=129,p=0.14
Adult females	7.58 (SE=3.78) n=12	12.57 (SE=6.50) n=7	U=65,p=0.03
All adults	5.86 (SE=0.66) n=35	9.19 (SE=1.44) n=16	U=377,p=0.03

Carbyn, 1983a; Messier and Crete, 1985; Bjorge and Gunson, 1989) or automobile kills (Pimlott et al., 1969). Fritts and Mech (1981) suggested that hunter kills, which provided their population sample, affected the age and sex distribution of the population and the animals killed by wolves. However, a selectivity for old animals has also been shown when kills were compared to ages of live-captured animals, or to theoretical age distributions (Peterson, 1977; Peterson et al., 1984; Ballard et al., 1987). Wolves probably do select for old animals in many systems, but the bias outlined above could overemphasize this selectivity, or create apparent selectivity where none exists.

Selection for body condition

Wolves are believed to take proportionally more sick and weak animals than occur in the population, particularly in species such as moose which are difficult to capture (Mech, 1970; Temple, 1987). However, evidence for this belief is often scanty or contradictory. Several studies have shown increased pathologies or low levels of femur marrow fat (an indication of very low energy reserves; Mech and DelGiudice, 1985) in moose killed by wolves (Peterson et al., 1984; Messier and Crete, 1985), but population comparisons are usually not available. Other studies have shown no differences between kills of moose and samples representing the population (Stephenson and Johnson, 1973; Rausch et al., 1974; Ballard et al., 1981; Ballard et al., 1987). Slower development and more prevalent jaw pathologies have been noted in white-tailed deer killed by wolves (Mech and Frenzel, 1971), but fat levels are high (Fritts and Mech, 1981) or do not differ from the population (Mech and Frenzel, 1971). Elk killed by wolves in Riding Mountain National Park had very high levels of fat (Carbyn, 1983a).

Jaw length is an index of body size and may indicate the long-term health of an animal during the four years elk require to attain full adult size (c.f. metatarsal length, Peterson et al., 1977). Longer, heavier antlers indicate healthier animals on an intermediate scale, the several months in summer when antlers are grown (Mech and

Frenzel, 1971). The lack of significant differences between jaw and antler measurements of wolf kills and the population indicate that wolves do not select animals on the basis of these long and intermediate term indicators of body condition. However, for all three antler measurements, the wolf kills were larger than the population, though only one comparison approached significance. This difference suggests the largest bulls of a given age may be more vulnerable to predation. A larger sample of kills is needed to test for this slight selectivity.

In contrast to these longer-term indices of condition, adult male and female elk killed by wolves were in significantly poorer average condition at the time of predation than the population. Low fat reserves would not directly render an animal more vulnerable to predation, since chases by wolves are short and should not exhaust the energy resources of even a starving animal. However, if the poor condition is caused by a disease or high parasite load, then these may make the animal susceptible. As an extreme example, one dead cow elk was found which had died while being chased by wolves, without any contact by the wolves. The carcass was found in the middle of a river, inaccessible to the wolves, and had a ruptured liver highly infested by giant liver flukes. If the animal had died on land it would have been an easy meal for the wolves. Alternatively, an animal approaching starvation may feed more and be more vulnerable than animals which can devote more time to vigilance or resting in cover (McNamara and Houston, 1987).

The observation that adults killed by wolves are in poorer condition than the population, while kills of calves which are much preferred by wolves (Table 3.6), are no different from the population, is consistent with Temple's (1987) hypothesis that predators should select for substandard individuals of prey that are most difficult to catch. Temple's hypothesis is based on the probability of an attack being successful in a series of sequential attacks. In wolf attacks on elk, attack success is undoubtedly important, as wolves' success typically ranges from 5 % on large prey (Haber, 1977; Peterson et al.,

1984) to over 40 % on smaller ungulates (Kolenosky, 1972). However, wolves encounter several elk simultaneously in a herd and so conscious selection or choice of substandard individuals is also possible. From interpretation of tracks on at least 4 occasions, wolves entered a bedded cow/calf herd, passed several large beds (probably cows) and moved directly to a small (calf) bed. A short chase ensued and a calf kill was found. The opposite situation, wolves ignoring calves to attack a cow, was never noted, though interpretation of tracks is never certain. Wolves appear to choose calves in simultaneous encounters with cows and calves, but it is uncertain whether wolves can identify substandard or vulnerable individuals upon encountering a herd, or whether differential attack success is the sole reason for the observed selectivity towards animals in poor condition.

Chapter 4. The effect of snow depth on kill rates, prey selectivity and scavenging by wolves in Banff National Park

Introduction

Snow is a ubiquitous component of the northern environment in winter and has numerous effects on the behaviour of wolves and their prey (Telfer and Kelsall, 1984; Fuller, 1991). Deep snow can hinder the movements of both wolves and ungulates, but wolves have a lighter foot loading than most ungulates (Mech et al., 1971; Telfer and Kelsall, 1984) and can often travel on top of a snow crust which will not support their prey (Peterson, 1977). Hunting success of wolves generally increases in deep snow (Kolenosky, 1972; Peterson and Allen, 1974; Haber, 1977) and kill rate may increase as the depth of the snow pack increases (Nelson and Mech, 1986). Correspondingly, the proportion of a carcass wolves eat before abandoning it declines with increasing snow depth (Pimlott et al., 1969; Mech et al., 1971; Carbyn, 1983a; Potvin et al., 1988), but generally remains over 80% (Fuller, 1991). Wolves will also return to old carcasses when snow levels drop in the spring (Pimlott et al., 1969; Mech et al., 1971).

Snow also affects the selectivity of wolves for different prey types, but a consistent pattern is not obvious. In several studies calves became a larger component of the diet in deeper snow (e.g. Peterson, 1977; Ballard et al., 1987), while in others adult females become more vulnerable (Mech and Frenzel, 1971; Haber, 1977), or there is no apparent effect of snow on selectivity (Fuller, 1991).

By affecting kill rates, selectivity and perhaps carcass use and scavenging, snow can alter the functional response of wolves and influence wolf-prey dynamics. Additionally, because food intake in winter affects pup production and survival, snow may also influence the numerical response of the wolves (Nelson and Mech, 1986).

This paper examines the effect of snow depth on the kill rate and prey selectivity of wolves in Banff National Park, Alberta, where elk (Cervus elaphus) are the main prey, but five other ungulates are also hunted by wolves, and considerable numbers of ungulate carcasses are available for scavenging. The study occurred from Sept. 1985 through May 1990. An intensive tracking of one pack in winter 1989-90 resulted in a more complete record of kills and scavenged carcasses, and a relatively unbiased assessment of kill rates (Fuller, 1991). I also used changes in kill rates to determine whether scavenging is a less preferred mode of foraging for wolves than hunting, and consider the implications of the results for predator-prey dynamics.

Methods

Kills and scavenging by wolves

Animals killed or scavenged by wolves were found while tracking wolves in the snow or during helicopter relocations of radio-collared wolves. Evidence that an animal was killed by wolves included an obvious chase sequence in the snow or evidence of a struggle, including damaged vegetation, extensive blood on the snow or canine slash marks on the animal (Haber, 1977). Scavenged animals included rail and road kills which showed clear evidence of impact, animals which had fallen through ice and drowned, road-killed animals set out as baits for collaring wolves, animals killed by other predators and old kills which wolves had abandoned at least several days previously. I have not included carcasses where I was unsure whether wolves had killed the animal or were scavenging.

Snow depth and selectivity for age classes of elk

The depth of the snow pack is recorded daily in the Bow Valley at meteorological stations at Banff, Lake Louise and midway between the two. Snow depth in the valley

bottom increases from Banff towards Lake Louise and, of course, changes through the winter. To summarize these two effects, contour plots of snow depths were calculated with date as one axis and position in the valley (from 0 at Banff to 55km at Lake Louise) as the other. The expected snow depth on a given date and at a given position in the valley bottom could be determined by finding the point representing these two variables and interpolating between snow depth contour lines (Fig. 4.1).

This technique was used to calculate the expected snow depths at all kills and scavenging events in the Bow Valley. This method was preferred to using snow depths recorded at kill sites for several reasons. First, snow depths were not recorded at many of the kills found in the early part of this study. Secondly, the area near a kill is frequently packed down by wolves and scavengers by the time the kill is found. Thirdly, the snow depth calculated from the contour plot gives the snow depths the animal was exposed to in the general area of the kill, rather than just at the kill site. For a few kills which occurred in side valleys or at high elevations on the edge of the Bow Valley the valley bottom data do not apply and snow depths recorded in the area of the kill were used.

Elk calves are seriously impeded by snow depths greater than 51cm, while adults are seriously impeded by depths over 58cm (Trottier et al., 1983). All elk killed by wolves in winter during the study (1986-90) were therefore tabulated as calf or adult in three snow depth categories - under 51 cm, 51-58 cm and over 58 cm.

Time since previous kill

The time elapsed since the wolves' previous kill was calculated for all kills and scavenging events when I was certain from snow-tracking and radio-telemetry that I had not missed a kill since the previous known kill. Missed kills were suspected when wolves spent more than one day in an area and no kill was found or scats collected at the time contained hairs of a species different from the known previous kill. Time since previous kill was not calculated if scavenging had occurred since the previous kill, since
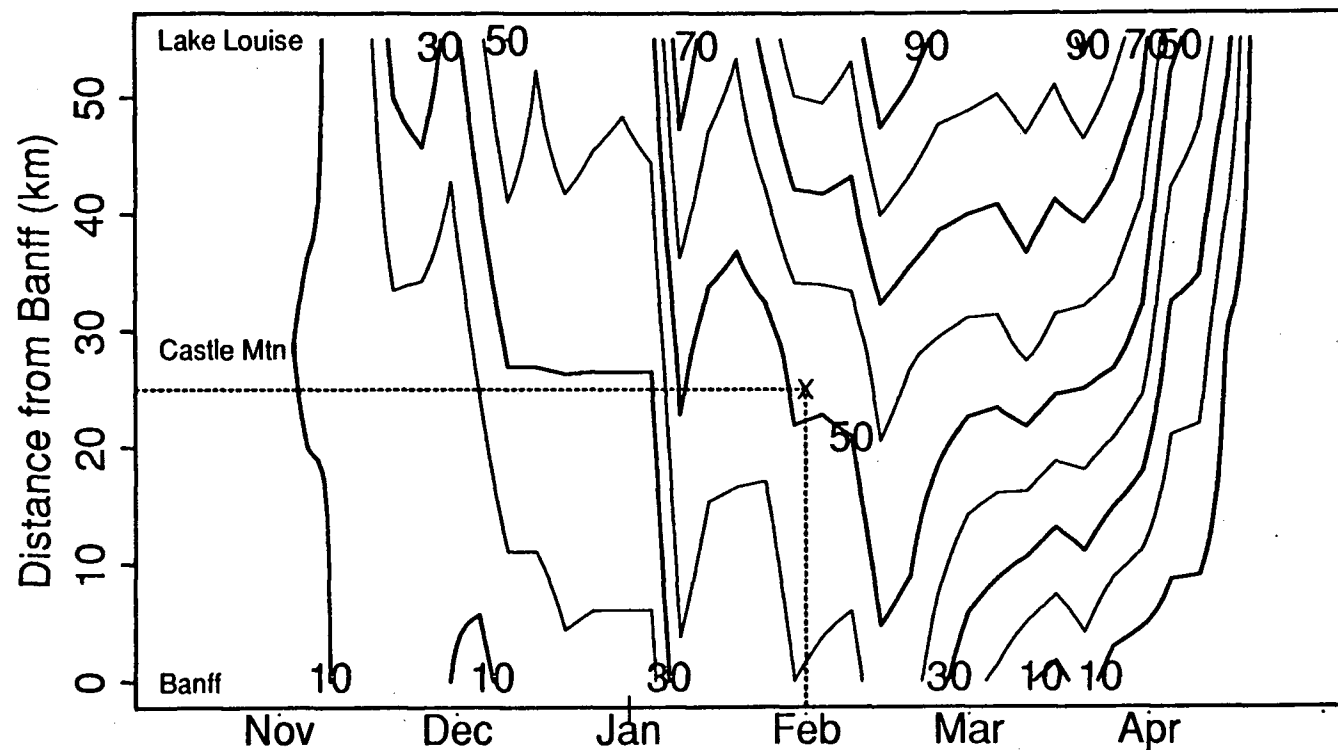
Fig. 4.1. An example of a contour plot used to calculate snow depths at a given date (X-axis) at a given position in the valley (Y-axis). Contour lines define points of equal snow depth (in cm). For example, on Feb. 1 at a position 25km up the valley from Banff ('X' on plot), the estimated snow depth was 52cm.

scavenging provided an unknown and variable amount of food to the pack. Therefore the first kill after a scavenging event or a series of scavenging events was not used in the time since previous kill data. Similarly, only the first scavenging event in a series of consecutive scavenging events could be used for these calculations. Time since previous kill was only calculated for kills made by one pack which was followed intensively in the winter of 1989-90.

Field observations indicated kills of elk calves or smaller ungulates provided full meals for a pack of wolves for roughly one day, while kills of adult elk provided food for two days. To estimate the time since the previous kill was abandoned, I subtracted one day from the time since the previous kill was made if the kill was a calf elk or smaller ungulate and two days if the kill was an adult elk.

Results

Snow depth and selectivity for prey types

Elk killed by wolves are tabulated by age class and snow depth in Table 4.1. The distribution of kills of elk was tested against 5 hypotheses of how snow depth might affect selectivity by wolves. These hypotheses assume that the ratios of calves to adults at depths under 51cm represent the selectivity of wolves without influence of snow. The mean snow depth of these kills was 26.8 cm.

Hypothesis 1. No effect. The ratio of calf and adult kills in the deeper two snow categories should be the same as in the under 51cm category. The observed distribution of kills is different at deeper snow depths (chi-squared = 13.3, 2 D.F., p < 0.005 (two-tailed)).

Hypothesis 2. Wolves specialize on their preferred class as snow depth increases. Calves are preferred over adults (Chap. 3, Fig. 3.2c), and calves should be increasingly

Table 4.1. Summary of elk killed by wolves found in winters from 1985-1990, by age class and snow depth category. Elk calves are hindered by snow depths over 50cm while adults are hindered by depths over 58 cm (Trottier et al., 1983)

Snow depth (cm)	Number of elk killed by wolves	
	Calves	Adults
<51	24	28
51-58	9	2
>58	0	9

represented in deeper snow categories. This does not occur (chi-squared = 5.6, 1 D.F., p < 0.01 (one-tailed)).

Hypothesis 3. Wolves take any elk which is impeded by snow, and when all elk are impeded (snow >= 58cm) should show their original preferences. There are more adults and fewer calves killed at snow depths greater than 58 cm than predicted by this hypothesis (chi-square=7.7, 1 D.F., p < 0.01 (two-tailed)). Cows with calves may leave areas of deep snow, but observations of calves in snow over 60cm indicates at least some calves are available.

Hypothesis 4. Wolves take any elk which is impeded by snow, and kill elk randomly when all are impeded. Calves comprise about 15% of the population in mid-winter and therefore only 1.35 of the 9 kills observed in the over 58cm category are expected to be calves. This is consistent with the observed distribution of kills (chi-squared = 1.6, 1 D.F., p > 0.2).

Hypothesis 5. Wolves take the largest animal which is impeded by snow. This hypothesis predicts that all 9 of the kills in the deepest snow category should be adults, as observed.

Both hypothesis 4 and 5 are consistent with the data and cannot be distinguished with current sample sizes. The prevalence of smaller ungulate species (deer and bighorn sheep) in the under 51cm category supports hypothesis 5, but these species may change their distributions and not be available under deep snow conditions. The 2 adults killed by wolves in the intermediate snow category are not strictly predicted by either hypothesis, but are expected given variation in local snow depths and conditions, variable effect of snow on ungulates, and especially the influence of chance on the hunting success of wolves. Additionally, though wolves may prefer calves in moderately deep snow, they will still attack herds they encounter which do not contain calves. Considering these sources of variation, the difference between kills at different snow depth classes is surprisingly pronounced.

Kill rate versus snow depth

The time between consecutive kills decreases with increasing snow depth (Fig. 4.2a), and therefore kill rate increases. This result does not simply reflect wolves switching at high snow depths to calf elk, which are consumed quickly. Adult elk kills are included at high snow depths, and several quickly-consumed deer kills and calf elk are included at low snow depths. When days since the wolves abandoned their previous kill (calculation explained above) is plotted against snow depth, the relationship persists (Fig. 4.2b). This demonstrates that the time without food available decreases with increasing snow depth. The observed relationship is also not simply a seasonal effect; data points for low snow depths were obtained from both early winter, before deep snow had accumulated and late winter as snow melted.

The linear distance between consecutive kills increases as the time between kills increases (Fig. 4.3). The actual distance travelled is probably higher than this linear distance, particularly when several days elapse between kills.

Scavenging

Wolves of the Spray pack in the winter of 1989-90 were observed scavenging on 4 rail-killed carcasses, 4 carcasses deployed as baits to capture an adjacent pack for radio-collaring, 3 drowned animals, 1 elk killed by a cougar (Felis concolor), 1 road-kill and 1 black bear (Ursus americanus) which died from injuries sustained during a translocation. Additionally, the pack visited old kills several times, up to 2 months after they were killed.

Snow depth when scavenging events occurred was significantly lower than when kills were made and time since previous kill was higher (Fig. 4.2a). Scavenging occurred both in early winter and late winter, and to a lesser extent during maximum snow accumulation in mid-winter. Old partially-consumed kills, drowned elk and rail-kills
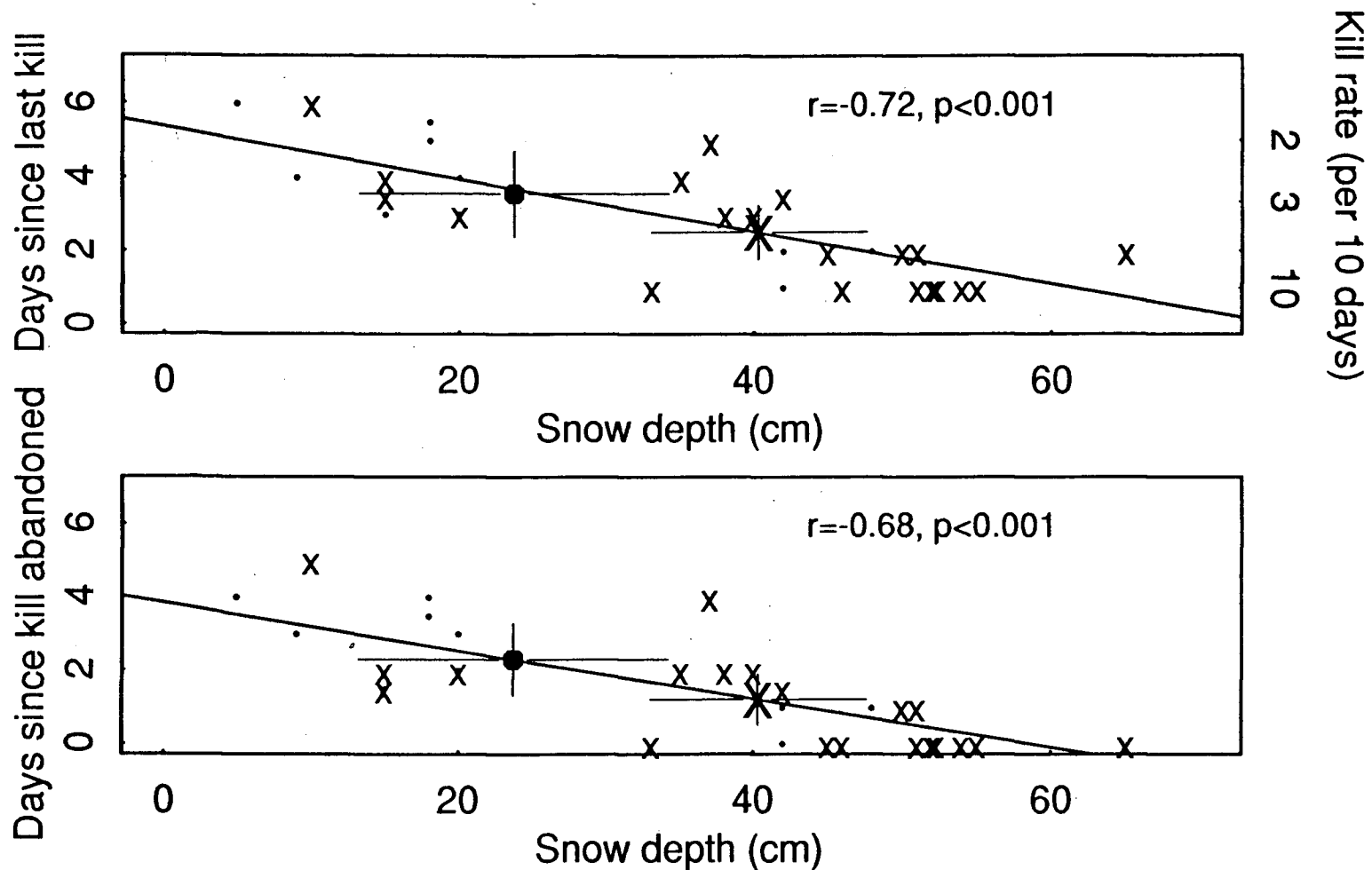
Fig. 4.2. a. Time between consecutive kills as a function of snow depth. X=wolf kill, dots=scavenging events. The large X is the mean conditions when kills occured, with 95% confidence intervals for both axes; the large dot is the same information for scavenging events. The regression line is fitted through the kill data only. b. The time since the previous kill was abandoned as a function of snow depth, based on two days to consume an adult elk and one day for smaller prey types. Symbols and regression as above.
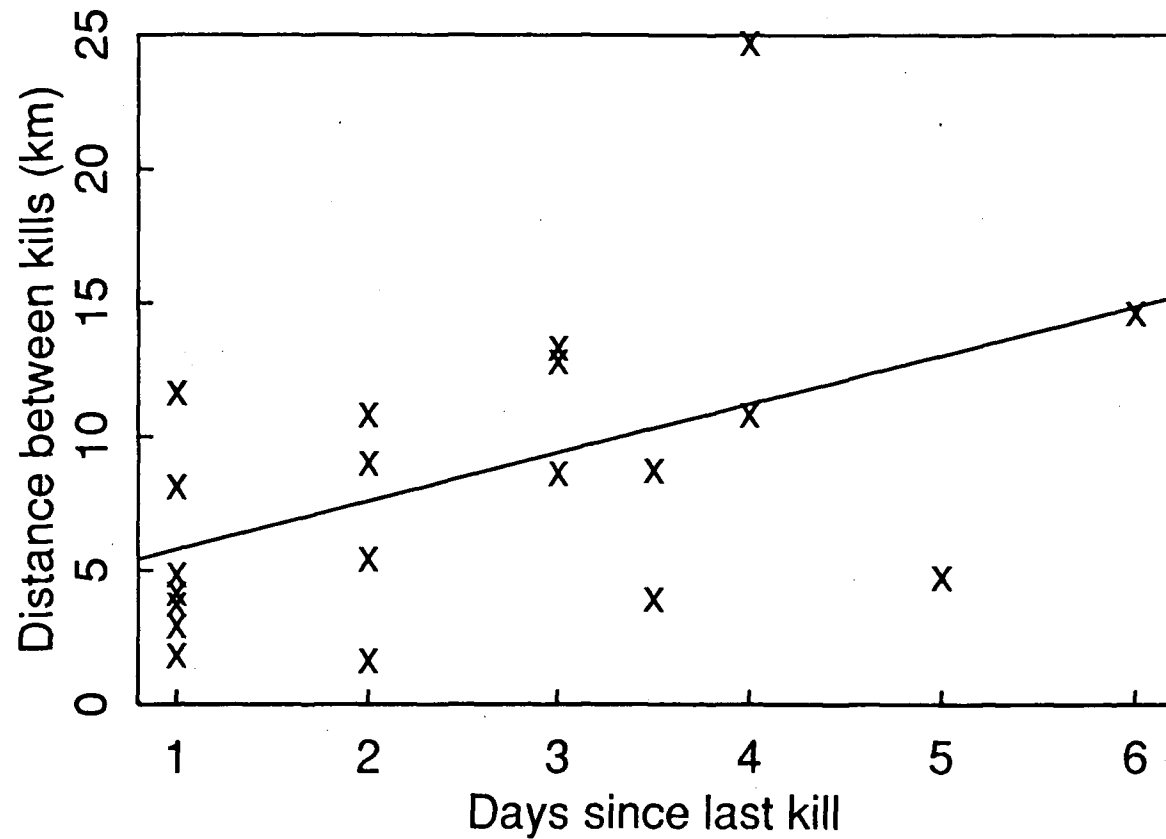
Fig. 4.3. The linear distance between kills as a function of the time between kills. The actual distance travelled by wolves is likely to be substantially longer, particularly when there are several days between kills.

were available throughout the winter (Woods, 1988). The mean snow depth and time since previous kill when scavenging occurred fall on the regression line of the two variables based on conditions when kills were made. In other words, at a given snow depth, wolves did not wait longer than the expected time to make a kill before beginning to scavenge.

The prevalence of scavenging events at low snow depths and kill rates could be because scavenging is a less profitable foraging mode than hunting and is only used when kill rates are low (1/0 rule; Stephens and Krebs, 1986); alternately, wolves may simply encounter fewer scavengeable carcasses at high snow depths and not avoid scavenging under any conditions. To differentiate between these alternatives, I estimated encounter rates for carcasses at high and low kill rates.

Assuming the abundance of carcasses is roughly the same throughout the winter, the number encountered by wolves, or their chance of encountering a carcass is proportional to the distance they travel. I calculated the total minimum distance wolves travelled when they made a kill or scavenged within 3 days of their previous kill (from the relationship in Fig. 4.3), and when more than 3 days elapsed since the previous kills. In the 3 days or less category there were more events (kills and scavenging) but less distance between them than in the greater than 3 day category, such that the total minimum distance travelled was the same (132km and 134km respectively). The number of carcasses scavenged was also the same in both categories, providing no evidence that the tendency of wolves to scavenge depended on the time since their previous kill. When time between kills is short, wolves were likely to make another kill before encountering a scavengeable carcass and, therefore, scavenging events were relatively rare when kill rates were high. This does not, however, imply that wolves avoided scavenging from a carcass when they encountered one.

Discussion

The effect of snow on prey selectivity

The results of Table 4.1 are based on combining the known kills from several years for 2 packs, the intensively studied Spray pack and the Baker pack from the north end of the Bow Valley. The Baker pack is somewhat larger, more cohesive and experiences deeper overall snow, but showed the same pattern as the Spray pack, particularly in concentrating on adult elk at depths greater than 58cm. The switch from calves in moderately deep snow to adults in very deep snow is similar to the pattern of predation on elk reported by Carbyn (1983a).

The variation in the effects of snow on selectivity reported in other studies (Fuller, 1991) could be explained by similar threshold effects of snow depth operating with other species. Fuller (1991) compared three mid-winters with snow over 40cm to three with snow under 26cm in Minnesota and found no difference in the proportion of white-tailed deer (Odocoileus virginianus) calves in the wolves' diets. He also reports that all white-tailed deer are hindered by snow between 40 and 50cm. The deep snow winters in Fuller's study may represent selectivity when all deer were hindered, while the low snow years represent selectivity when none were hindered. Trottier et al. (1983) consider that adult and calf deer are hindered at snow depths of 40cm and 32 cm respectively. At intermediate snow depths, calves but not adults may be hindered and become a greater proportion of the diet.

Haber (1977) reports the same proportion of moose (Alces alces) calves in kills under 53 cm and in kills over 53 cm. Peterson and Allen (1974), however, found a higher proportion of calves in kills in snow over 76 cm deep on Isle Royale. Haber (1977) suggests the difference is because moose in his study area challenge attacking wolves while moose on Isle Royale flee. Alternatively, Haber's 53 cm criterion may be

below the level where moose calves are hindered, while Peterson and Allen's 76 cm separate hindered and unhindered calves.

In the current study, the 51 and 58cm limits suggested by Trottier et al. (1983) clearly separated out the kills of the different age classes. If a comparison had been made between kills under 51cm with kills over 51 cm, no difference would have been found. The possible importance of these threshold effects of snow depth for predator-prey dynamics is discussed below.

The effect of snow on kill rate

The procedure of using only kills which were known to be consecutive substantially reduced the sample size for the kill rate and scavenging analysis. The more days which elapsed between kills, the greater the probability of losing the wolves for a day. Therefore, extremely long intervals between kills are not likely to be included in the data, biasing the kill rate upward. However, the observed trend of decreasing kill rates with increasing snow is still valid.

Kill rate may increase with snow depth (Fig. 4.2a) for a number of reasons. Some prey species tend to congregate in small areas in deeper snow as forage becomes unavailable elsewhere (white-tailed deer, Fuller, 1991; moose, Peterson, 1977). In Banff, elk tended to occur along the river or railway right-of-way in deep snow, and wolves used these as travel corridors. Whether intentionally seeking out prey or simply for ease of travel, this pattern would increase the encounter rate of wolves with prey. The Baker pack, hunting in deep snow, encountered more prey (indexed by prey tracks crossing tracks of wolves) than were encountered on random transects in the area, while the Spray pack in shallower snow encountered prey at the same rate as random transects in the area (Chap. 2, Table 2.5). Deep snow also enhances hunting success of wolves which have encountered prey (Kolenosky, 1972; Haber, 1977). Chases were rarely observed directly in Banff, and most successful chases reconstructed from tracks in the snow were short, so

it seems likely that deeper snow increased the wolves' encounter rate with prey, rather than affecting their hunting success.

Kill rates of wolves are far easier to determine in the winter using snow-tracking than in the summer when intensive aerial tracking is necessary. However, because of the effect of snow, winter kill rates must not be extrapolated directly to snow-free periods. In Banff, the mean kill rate, when consecutive kills were found, was one ungulate per 2.5 days, whereas the 0-intercept of the regression line (Fig. 4.2a) was at less than half this rate, one kill per 5.4 days. Different prey are available in summer, but this lower kill rate is the best estimate of kill rates in the snow-free spring and fall periods.

Scavenging

Profitability of food types is defined as the ratio of net energy gain to handling time (Stephens and Krebs, 1986), and for wolves feeding on ungulates it is largely determined by the amount of energy from a stomachful of meat and the time needed to digest it (Chap.2). Killing and eating times are negligible. Many carcasses which wolves scavenged had already been visited by other scavengers, or wolves had fed on them previously, and little remained except bones and hide. A meal of hide or bones probably takes at least as long to digest as a meal of fresh meat, but will provide far less energy. Some carcasses contained frozen meat which other scavengers could not remove. In this case, the time to gnaw off the hard flesh may become a substantial component of handling time and thus reduce profitability. With reduced profitability, scavenging should be a lower-ranked foraging mode than hunting and should not occur when kill rates are high and food is abundant (a prediction from the prey selection models of foraging theory; Stephens and Krebs, 1986). However, my results do not indicate that scavenging is ever avoided. Though the mean kill rate when scavenging occurs is lower than when kills are made, the scavenging rate (per unit distance travelled and therefore per carcass encountered) is the same at high and low kill rates.

Messier and Crete (1985) reported that the ratio of moose scavenged by wolves to moose killed by wolves was roughly 4 times higher in an area of moderate moose density than in an area of high moose density. Search time, the time between kills, was 5 times higher in the moderate density area and, if the density of moose carcasses was comparable between the areas, the wolves would have encountered 5 times as many scavengeable carcass per moose killed. These results also indicate no tendency for wolves to scavenge less at high prey densities and kill rates. In contrast, Fuller (1991) reports that in winters with deep snow wolves travelled shorter distances between kills, but scavenged a higher percentage of known deer carcasses. It is unclear why this occurred, but carcasses may be more abundant in deep snow as deer starve, or wolves may have more known kills to revisit in late winter when deep snow allowed a higher kill rate.

Wolves may not avoid scavenging at high kill rates because the profitability of scavenging, though lower than hunting, is still greater than the average energy intake from hunting, which also includes the search time (simple prey selection model of foraging theory; Stephens and Krebs, 1986). However, search time (time between kills) is low at high kill rates (Fig. 4.2b), so the profitability of a scavenged meal would have to approach that of a hunted meal for scavenging to be 'optimal' under conditions of high kill rates, which is unlikely. Scavenging does avoid the danger inherent in capturing a large prey animal. Alternatively, the deep snow conditions which allow high kill rates are infrequent in Banff and wolves may simply scavenge whenever possible, even if this is not the energy-maximizing behaviour in deep snow.

Implications for population dynamics

The kill rate multiplied by the number of wolf packs determines the impact of wolf predation on prey populations at a particular prey density. Because the kill rate is closely linked to snow depth, unpredictable variation in yearly snowfall may add

substantial, density-independent noise to wolf-prey interactions. Similarly, snow depth will also affect which classes of the prey species are taken.

In Table 4.2, I have taken the daily snow depths in the middle of the Bow Valley and calculated the expected daily kill rate of a pack hunting in this area. For instance, if the snow depth on a certain day was 20cm, the kill rate would be 1 kill per 4 days, or 0.25 per day (Fig. 4.2a). These values were calculated for each day of the winter and summed to indicate the predicted number of kills for each of the last five winters. Similarly, the ratio of calves to adults in the elk kills was predicted for the snow depth each day based on Table 4.1. The predicted kill rates vary from a maximum of 113 in 1986-87, a winter with deep snow, to 65 in 1985-86 with little snow. In the deepest snow year, predation on adults increased (the snow was often over 58cm), but roughly the same number of calves were expected to be killed every winter.

The ratios of adult to calf elk are known for the fall and spring elk populations in the area of the Bow Valley used by wolves (data from J. Woods). If wolf predation has a significant impact on the population, one would expect the least overwinter change in these ratios in the winters when adults comprise the major part of the wolves predicted diet. In winters in which calves are a large part of the predicted diet, the number of calves, which are relatively rare in the population, would decline substantially and the spring adult to calf ratio would be much higher than the fall ratio. As expected, the least overwinter change in the adult to calf ratio occurred in 1986-87 when the predicted proportion of calves in the winter diet was lowest, and the second lowest overwinter change in ratios occurred in 1988-89 when the predicted proportion of calves was second lowest. The overwinter changes in the ratios were larger for the other three years, as were the predicted proportions of calves in the winter diets. Rigorous testing of these predictions, particularly the total number of ungulates consumed, requires precise estimates of the fall and spring populations, which are not available. However, the trend in the changes in the adult to calf ratios is as predicted by the relationship between

Table 4.2. Predicted total number of kills and adult/calf proportions for a wolf pack in the middle Bow Valley, based on the daily snow depths through 5 winters and the relationships between snow depth and kill rate, and between snow depth and selectivity. The observed change in the ratio of adults to calves between fall and spring is also presented for each winter.

| Winter | Predicted overwinter kill | | | Change in adult:calf ratio |
	Total number	Calves (%)	Adults (%)	
1985-86	65	48.4	51.6	0.177
1986-87	113	25.3	74.7	0.068
1987-88	66	46.3	53.7	0.165
1988-89	90	41.6	58.4	0.083
1989-90	83	50.8	49.2	0.146

selectivity and snow depth, suggesting that snow depth can have a substantial effect on predator-prey dynamics. Other factors, such as mortality caused by humans, movements between areas without wolves and the direct impact of snow on ungulates (e.g. Walters et al., 1981) also clearly have effects on the Bow Valley ungulate populations.

If wolves scavenge whenever they encounter a carcass, then wolf predation rates may be reduced if other mortality sources are generating scavengeable carcasses. For instance, in winters with very deep snow, predation rates are expected to be high, but if animals are dying from other causes, such as starvation, a substantial proportion of the wolves' diet may be from scavenged food and predation rates may decrease. In this case, scavenging allows wolf predation to be at least partially compensatory with other mortality sources. This is not predicted if scavenging is a secondary foraging mode, only used when kill rates were low.

Chapter 5. Telemetry relocation error and assessment of habitat use in a mountainous environment

Introduction

Many field studies of large vertebrates rely on radio-telemetry locations for much of their information on home ranges, movement patterns, associations of animals and habitat use (e.g. studies and references in Amlaner, 1989). However, a radio relocation provides only an estimate of an animal's location, and has an associated error, the distance between the apparent and true locations. Several papers have examined the magnitude of telemetry errors and the factors which generate error, generally using relocation bearings taken from fixed towers and covering a defined study area (Heezen and Tester, 1967; Springer, 1979; Hupp and Ratti, 1983; Lee et al. 1985; Garrott et al., 1986). Fixed towers are rarely practical in studies of large, mobile mammals, and in these studies most ground relocations are made using hand-held or vehicle-mounted antennas, with the observer moving along a road or trail system. Usually, multiple bearings are taken until several bearings cross near each other, or the area of the map error polygon (Fig. 5.1) is less than a certain size, or until the observer subjectively feels confident in the relocation. The accuracy and precision of relocations from handheld antennas, the factors affecting precision and the utility of the map error polygon as an indicator of accuracy of the location have received little attention.

When radio-telemetry relocations are used to assess habitat use and preference, location error may introduce a bias (Nams, 1989). Highly preferred or avoided habitats appear less so in telemetry data, and this bias increases as the telemetry error becomes large relative to the size of the habitat units. To correct for this, Nams (1989) recommended multiplying the vector of observed habitat use by a bias matrix to obtain the vector of true habitat use. He suggested that the bias matrix could be calculated by
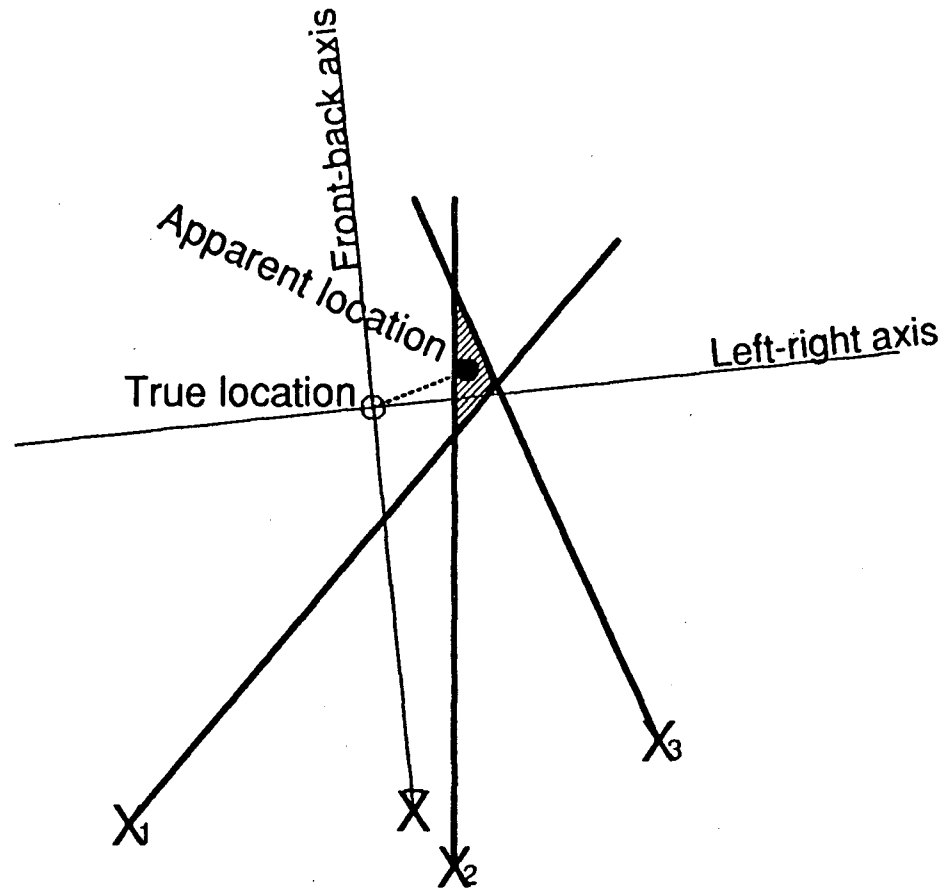
Fig. 5.1. Definitions of terms. Good bearings (thick lines) were taken at observer positions X1, X2 and X3. X̃ is the geometric mean observer position. The dotted line between the true location (O) and the apparent location indicated by telemetry (●) is the error distance. The shaded triangle is the map error polygon. In this example, the apparent location is to the right of the true location (i.e. positive value along the left-right axis) and slightly behind the true location (i.e. positive value along the front-back axis).

determining the distribution of telemetry error, then applying this error distribution to a large number of random locations on a habitat map of the study site. The bias matrix is calculated by comparing the habitat type of the random locations (the "true" locations) to the habitat type of the same random location with telemetry error added (the "apparent" location).

In this paper, I report the error of relocations of large-mammal radio-collars in different topography types in a broad mountain valley, and assess some factors associated with this error. I then use these errors and a habitat map of the study area to calculate bias matrices (Nams, 1989) for evaluating habitat use of radio-collared animals in this environment.

Methods

Study area

This study was conducted as part of a study of wolf ecology in the Bow Valley of Banff National Park, Alberta. The Bow Valley is a broad (3-4 km wide), U-shaped valley surrounded by steep, rock cliffs and mountain slopes. The habitats in the park have been classified into "ecosites", polygons encompassing areas of similar bedrock, soil type and vegetation (Holland and Coen, 1983). The ecosites can be combined into 8 broad vegetation types: pine, spruce, mixed coniferous and aspen forests, dry forests on south-west facing slopes, open wet areas, grasslands and alpine areas.

The valley topography was divided into 4 classes based on Holland and Coen's (1983) classification of the park:

        1: Flat, 0 degrees to 5 degrees.

        2: Gentle slope, 5 to 15 degrees.

        3: Moderately steep, 15 to 45 degrees.

        4: Steep, greater than 45 degrees.

Within each slope class, Holland and Coen (1983) classified the topography as "simple" if it had a fairly uniform slope, or "complex" if it had variable local topography. Thus, a complex, class 1 area indicates rolling hills with no overall trend in elevation; a complex, class 3 slope might contain small cliffs, mixed with terraces, or gullies in a moderately steep overall slope.

Determining the distribution of telemetry error

Large-mammal radio-collars were placed on branches of trees approximately 1m from the ground. Collars were placed haphazardly within each of the eight topography types, generally near a road to allow an accurate determination of their true location (within 50m, plotted on a 1:50,000 map). In complex topography classes, collars were intentionally put at locations in all types of available local topography, to represent the variability of topography in the complex areas.

I relocated the collars from a road on the opposite side of the valley, using a hand-held 2-element Yagi antenna. I determined the bearing of a signal based on a combination of the null-point and peak signal methods (Springer, 1979), and determined my location based on local features of the road, river and topography, and distance from known points. My location and the bearing were then plotted on a 1:50 000 map. Bearings were repeated at different locations on the road until the map error polygon defined by the 3 bearings in which I had the most confidence was 5 ha or less. When I could not achieve this precision or was not confident in the bearings, the collar was considered unlocatable from the road I was on. The geometric center of the error polygon of successful relocations was used as the relocation point. In general, this is how animals were relocated in the associated wolf ecology project and other large mammal studies in the area (J. Woods, Canadian Parks Service, pers. comm.).

Error distances were calculated as the Euclidean distance between the true location and the telemetry relocation. This is the horizontal, map distance, which will be

less than the true, ground distance on steep slopes. No correction was made for slope because this is rarely done in applications of telemetry data, such as determining home range size, and the geographical information system used in this study (discussed below) does not adjust areas on slopes. Error distance along the front-back axis was defined as the component of the error distance along the line between the mean observer position and the true location; error along the left-right axis is the error component along the perpendicular axis running through the true location (Fig. 5.1). Mean relocation distance was the mean distance from the three points where bearings were taken to the triangulated location.

Statistical analysis of telemetry error distribution

Distances on the 1:50,000 maps could only be recorded to the nearest 100m in the x- and y-dimensions, and therefore Euclidean error distances occurred in discrete categories (i.e. 0m, 100m, 144m, etc.). Error distances, which cannot be less than 0, are clearly not normally distributed. Error distances for all relocations in simple topography were compared to error distances in complex topography using a Mann-Whitney U-test. Spearman rank correlation was used to examine the relationship between the square root of the area of the map error polygon and the actual error distance, and between the error distance and mean relocation distance.

Calculation of the bias matrices

To calculate a bias matrix (Nams, 1989), a random point (representing the "true location" of an animal) was selected in the study area and the ecosite, vegetation type and topography class at that point were determined using a digitized map of the study area on a geographical information system (G.I.S.). Telemetry error in the left-right and front-back axes was simulated by selecting points randomly from a normal curve fit to the distributions of error along these axes observed in the telemetry tests. Separate error
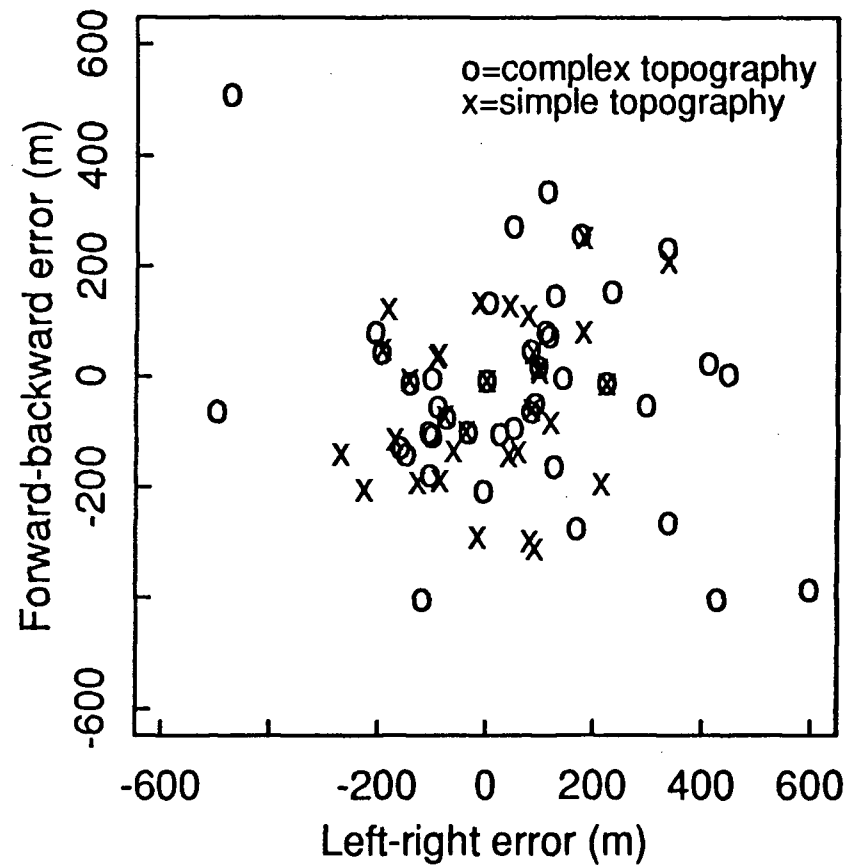
Fig. 5.2. The distribution of apparent locations indicated by telemetry in the trials, relative to the true location (0,0). Error distances could only be determined to the nearest 100m on the 1:50,000 scale map. Eight relocations in simple topography and 3 in complex topography occured at the true location (0,0).

distributions were calculated for simple and complex topography and telemetry error was simulated using the appropriate distribution for the topography type of the true location. These errors were then added to the true location to generate the "apparent location" (representing the telemetry relocation of the animal), and the ecosite, vegetation type and topography were determined at that point. This procedure was repeated 10,000 times. The resolution of the G.I.S. system is approximately 1m for this study area, far smaller than the telemetry error distance.

Bias matrices were calculated separately for ecosites, broad vegetation type and topography classes. The bias matrix has the attributes (ecosite, vegetation or topography) of the true locations as the rows of the matrix and the attributes of the associated apparent locations as the columns. Cells on the main diagonal of the bias matrix therefore represent points which were relocated by telemetry in the true or correct ecosite, vegetation or topography class, while all other cells contain cases where the telemetry relocation misrepresents the attribute of the true location. The values in a row of the matrix are expressed as a percentage of the row total, to indicate the percentage of time an animal in the true habitat would be relocated in the apparent habitat.

To calculate the vector of apparent habitat use a researcher would expect given the vector of true habitat use, the latter was multiplied by the bias matrix. To calculate a vector of true habitat use based on an apparent vector, the apparent vector was multiplied by the generalized inverse of the bias matrix (Nams, 1989).

Results

Telemetry error

The distribution of relocation errors is shown in Fig. 5.2. The mean error distance of relocations in complex topography was greater than those in simple topography (Table 5.1; U=1052.5, one-tailed p=0.037). In complex topography, the error in the front-back

Table 5.1. Summary of telemetry tests, relocation error and relocation bias in simple and complex topography.

Measurement	Simple	Complex	Combined
Number of tests	48	48	96
No triangulation	9	4	13
Useable relocations	39	44	83
Error			
Mean error distance (m)	156.4	234.0 *	197.5
S.E.	17.2	26.1	16.4
Left-right error (m)	102.1	168.6	136.1
Back-front error (m)	100.5	131.8	116.1
Bias			
Distance from mean apparent location to true location	32.7	54.2	36.1
Mean left-right position (m right)	-0.1	50.7	27.6
Bootstrapped quantiles	-39.6 - +41.8	-13.0 - +117.4	-14.8 - + 67.2
Mean back-front position (m back)	-32.0	-17.9	-22.9
Bootstrapped quantiles	-74.9 - +10.8	-74.0 - +37.9	-57.6 - + 13.5

N.B. Bootstrap analysis comparing left-right error and front-back error showed no significant differences for simple or complex topography or for both combined. The bootstrap quantiles (2.5% and 97.5%) for the bias components approximate 95% confidence intervals and indicate that the mean apparent locations are not significantly biased.

axis was less than the left-right error (Table 5.1), indicating an elliptical error distribution. The mean apparent location was to the right and in front of the true location. To test the significance of this bias, the apparent locations were resampled ("bootstrapped", following Krebs, 1989) and the mean apparent locations recalculated 1000 times. 22.2% of the 1000 bootstrapped mean apparent locations were farther from the original apparent location than the true location was. This indicates that the relocations were not biased significantly.

Error distance and mean location distance were positively correlated (rho=0.26, n=83, p=0.02), but the mean location distance explained little of the variance in error distance (Fig. 5.3a). The square root of the map error polygon is also correlated weakly with the error distance (rho=0.40, n=83, p<0.01) (Fig. 5.3b).

Bias matrices

Forty-four ecosite types occurred in the study area, and a portion of the 44 X 44 bias matrix for ecosite determination is shown in Table 5.2. The number of points in each cell has been expressed as a percentage of the row total, to indicate the percentage of the time that an animal is in the true ecosite that it will be relocated in the apparent ecosite. The main diagonal, which represents correct ecosite determination, ranges from 0% to 89% in the 44 X 44 matrix. In fig. 5.4, these percentages of correct allocation for each ecosite are plotted against the percentage of the study area that each ecosite represents. The percent of correct allocations increases for more common ecosites, reaching an asymptote at roughly 80%. The distribution and configuration of individual ecosite types adds variance to this relationship (examples in Fig. 5.4).

The bias matrix for broad vegetation type is shown in Table 5.3. Tables 5.4a-c provide examples of how telemetry error can affect assessment of habitat use. In a., animals are assumed to occur in each vegetation type equally often, which represents a strong preference for the rare types and avoidance of the common types. This true
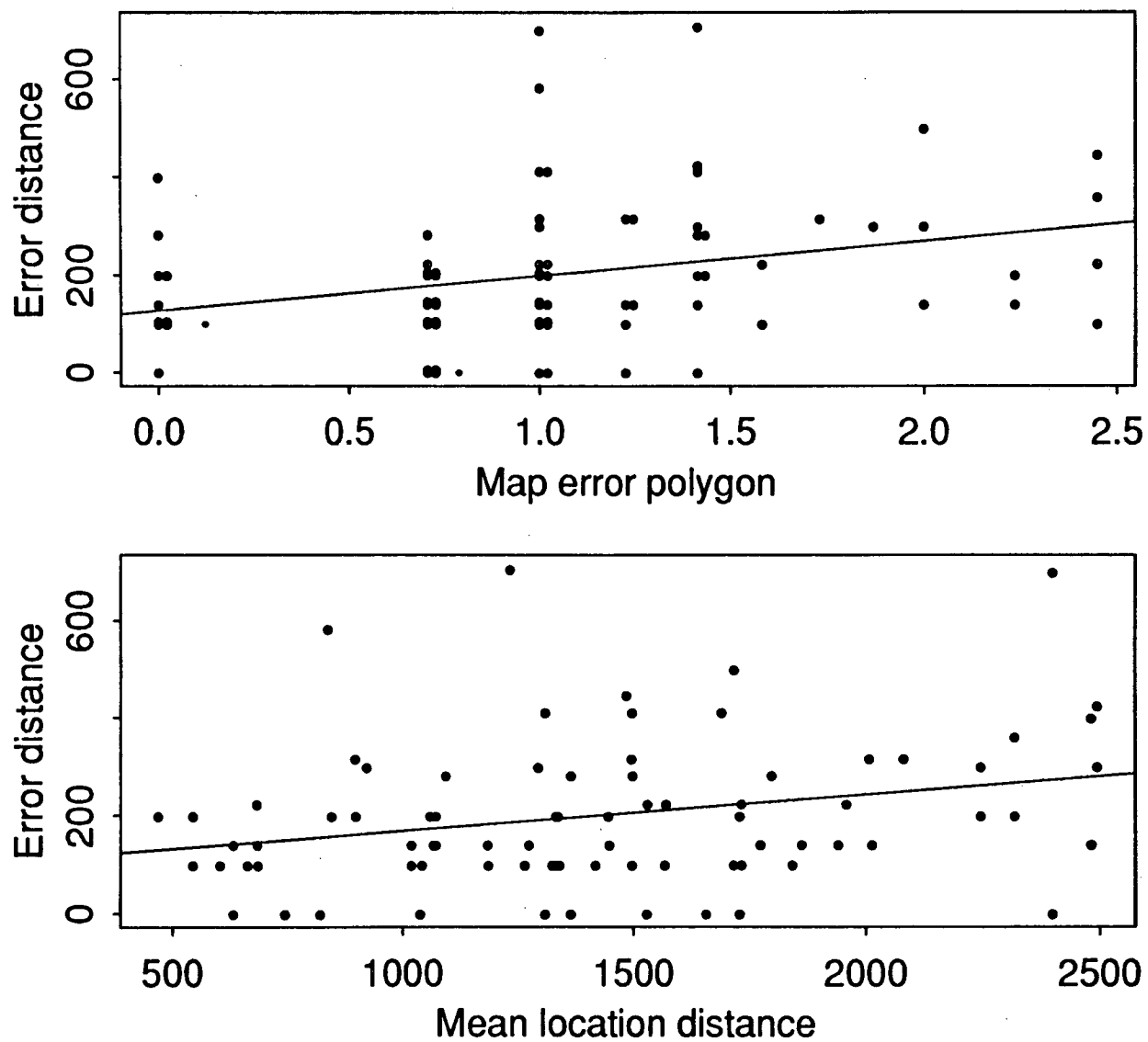
Fig. 5.3. The correlations between map error polygon and error distance (a.), and between mean location distance and error distance (b.).

Table 5.2. Part of the bias matrix for ecosite assignment. The complete matrix is 44 X 44, and only 6 representative ecosites are shown with the rest combined into the "other" column. Points with true habitat types of "other" are not presented.

TRUE	FR1	GA1	APPARENT PR2	PR4	VL4	HD1	OTHER
FR1	**67.44**	0.00	0.66	0.17	0.83	6.94	23.97
GA1	0.87	**89.08**	1.31	0.00	0.00	0.22	8.52
PR2	0.80	0.33	**79.91**	0.07	0.00	0.00	19.09
PR4	2.86	0.00	0.00	**53.33**	4.76	0.00	39.05
VL4	3.27	0.00	0.47	4.70	**75.23**	2.34	14.02
HD1	11.85	0.00	0.00	0.00	2.09	**65.51**	20.56
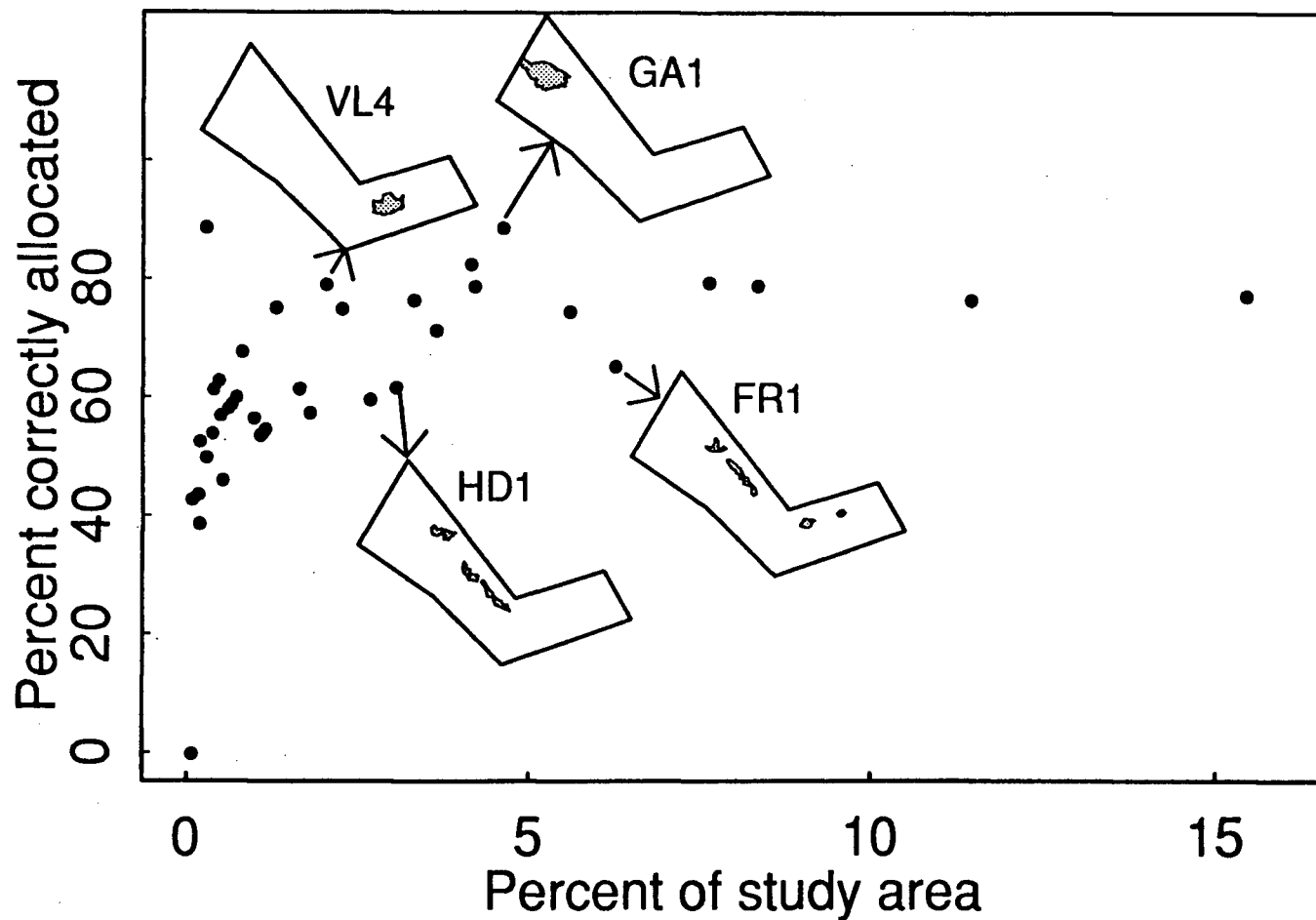
Fig. 5.4. The relationship between the percent of locations which were correctly allocated to the true ecosite and the percentage of the study area comprised of the true ecosite type. Each point represents an ecosite type. Examples of the distribution of four ecosites in the study area (L-shaped area) are given. VL4 and GA1 are large, roughly circular units of spruce and pine forests; HD1 and FR1 are thin, disjunct units of aspen and dry pine forests.

Table 5.3. Bias matrix for broad vegetation types in the study area. The value in each cell represents the percentage of the time that a collar in the true habitat type will be located in the apparent habitat type.

			APPARENT					
TRUE	Pine	Mixed	Spruce	Wet	Dry	Aspen	Grass	Alpine
Pine	<u>83.9</u>	3.7	5.5	0.6	3.3	1.7	1.1	0.2
Mixed	11.6	<u>82.6</u>	2.6	0.2	0.2	0.0	0.0	2.9
Spruce	11.5	2.6	<u>77.6</u>	3.8	1.8	1.7	0.5	0.5
Wet	6.8	1.6	17.3	<u>72.6</u>	0.0	1.6	0.0	0.0
Dry	13.6	0.4	3.6	0.0	<u>78.1</u>	0.2	1.6	2.5
Aspen	17.0	0.0	9.2	3.9	2.8	<u>66.4</u>	0.7	0.0
Grass	16.4	0.0	6.0	0.0	14.2	2.2	<u>61.2</u>	0.0
Alpine	3.2	7.2	1.4	0.0	4.1	0.0	0.0	<u>82.6</u>

habitat use vector is multiplied by the bias matrix (Table 5.3) to give the vector of apparent (telemetry) habitat use. Using this apparent vector, preferred or avoided habitats are still preferred or avoided, but to a lesser extent. Twice as many apparent locations are in the common pine habitat as in the rare aspen or grass habitats, although the animals were assumed to use each type equally often. Conversely, in Table 5.4b, I assume that telemetry indicates that all habitats are used equally often. Correcting this apparent habitat use vector (i.e. multiplying by the inverse of the bias matrix) shows that animals rarely use the common pine forest but are often in the rarer aspen or grasslands. Again, the true preference for or avoidance of habitats is much more pronounced than indicated by telemetry. Table 5.4c provides a real example of habitat use by wolves, observed by telemetry, and the true, corrected use this represents. Habitat selectivity is less pronounced here than in the hypothetical examples, but applying the correction for bias still produces substantial changes in the habitat use pattern.

Table 5.5 shows the bias matrix for simple versus complex topography. Points in complex topography, with greater relocation error distances, are less often correctly relocated in complex topography than points in simple topography.

Discussion

Telemetry bearings taken using large, tower-mounted antennas should be more precise than bearings from small, handheld antennas (Kenward, 1987). However, in mountainous environments, signal bounce can cause serious bearing errors (Garrott et al., 1986). Observers using mobile telemetry equipment can reduce the effects of bounce by moving to locations where bounce does not appear to occur, but this requires the observer to evaluate the likely sources of bounce from the topography in the area and to take multiple bearings to identify clearly erroneous bearings. The mobile observer can also reject uncertain relocations and move closer to the animal for a better relocation. These

Table 5.4. Examples of the effect of telemetry error on habitat use assessment, and correcting observed habitat use for the bias introduced by telemetry error. Preference for a habitat type is summarized as the ratio of the proportions of locations in a habitat type to the proportion of that habitat available. A ratio less than 1 indicates avoidance; a ratio greater than 1 indicates preference. Numbers in bold are the known/assumed values.

a. The number of relocations expected in each broad vegetation type given an assumed true pattern of habitat use.

Habitat	True use	True Preference->	Apparent use	Apparent Preference
Pine	**1000**	**0.30**	1639	0.49
Mixed	**1000**	**0.79**	981	0.78
Spruce	**1000**	**0.64**	1231	0.79
Wet	**1000**	**3.38**	811	2.74
Dry	**1000**	**1.19**	1045	1.25
Aspen	**1000**	**4.40**	739	3.26
Grasslands	**1000**	**9.30**	652	6.07
Alpine	**1000**	**2.82**	887	2.50

b. The number of true locations expected based on the apparent pattern of habitat use from telemetry relocations.

Habitat	True use	True Preference<-	Apparent use	Apparent Preference
Pine	82	0.02	**1000**	**0.30**
Mixed	1059	0.84	**1000**	**0.79**
Spruce	617	0.39	**1000**	**0.64**
Wet	1266	4.27	**1000**	**3.38**
Dry	861	1.02	**1000**	**1.19**
Aspen	1400	6.15	**1000**	**4.40**
Grasslands	1588	14.78	**1000**	**9.30**
Alpine	1144	3.21	**1000**	**2.82**

c. The true use of habitats based 520 winter telemetry locations of collared wolves in the study area, corrected for the bias caused by telemetry error. Habitat use is expressed as the proportion of locations in that habitat. Alpine habitat was not included in this study area.

Habitat	True use	True Preference<-	Apparent use	Apparent Preference
Pine	0.19	0.45	**0.25**	**0.59**
Mixed	0.13	0.82	**0.13**	**0.81**
Spruce	0.49	2.54	**0.42**	**2.16**
Wet	0.10	2.74	**0.09**	**2.59**
Dry	0.02	0.17	**0.03**	**0.31**
Aspen	0.06	1.98	**0.05**	**1.80**
Grasslands	0.01	0.93	**0.01**	**0.97**

Table 5.5. Bias matrix for simple versus complex topography. Matrix gives the percentage of the time that an animal is in the true topography type that it will be located in the apparent type.

TRUE	APPARENT Simple	Complex
SIMPLE	90.44	9.56
COMPLEX	16.44	83.56

are subjective procedures and the only way to quantify the expected error associated with the resulting relocation is the empirical method of relocating collars in a known position, as was done in this paper.

The map error polygon (Fig. 5.1) may be used in the field as an indication of the precision of a relocation - it is small when all 3 pairs of bearings cross nearby. However, it is not a good index of the accuracy of the location. The square root of the area of the map error polygon is often less than the actual error distance, and is only weakly correlated with the actual error distance (Fig. 5.3a). The mean bearing distance is also an unreliable indicator of the accuracy of the relocation (Fig. 5.3b), as Kufeld et al. (1987) also found. The maximum angle of intersection of the 3 bearings generally ranged from 50 to 100 degrees in this study, and was also only weakly correlated with the error distance. There does not appear to be a simple reliable indicator of the accuracy of single relocations.

Error distance was greater in complex topography than in simple topography (Table 5.1) and all 9 error distances of 400m or more came from collars in complex topography. However, 9 of the 13 collars which could not be relocated were in simple topography. Rock faces or cliff bands were obvious sources of bounced signals in this study, and signal strength in the direction of the bounce could be stronger than in the direction of the collar, particularly when the collar was behind a protruding landform ("non-line-of-sight"; Garrott et al., 1986). This happened occasionally when the collar was in simple topography, in which case some bearings would be towards the bounce source; from other observer locations, the collar would not be obscured and the bearing would be towards the collar. This produced 2 general areas where bearings intersected (near the collar and towards the bounce source). The observer, not being able to resolve which was the true relocation point, would reject the relocation. In contrast, some collars in complex topography could be behind a landform for all observer positions (e.g. behind a hummock or in a gully), in which case the bearing would consistently be directed at a

bounce source. This would produce an apparently precise, but inaccurate, relocation which the observer would accept.

These telemetry errors can cause incorrect assessment of habitat use, particularly with rare habitat types (Fig. 5.4). The relationship in Fig. 5.4 can be used to determine how finely the habitat can be divided for telemetry studies - in this case, habitat units comprising less than 2% of the study area will frequently be misallocated, and this could represent a lower limit on the size of useable habitat groups. Telemetry information about the use of many of the rare ecosites in this study area would be unreliable, and even assignments to broad habitat types will be incorrect about 20% of the time.

In addition to the overall abundance of the habitat units, the following factors combine to determine the bias matrix:

1. Relative size of the habitat units. The percentage of successful assignments is greater for habitats which occur as large, contiguous patches. For example, only 83% of points in pine forest, which comprises 41.8% of the study area, were correctly assigned to 'pine' (Table 5.3), because pine occurs in small patches, interspersed among other habitat types. Mixed forest comprises only 15.7% of the study area, but because it occurs as large patches, the same percentage of assignments are successful.

2. Shapes of habitat units. Points are less likely to be assigned correctly to long, thin habitat units than to circular ones of the same area. For example, VL4 and GA1 are comprised of roughly circular units and points in these ecosites are more often correctly assigned than points in HD1 or FR1 which occur in strips along the base of the valley walls (Fig. 5.4).

3. Association of habitat units. Incorrectly assigned points are not distributed randomly among the remaining habitats because certain habitat types tend to be adjacent to each other. For example, incorrectly assigned points from grassland habitats are assigned to dry forest much more often than expected (Table 5.3). Of

the 39% of misassigned points from grasslands, we would expect by chance about 3.9% to fall in dry forest, which comprises about 10% of the non-grassland area. Because dry forest is frequently adjacent to grassland, the actual value is 14.9%. Due to this association, animals which show a strong preference for grassland, will also show an apparent preference for dry forest, even if they avoid this habitat.

4. Topography associations. Correct assignment is lower for habitats associated with complex topography, where relocation errors are larger.

Conclusions and management implications

Telemetry relocations can be highly inaccurate in mountainous areas. Beyond rejecting relocations that the observer feels are clearly uncertain, no useful way was found to assess the inaccuracy of a single relocation. In particular, some relocations in complex topography appeared precise, but were highly inaccurate.

Establishing and relocating collars in known locations, calculating telemetry error and generating bias matrices through simulations on G.I.S. systems is laborious and time-consuming. However, any study relying on telemetry to provide information on habitat use is likely to produce inaccurate results if the habitat use data are not corrected with a bias matrix. Because many factors, such as the relative area, size, shape, configuration and association of habitat units and the magnitude and orientation of the telemetry error affect the bias matrix and are specific to the study area, each project would have to calculate its own bias matrix.

The bias introduced by telemetry error is particularly pronounced for small, highly preferred habitats, which are likely to be of prime interest to wildlife managers. For instance, small patches of grasslands, open slopes or small wetlands may be highly

preferred habitats, but telemetry error is likely to mask this preference, and the importance of these habitats will be underestimated. This problem is not unique to ground triangulation and should also be considered with aerial telemetry when the animal is not seen, and with satellite telemetry.

Chapter 6. General Conclusion

Wolf studies have been conducted in more than 25 locations across northern North America, encompassing a wide variety of physical environments and available prey bases. A large number of studies, over a range of ecological conditions, should allow us to discern general features of the prey selectivity of wolves through comparison. However, few generalities are apparent. Several studies have found that non-ungulates are less preferred than ungulate prey (e.g. Voigt et al., 1976; Ballard et al., 1981), that all available ungulates are eaten, though usually not in proportion to their abundance (e.g. Haber, 1977; Carbyn, 1983) and that calves or old animals are preferred (e.g. Pimlott et al., 1967; Peterson, 1977; Fuller and Keith, 1980; Peterson et al., 1984). For each of these general phenomena, however, there are studies which have failed to find this pattern (e.g. old adults: Kolenosky, 1972; calves: Messier and Crete, 1985), or have found the opposite (e.g. non-ungulates: Shelton and Peterson, 1983).

This variability may initially suggest that no general principles underlie selectivity by wolves, and that selectivity under a given set of environmental conditions can never be predicted a priori. Previous studies of wolves have generally taken a "black-box" approach to selectivity (Taylor, 1984), in which the number of available prey individuals is measured and the wolves' diet quantified. Selectivity is then described by comparing the two, with little insight into the underlying causes and limited ability to predict how the "black box" will respond to changing prey densities or environmental conditions. By looking at the components of the system which generate selectivity, as I have done in this thesis, we will be able better to predict how different or changing conditions will affect selectivity.

The first important component of selectivity I measured was the degree of overlap of the prey species with wolves. Bighorn sheep and mountain goats use habitats away from wolves and are therefore encountered and killed less often than expected on the

basis of overall numbers. This refuge effect would decrease as abundances of sheep or goats increased and they began to use lower elevation habitats or it became profitable for wolves to hunt in higher areas, resulting in a predicted functional response of the type III (Holling, 1959a) form. A more sophisticated approach could predict habitat overlap based on the energetic benefits of hunting at high elevations for wolves (i.e. patch use model; Stephens and Krebs, 1986), or the trade-off between foraging and predation risk (McNamara and Houston, 1987) for sheep or goats at different densities. Habitat overlap with wolves is high for the other species in the Banff system, and differential habitat overlap is relatively unimportant in determining selectivity within elk.

The second influence on selectivity I examined is the aggregation of prey species into herds. Biologists typically count the numbers of individuals of a species, and assume that individuals are the unit of available prey for predators. However, I argued that the small size of herds compared to the distances between them, the coordinated response of herds, the increased wariness and presumed decreased vulnerability of the entire herd following an attack and the fact that consecutive kills are almost always from different herds suggest that considering the herd as the unit encountered by wolves is more realistic biologically. In this case, the size of herds is an important determinant of overall selectivity. This is especially true for selectivity within elk, where males are less common than females, but occur in smaller herds and are therefore encountered as often, producing an overall selectivity for males over females. Calves, on the other hand, are preferred by wolves over adults, but are not highly selected overall because they occur in relatively few herds. The association of females with calves probably reduces predation on females. Herd dynamics, the changes in herd sizes and composition with changes in prey numbers, is therefore a critical component of predator-prey dynamics in systems with herding species, and merits greater attention in studies of wolf ecology. In addition, the use of predictable herds by wolves violates the assumption of random search used to

generate classical functional responses and could lead to less stable interactions between wolves and elk, or other species which predictably use certain areas.

The third component of selectivity I examined was the preference of wolves for certain species upon encounter (i.e. whether wolves avoid attacking species of low profitability). Simple prey selection models of foraging theory (Stephens and Krebs, 1986) suggested that all ungulate prey is of similar profitability, and in sequential encounters wolves should attack any herd they encounter, regardless of species or age/sex composition. However, when different prey types are encountered simultaneously in a mixed herd (e.g. cow and calf elk) the sequential encounter model does not apply and wolves should show preference for certain prey types. This is particularly true when herds become more wary and less vulnerable following an attack by wolves; if wolves attack an animal they are unlikely to catch, the whole herd, including the more vulnerable animals, becomes unavailable temporarily.

Several components which affect selectivity remain unquantified. The relative detectability of different prey types and the attack success of wolves both contribute in determining the wolves' diet, but are very difficult to measure. I have assumed that these are either similar among different prey types, or do not change with prey density and therefore do not alter the predicted functional responses. Future studies should analyze this assumption.

Separating the dynamics of predators into the numerical and functional response simplified the analysis of complex predator-prey interactions, allowing insights into the mechanisms causing complex behaviour in systems. Similarly, analyzing the components which generate the selectivity of predators can allow better prediction of their functional responses. This is particularly true for wolf predation, where the form of the functional response is critical for understanding and managing the large mammal systems, but where this response can rarely be measured directly. Future studies of wolf

predation would benefit by examining the various components producing the overall selectivity they observe.

References cited

Abrams, P.A., 1982. Functional responses of optimal foragers. Am. Nat. 120:382-390.

Abrams, P.A., 1987. The functional responses of adaptive consumers of two resources. Theor. Pop. Biol. 33:262-288.

Altmann, M., 1960. The role of juvenile elk and moose in the social dynamics of their species. Zoologica 45:35-39.

Amlaner, C.J. (ed.), 1988. Biotelemetry X: Proceedings of the tenth international symposium on biotelemetry. Univ. of Arkansas Press, Fayetteville. 733pp.

Armstrong, R.A., 1976. The effects of predator functional response and prey productivity on predator-prey stability: a graphical approach. Ecol. 57:609-611.

Ballard, W.B., R.O. Stephenson and T.H. Spraker, 1981. Nelchina Basin wolf studies. Alaska Dept. Fish and Game. Fed. Aid in Wildl. Rest. Final report project W17-8 through W17-11. 201pp.

Ballard, W.B., .S. Whitman and C.L. Gardner, 1987. Ecology of an exploited wolf population in southcentral Alaska. Wildl. Monogr. No. 98. 51 pp.

Belovsky, G.E., 1978. Diet optimization in a generalist herbivore: the moose. Ecol. 62:1020-1030.

Bertch, B., 1989. Goat monitoring report, 1988. Can. Parks Serv. document, Banff, Alberta. 33pp.

Bibikov, D.I., 1979. Wolf ecology and management in the USSR. In: Wolves of the world, F.H. Harrington and P.C. Paquet (eds.). Noyes Publications, Park Ridge, N.J. pp. 120-133.

Bjorge, R.R. and J.R. Gunson, 1989. Wolf, *Canis lupus*, population characteristics and prey relationships near Simonette River, Alberta. Can. Field-Nat. 103:327-334.

Boutin, S. and H.D. Cluff, 1989. Coyote prey choice: Optimal or opporunistic foraging? A comment. J. Wildl. Manage. 53:663-666.

Carbyn, L.N., 1974. Wolf predation and behavioural interactions with elk and other ungulates in an area of high prey diversity. PhD thesis, Univ. Toronto, Toronto. 233pp.

Carbyn, L.N., 1983a. Wolf predation on elk in Riding Mountain National Park, Manitoba. J. Wildl. Manage. 47:963-976.

Carbyn, L.N., 1983b. Wolves in Canada and Alaska: their status, biology and management. Can. Wildl. Serv., Ottawa. 135pp.

Charnov, E.L. and G.H. Orians, 1973. Optimal foraging: some theoretical explorations. Unpub. MS.

Charnov, E.L., G.H. Orians and K. Hyatt, 1976. Ecological implications of resource depression. Am. Nat. 110:247-259.

Chesson, J., 1978. Measuring preference in selective predation. Ecol. 59:211-215.

Clutton-Brock, T.H., F.E. Guinness and S.D. Albon, 1982. Red deer: Behaviour and ecology of two sexes. Univ. of Chicago Press, Chicago. 378pp.

Corbett, L.K., 1989. Assessing the diet of dingoes from feces: a comparison of 3 methods. J. Wildl. Manage. 53:343-347.

Cowan, I. McT., 1947. The timber wolf in the Rocky Mountain National Parks of Canada. Can. J. Res. 25D:139-174.

Cowan, I. McT., 1950. Some vital statistics of big game on over-stocked mountain range. Trans. N. Am. Wildl. Conf. 15:581-588.

Emlen, J.E., 1984. Natural selection and population density-feedback II. The evolution of functional response curves. Theor. Pop. Biol. 25:62-77.

Fancy, S.G., 1980. Preparation of mammalian teeth for age determination by cementum layers: a review. Wildl. Soc. Bull. 8:242-248.

Flook, D., 1970. Causes and implications of observed sex differential in the survival of wapiti. Can. Wildl. Serv. Rep. Ser. 11. 77pp.

Floyd, T.J., L.D. Mech and P.A. Jordan, 1978. Relating wolf scat content to prey consumed. J. Wildl. Manage. 42:528-532.

Fritts, S.H. and L.D. Mech, 1981. Dynamics, movements and feeding ecology of a newly-protected wolf population in northwestern Minnesota. Wildl. Monogr. No. 80. 79pp.

Fuller, T.K., 1990. Dynamics of a declining white-tailed deer population in north-central Minnesota. Wildl. Monogr. No. 110. 37pp.

Fuller, T.K., 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. Can. J. Zool. 69:283-287.

Fuller, T.K. and L.B. Keith, 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J. Wildl. Manage. 44:583-602.

Garrott, R.A., G.C. White, R.M. Bartmenn and D.L. Weybright, 1986. Reflected signal bias in biotelemetry triangulation systems. J. Wildl. Manage. 50:747-752.

Haber, G.C., 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. thesis, Univ. British Columbia, Vancouver.

Hassell, M.P., 1978. The dynamics of arthropod predator-prey systems. Monogr. Pop. Biol. No. 13, Princeton Univ. Press, Princeton.

Heezen, K.L. and J.R. Tester, 1967. Evaluation of radio-tracking by triangulation with special reference to deer movements. J. Wildl. Manage. 31:124-141.

Holland, W.D. and G.M. Coen, 1982. Ecological (Biophysical) land classification of Banff and Jasper national parks, volume II: Soil and vegetation resources. Alta. Inst. Pedology Pub. SS-82-44. 540pp..

Holland, W.D. and G.M. Coen, 1983. Ecological (biophysical) land classification of Banff and Jasper national parks, volume I: Summary. Alta. Inst. Pedology Pub. M-83-2 193pp.

Holling, C.S., 1959a. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91:293-320.

Holling, C.S., 1959b. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91:365-398.

Holling, C.S., 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45:1-60.

Holling, C.S., 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48:1-86.

Holroyd, G.L. and K.J. Van Tighem, 1983. Ecological (Biophysical) Land Classification of Banff and Jasper National Parkks, Vol. III: The Wildlife Inventory. Can. Wildl. Serv., Edmonton. 691pp.

Hupp, J.W. and J.T. Ratti, 1983. A test of radio telemetry triangulation accuracy in heterogeneous environments. Proc. Int. Wildl. Biotelem. Conf. 4:31-46.

Kennedy, A.J. and L.N. Carbyn, 1981. Identification of wolf prey using hair and feather remains with special reference to western Canadian national parks. Can. Wildl. Ser. Rep. 65pp.

Kenward, R., 1987. Wildlife radio tagging. Academic Press, London. 222pp.

Kolenosky, G.B., 1972. Wolf predation on wintering deer in east-central Ontario. J. Wildl. Manage. 36:357-369.

Krebs, C.J., 1989. Ecological methodology. Harper and Row, New York. 654pp.

Kufeld, R.C., D.C. Bowden and J.M. Siperek, 1987. Evaluation of a telemetry system for measuring habitat usage in mountainous terrain. Northwest Sci. 61:249-256.

Kunelius, R., 1985a. Bighorn sheep monitoring, Banff National Park. Can. Parks Serv. document, Banff, Alberta, 37pp.

Kunelius, R., 1985b. Methodology for Bow Valley aerial elk surveys, Banff National Park. Can. Parks Serv., Banff, Alta.

Lee, J.E., G.C. White, R.A. Garrott, R.M. Bartmann and A.W. Alldredge, 1985. Assessing the accuracy of a radiotelemetry system for estimating animal locations. J. Wildl. Manage. 49:658-663.

Levin, S.A., 1977. A more functional response to predator-prey stability. Am. Nat. 111:381-383.

Manly, B.F.J., 1974. A model for certain types of selection experiments. Biometrics 30:281-294.

May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471-477.

McMurtie, R., 1978. Persistence and stability of single-species and prey-predator systems in spatially heterogeneous environments. Math. Biosci. 39:11-51.

McNair, J.N., 1980. A stochastic foraging model with predator training effects. I. Functional response, switching, and run lengths. Theor. Pop. Biol. 17:141-166.

McNamara, J.M. and A.I. Houston, 1987. Starvation and predation as factors limiting population size. Ecol. 68:1515-1519.

Mech, L.D., 1970. The wolf: ecology and behaviour of an endangered species. The Natural History Press, New York.

Mech, L.D., 1977. Wolf pack buffer zones as prey reservoirs. Science 198:320-321.

Mech, L.D. and G.D. DelGiudice, 1985. Limitations of the marrow-fat technique as an indicator of body condition. Wildl. Soc. Bull. 13:204-206.

Mech, L.D., L.D. Frenzel, Jr. and P.D. Karns, 1971. The effect of snow conditions on the vulnerability of white-tailed deer to predation. U.S. Dept. Agr. Res. Paper N.C. 52:51-59.

Mech, L.D. and L.D. Frenzel Jr., 1971. An analysis of the age, sex, and condition of deer killed by wolves in northeastern Minnesota. U.S. For. Serv. Res. Pap. No. NC-52, pp. 35-50.

Mech, L.D. and P.D. Karns, 1977. Role of the wolf in a deer decline in the Superior National Forest. U.S. Dept. Agric. For. Serv., Res. Pap. NC-143. 23pp.

Messier, F. and M. Crete, 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecol. 65:503-512.

Mickle, D., G. Fortin and R. Kunelius, 1986. Status of wolves, Banff National Park. Can. Parks Serv., Banff, Alberta. 31 pp.

Mitchell, W.A. and J.S. Brown, 1990. Density-dependent harvest rates by optimal foragers. Oikos 57:180-190.

Moore, T.D., L.E. Spence and C.E. Dugnolle, 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Dept.

Morgantini, L.E. and R.J. Hudson, 1988. Migratory patterns of the wapiti, *Cervus elaphus*, in Banff National Park, Alberta. Can. Field-Nat. 102:12-19

Murdoch, W.W., 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39:335-354.

Murie, A., 1944. The wolves of Mount McKinley. U.S. Natl. Park Serv. Fauna Ser. 238pp.

Nams, V.O., 1989. Effects of radiotelemetry error on sample size and bias when testing for habitat selection. Can. J. Zool. 67:1631-1636.

Neff, D.J., 1968. The pellet-group count technique for big game trend, census, and distribution: a review. J. Wildl. Manage. 32:597-614.

Nelson, M.E. and L.D. Mech, 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildl. Monogr. No. 77. 53pp.

Nelson, M.E. and L.D. Mech, 1985. Observation of a wolf killed by a deer. J. Mammal. 66:187-188.

Nelson, M.E. and L.D. Mech, 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. J. Wildl. Manage. 50:471-474.

Nishimura, K. and M.T. Abe, 1988. Prey susceptibilities, prey utilization and variable attack efficiencies of Ural owls. Oecol. 77:414-422.

Oosenbrug, S.M. and L.N. Carbyn, 1985. Wolf predation on bison in Wood Buffalo National Park. Can. Wildl. Serv., Edmonton, Alberta. 264pp.

Orians, G.H. and N.E. Pearson, 1979. On the theory of central place foraging. In: A.C. Kamil and T.D. Sargent (eds.), Analysis of ecological systems. pp. 154-177. Ohio State Univ. Press, Columbus.

Palmer, A.R. and C. Strobeck, 1986. Fluctuating asymmetry: measurement, analysis, patterns. Ann. Rev. Ecol. Syst. 17:391-422.

Peterson, R.O., 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Natl. Park Serv., Scientific Monogr. Series, No. 11. 210pp.

Peterson, R.O. and D.L. Allen, 1974. Snow conditions as a parameter in moose-wolf relationships. Nat. Can. 101:481-492.

Peterson, R.O., J.D. Woolington and T.N. Bailey, 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Mongr. 52pp.

Pimlott, D.H., J.A. Shannon and G.B. Kolenosky, 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ont. Dept. Lands For. Res. Rep. Wildl. No. 87. 92pp.

Potvin, F., H. Jolicoeur and J. Huot, 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. Can. J. Zool. 66:1274-1279.

Pyke, G.H., 1984. Optimal foraging theory: a critical review. Ann. Rev. Ecol. Syst. 15:523-575.

Rausch, R.A., R.J. Somerville and R.H. Bishop, 1974. Moose management in Alaska. Nat. Can. (Que.) 101:705-721.

Real, L.A., 1979. Ecological determinants of functional response. Ecol. 60:481-485.

Rogers, D.J., 1972. Random search and insect population models. J. Anim. Ecol. 41:369-383.

Saltz, D. and G.C. White, 1990. Comparison of different measures of the error in simulated radio-telemetry locations. J. Wildl. Manage. 54:169-174.

Scott, B.M.V. and D.M. Shackleton, 1980. Food habits of two Vancouver Island wolf packs: a preliminary study. Can. J. Zool. 58:1203-1207.

Shelton, P.C. and R.O. Peterson, 1983. Beaver, wolf and moose interactions in Isle Royale National Park, U.S.A. Acta Zool. Fennica 174:265-266.

Solomon, M.E., 1949. The natural control of animal populations. J. Anim. Ecol. 18:1-35

Springer, J.T., 1979. Some sources of bias and sampling error in radio triangulation. J. Wildl. Manage. 43:926-935.

Stenlund, M.H., 1955. A field study of the timber wolf (Canis lupus) on the Superior National Forest, Minnesota. Minn. Dept. Conserv. Tech. Bull. No. 4.

Stephens, D.W. and J.R. Krebs, 1986. Foraging Theory. Princeton Univ. Press, Princeton, N.J. 247pp.

Stephenson, R.O. and D. James, 1979. Wolf movements and food habits in northwest Alaska. In: Wolves of the world, F.H. Harrington and P.C. Paquet (eds.). Noyes Publications, Park Ridge, N.J. pp. 26-42.

Stephenson, R.O. and L.J. Johnson, 1973. Wolf report. Vo.. XI. Annual project segments report. Alaska Dept. of Fish and Game. 52pp.

Taber, R.D., 1971. Criteria of sex and age. In: Wildlife management techniques. The Wildlife Society, Washington. pp 325-401.

Taylor, R.J., 1979. The value of clumping to prey when detectability increases with group size. Am. Nat. 113:299-301.

Taylor, R.J., 1981. Ambush predation as a destabilizing influence upon prey populations. Am. Nat. 118:102-109.

Taylor, R.J., 1984. Predation. Chapman and Hall, New York. 166pp.

Temeles, E.J., 1989. Effect of prey consumption on foraging activity of northern harriers. Auk 106:353-357.

Temple, S.A., 1987. Do predators always catch substandard individuals disproportionately from prey populations? Ecol. 68:669-674.

Theberge, J.B. and T.S. Cottrell, 1975. Food habits of wolves in Kluane National Park. Arctic 30:189-191.

Theberge, J.B., S.M. Oosenbrug and D.H. Pimlott, 1978. Site and seasonal variation in food of wolves, Algonquin Park, Ontario. Can. Field-Nat. 92:91-94.

Trottier, G.C., S.R. Rollans and R.C. Hutchison, 1983. Range, habitat and foraging reloationships of ungulates in Riding Mountain National Park. Can. Wildl. Serv. (Large mammal systems studies, rep. no. 14).

Verme, L.J. and J.C. Holland, 1973. Reagent-dry assay of marrow fat in white-tailed deer. J. Wildl. Manage. 37:103-105.

Voigt, D.R., G.B. Kolenosky and D.H. Pimlott, 1976. Changes in summer food of wolves in central Ontarion. J. Wildl. Manage. 40:663-668.

Walters, C.J., M. Stocker and G.C. Haber, 1981. Simulation and optimization models for a wolf-ungulate system. In: Fowler, C.W. and T.D. Smith (eds). Dynamics of large mammal populations. John Wiley and Sons, New York, pp 317-337.

Wanink, J. and L. Zwarts, 1985. Does an optimally foraging oystercatcher obey the functional response? Oecol. 67:98-106.

Weaver, J.L. and S.H. Fritts, 1979. Comparison of coyote and wolf scat diameters. J. Wildl. Manage. 43:786-788.

Woods, J.G., 1991. The ecology of a partially migratory elk population. PhD. thesis, Univ. B.C.