

ECOLOGY AND BEHAVIOUR OF WOLVERINE IN YUKON

by

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ABSTRACT

Wolverine carcasses were submitted by trappers over 3 winters, between 1982–1985. The mean *in utero* litter size was $3.2 \pm \text{S.D. } 0.8$ young. Not all females within adult age classes were pregnant. Seasonal food habits were determined from winter stomachs, scats and observations. In order of importance, prey in the winter diet consisted of ungulate supplemented by snowshoe hare, sciurids, birds and small mammals. Home range and habitat use were investigated using radio-telemetry in the Kluane Game Sanctuary of southwest Yukon. Home ranges were small compared to those of wolverine in other areas. Only 1 of 3 adult females had kits. The demands of raising young are high and may reduce a female's probability of reproducing the following year. Individual variability was apparent in use of forest cover types, slopes, elevations and aspects. Home range and habitat use are functions of the distribution and availability of prey and likely vary across Yukon. A density of 1 resident wolverine per 177 km² was estimated within the study area. A consistent bias towards males was apparent in Yukon harvests. This vulnerability to trapping was attributed to the larger home ranges and greater movements of males than those of females. Yearly differences in trapper effort may alter expected harvest patterns. Prey distribution and availability affect vulnerabilities of all age classes. A productivity index for ecoregions of Yukon was derived using harvest statistics. Diversity in habitat promotes diversity in prey and is important in determining productivity of ecoregions for wolverine. A population size for Yukon after reproduction and before trapping was estimated as 4380. Wolverine populations in Yukon do not appear to be declining. Population indices could not be derived because harvest data are confounded by trapper effort and differential vulnerability of sex/age classes. The relationship between trapper effort and harvest should be quantified. Education of trappers for management of wolverine is recommended.

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PART A
INTRODUCTION

The wolverine (*Gulo gulo*), the largest member of the Mustelidae, is one of the least known carnivores in North America. Wolverine occur at low densities, have a solitary nature and are residents of sparsely inhabited tundra, boreal forest and mountainous regions. These attributes have made the study of this species logistically difficult and the literature on its biology is meagre. Distribution of wolverine in North America has been described by van Zyll de Jong (1975) and Kelsall (1981). Historically, wolverine ranged over most of Canada and the northern United States with the exceptions of Newfoundland, Prince Edward Island, the southern Prairies and the Queen Charlotte Islands. In eastern Canada, the species has become rare and restricted in distribution. The limit of wolverine range in Alberta, Saskatchewan and Manitoba has receded to the northern fringes of these provinces. Only British Columbia, Yukon and Northwest Territories contain significant remnants of original wolverine populations.

Reproduction of Yukon and Alaskan wolverine has been reported on by Wright and Rausch (1955) and Rausch and Pearson (1972). Holbrow (1976) undertook a comprehensive review on the biology, mythology, distribution and management of wolverine in western Canada. Liskop et al. (1981) presented reproductive data taken from carcasses of wolverine trapped in northern British Columbia from 1976 to 1979. Banci (1982) reported on age determination methods and reevaluated the status of Vancouver Island wolverine, *Gulo gulo vancouverensis*. Researchers in Scandinavia, notably Krott (1959), Pulliainen (1963), Myhre (1967) and Myrberget et al. (1969), have studied wolverine in the wild using snow-tracking. The advent of radio-telemetry facilitated field studies of wolverine, first used by Hornocker and Hash (1981) in Montana. Subsequently, Magoun (1985) radio-tracked wolverine in arctic Alaska, and Whitman and Ballard (1983) and Gardner (1985) in south-central Alaska. This thesis describes the first radio-tracking study of wolverine in Canada.

Wolverine occur throughout Yukon, in all forested, alpine tundra and arctic regions. The species is classified both as a fur-bearer and a big game animal in the territory. Trapping occurs in most areas excepting Kluane National Park, Kluane Game Sanctuary, McArthur Game Preserve and the North Slope. The trapping season extends from 1 November to 31 March; there is no limit on the number

harvested. The hunting season extends from 1 August to 31 October; the limit is one per hunter per year. Since 1972/73, hunter take represents 2.5–9.7% of the annual harvest.

The average selling price of Yukon wolverine pelts has increased dramatically in the last 15 years, from \$26 in 1970/71 to \$263 in 1984/85. Pelt value affects the allocation of trapper effort and an increase in price may be equated with increasing demand. Canadian harvest of wolverine, from 1971 to 1982, increased with price paid per hide (Slough 1982). However, this trend was reversed in Yukon. Up to 1982/83, pelt values increased while harvests declined (Fig. 1.0, subsequent to 1982/83, harvest has increased). At that time, the Yukon Department of Renewable Resources identified a need for information on the biology of wolverine in the territory and for a method of assessing the status of populations (Slough 1982). This study was initiated in 1983 in conjunction with Government of Yukon and World Wildlife Fund (Canada) to pursue these objectives. My primary aim is to describe population parameters using morphological data from carcasses and behavioural data collected from live wolverine. Specific objectives of the thesis are to determine and describe:

1. Reproduction.
2. Morphology and condition in winter.
3. Seasonal food habits.
4. Home range and habitat use.
5. Harvest vulnerability patterns.
6. Habitat quality (productivity) of ecoregions and density.

Knowledge of spatial patterns, habitat use, food habits, age specific natality and mortality, estimates of density, and an understanding of how population growth is regulated are necessary to assess the status of harvested populations and to provide a sound base for management decisions. The process by which an animal copes with its environment is integrated and complex. An understanding of this process is gained by measuring population sizes, birth and death rates, the supply and use of energy and nutrients in the environment, spatial strategies and other facets of an animal's behaviour. Environments are not static but change daily,

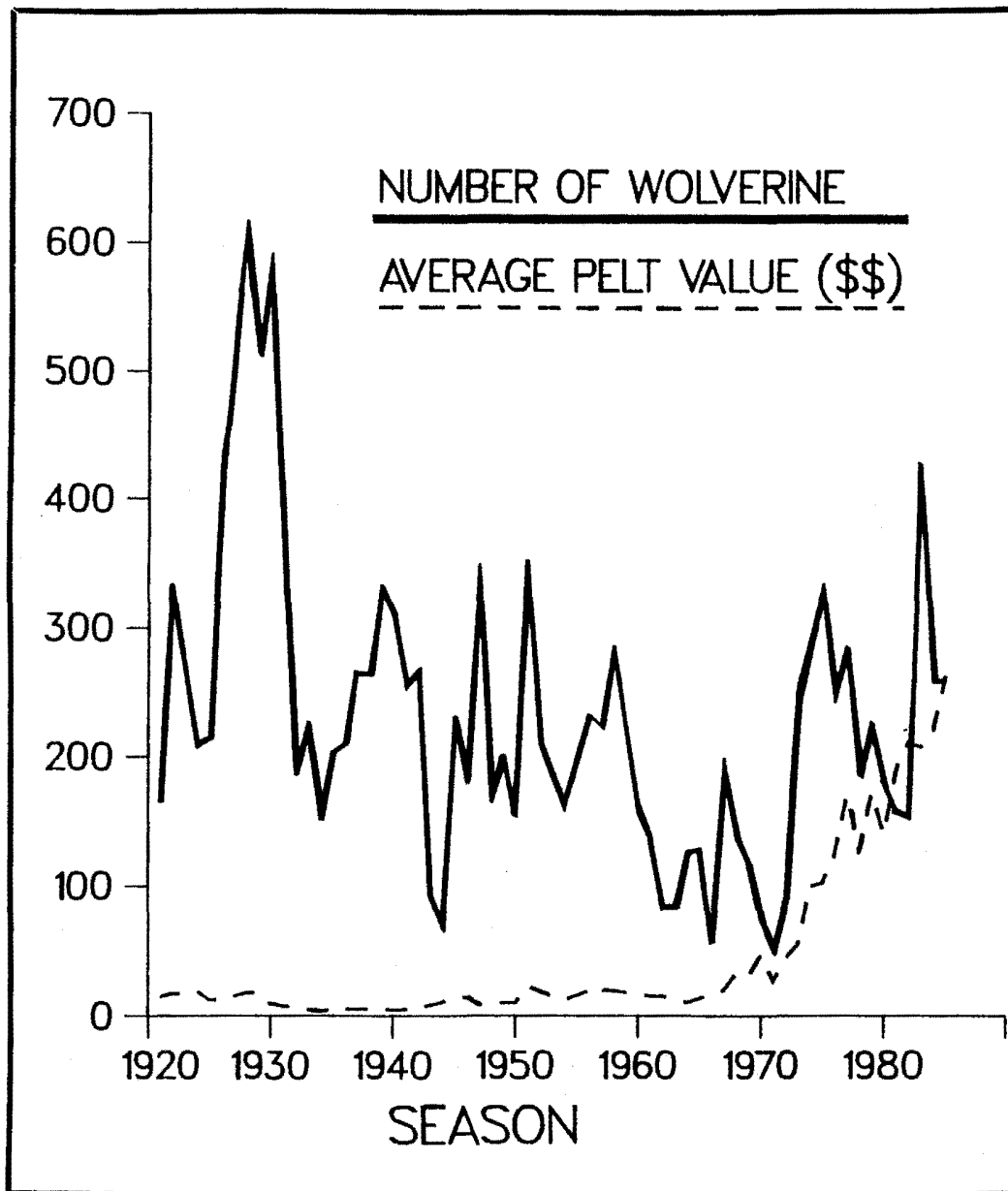


Fig. 1.0. Size and value of wolverine harvest in Yukon from 1920/21 to 1984/85.

Hunter take is included beginning 1971/72.

seasonally and yearly. Such variability necessitates that an animal's behaviour also be flexible. The capacity to deal with a variable environment does not remain constant throughout an animal's life but is affected by experience, reproductive status and physiological condition.

The addition of humans into the environment opens up a niche, that occupied by the wildlife manager. Man interacts with wild species by harvesting or through the use and alteration of habitats. The responsibility of a manager of a harvested furbearer is to maintain populations at some acceptable level while accommodating use by man, both consumptive and non-consumptive. When a management action becomes necessary, a manager has two basic options, to manipulate animals or to manipulate humans. The former may involve provision of high capability habitat; the latter may be achieved by controlling harvests. Furbearers are a diverse group occupying diverse areas and direct manipulation of populations and their habitats is difficult. Thus, managers attempt to manipulate harvests. Harvest data, the numbers of furbearers which are trapped, are easily collected. The sex and age of harvested animals may be determined with minimal additional effort. The collection and analysis of carcasses and the use of radio-telemetry for tracking wild species, however, are expensive and not routine management tools. A manager's objective is to obtain required information at the least cost and effort. However, harvest data are a function of differential vulnerability of sex/age classes to trapping and trapper effort as well as the abundance of animals. An understanding of the relationships between these variables and how the behaviour of furbearers is reflected in harvest data are necessary to interpret harvest patterns.

The nutritional requirements of pregnancy and lactation are great and the periods of reproduction are the most stressful and critical in the life of a mammal. For wolverine, reproduction occurs during the season of harvest. By knowing when pregnancy and parturition occur, periods of vulnerability within the trapping season may be identified. Age-specific natality, age at first reproduction and success of reproduction interact to determine a population's rate of growth. These life history parameters are readily determined from a sample of carcasses. However, accurate aging is crucial for their valid interpretation. Difficulties in aging wolverine using

standard techniques were apparent and required that I address these concerns.

An animal's physiological condition reflects the quality of its environment. Determining the condition or health of wolverine will allow me to identify periods of vulnerability. Body size, sex, age and reproductive status determine nutritional requirements and affect the ability or resilience of animals to withstand times of stress or low food availability. These factors must be considered when assessing the health of wolverine. The acquisition of food is central to understanding what habitats a furbearer uses, its activity patterns, health and vulnerability to trapping. Observations of feeding activity are difficult to obtain for furbearers, such as wolverine, that are rarely sighted and food habits are often determined using stomach contents or scats. Such data, however, may be biased because of the incidence of bait in the diet of a trapped species and the differential retention of prey remains within the gastro-intestinal tract. Thus, to assess the importance of prey found in the diet, the distribution and availability of prey within the environment must be known. These data are difficult to collect for wolverine and qualitative information is used to estimate prey availability.

Reproduction, physiological condition and food habits determined using carcasses provide the framework for interpreting behaviour observed from radio-collared wolverine. Insight into natural mortality factors, reproductive success, and prey distribution and availability is also gained by observing wolverine in their environment. Fulfillment of my first four objectives will assist in understanding the relationships between reproduction, condition, food, habitat use and spatial strategy, and will illustrate how these factors determine the vulnerability of wolverine to trapping and other mortality factors. The status of wolverine populations in Yukon is unknown and a readily applied index to population size or density is not available. Since 1951/52, the Yukon Department of Renewable Resources has collected extensive records on numbers of furbearers harvested. I use these harvests, an estimate of density determined from radio-tracking, knowledge of habitat use, home range size and prey requirements to assess the habitat capability of ecoregions of Yukon for wolverine. Current management regulations for wolverine in Yukon are reviewed and assessed. Sections are self contained

with respect to introduction, materials and methods, results and discussion. References are positioned at the end of the thesis.

The use of models and simulations to forecast future trends in population size has become common in wildlife biology. A population model based on information collected in this study is developed for wolverine. Data regarding the contribution of natural mortality factors and population size are lacking, thus the model is incomplete and preliminary. It is intended as an initial step in the attempt to manage wolverine populations using a theoretical, predictive model and has the capability to be improved as information becomes available. This model is outlined in the appendices.

PART B
ANALYSIS OF CARCASSES

CHAPTER I

REPRODUCTION

Simply stated, population growth is equivalent to the difference between the number of animals that are born and the number of animals that die. Age at first reproduction, litter size, breeding interval and age-specific differences in productivity interact to determine births, or a population's reproductive rate. A quantitative description of reproduction is at the core of understanding the dynamics of a population and essential for determining optimal timing and rates of harvests. There have been three studies on reproduction of wolverine (*Gulo gulo*). Wright and Rausch (1955) examined 22 males and 11 females from northern Alaska. Rausch and Pearson (1972) analyzed 366 females from Alaska, 51 females from Yukon and 43 males from both areas, harvested over an 8 year period (1960–1968). Liskop et al. (1981) examined 40 females and 44 males from northern British Columbia. Because of the preponderance of juvenile animals in these harvested samples and limitation of specimens to the trapping season, generally November through March, timing of implantation and parturition, gestation length, and age of sexual maturity were still not clearly defined.

Wright and Rausch (1955) established that wolverine, like many of the Mustelidae, have delayed implantation. Female wolverine are monestrous and males polygynous. Whether females are promiscuous is unknown. Breeding is thought to occur between April and October but primarily in mid-summer (Wright and Rausch 1955). Captive wolverine have bred in May (Mehrer 1976) and July (Mohr 1938). Wolverine have been observed breeding in the wild in Alaska during June (Krott and Gardner 1985) and August (Magoun and Valkenburg 1983). Implantation of blastocysts is from December through March (Rausch and Pearson 1972). Birth of 2 to 4 kits occurs in late winter and spring (Wright and Rausch 1955, Rausch and Pearson 1972, Liskop et al. 1981).

As part of a population study, the Yukon Department of Renewable Resources collected wolverine carcasses from trappers over 3 winters, 1982/83 to 1984/85. The trapping season in Yukon extends from 1 November to 31 March and this

description of reproduction is limited to this period. Reproduction is stressful for females because of the increased nutritional requirements of pregnancy and lactation. Knowing the timing of estrus, implantation and parturition will aid in establishing when during the trapping season females are most vulnerable. This information is necessary for setting or altering trapping seasons if natality is to be maximized.

The objectives of this study were to determine:

1. Extent and timing of proestrus.
2. Age of sexual maturity for males and females.
3. Incidence of non-reproducing females in age groups that are sexually mature.
4. Timing of implantation and parturition.
5. Age-specific natality.
6. Relationships between bacula measurements and age.

Age-related characteristics of the baculum have been used to distinguish young from adult mustelids (King 1980 and refs. within). Wolverine are inherently difficult to age (Banci 1982) and the large sample presented an opportunity to investigate the utility of bacula for aging male wolverine.

Age Determination

Accurate age classification is crucial for interpreting life history parameters. Use of cementum analysis to age mammals is the most prevalent technique in wildlife biology (Morris 1972). The underlying assumption in this method is that the number of cementum bands deposited (usually 2 per year) are equivalent to the age of the animal. However, as rate of deposition is typically unknown, validity of the technique for wild mammals has been rarely demonstrated. Rausch and Pearson (1972) and Banci (1982) investigated a number of alternative methods for aging wolverine. Both found that utility of skull measurements was limited to distinguishing young of year from adults. Extension of the sagittal crest for males and degree of closure of internasal and zygomatic sutures for both sexes were the most useful characteristics (Banci 1982). Banci (1982) acknowledged that her

comparison of skull attributes to age determined from cementum analysis was not entirely valid. However, uncertainty in the accuracy of a technique does not override the necessity of providing estimates of age.

North American studies on wolverine have relied on cementum analysis for aging (Liskop et al. 1981, Hornocker and Hash 1981, Gardner 1985, Magoun 1985). Limited data from Myhre (1967) and Magoun (1985) suggest cementum bands correspond to age in years for wolverine. The assumption that cementum analysis provides reliable estimates of age for wolverine is likely valid. However, differing methodology, even within the same technique, can bias results and make comparisons between studies untenable. Additionally, the clarity of cementum bands depends on the degree to which animals are affected by the environmental factors responsible for the rate of deposition of tissues (Morris 1972). Wolverine are one of the most difficult of mammals to age using cementum analysis, possibly because the distinction between a "good" season and a "poor" season in terms of available food is not clear (Banci 1982). Such difficulties require that complete documentation of the technique used is reported.

As teeth do not erupt in the same sequence, the choice of tooth used in cementum analysis may also be important. Shilo and Tamarovskaya (1981) documented the eruption sequence of teeth for wolverine. Permanent dentition begins to appear at 85 days of age. Incisors erupt first, followed by molars, premolars and canines. By day 150, all teeth are permanent. Differences in cementum deposition among teeth of wolverine has not been investigated. However, limited data using both premolars and incisors from the same wolverine indicated either tooth is suitable (Banci, unpub. data). Canines do not appear to be suitable candidates for aging as the cementum bands are close together and difficult to distinguish (Banci, pers. obs.).

Materials and Methods

Upper premolars were obtained from each carcass. If unavailable, other teeth used in order of selection were lower premolars, upper incisors or canines. Two teeth were processed for each wolverine. Teeth were decalcified, sectioned at 10 microns using a freezing microtome, and stained with Tolulene Blue. Most teeth were processed by the Wildlife Lab of Yukon Department of Renewable Resources, Whitehorse (Appendix 1.). A sample was sectioned at Simon Fraser University and approximately 60 teeth were sectioned by a commercial histologist (Matson's, P.O. Box 308, Milltown, Montana 59851) using the same procedure. Ages were estimated from annuli and age class was estimated using skull characteristics. As young are born during late winter through summer, age at capture of young of year in winter will be about 0.5 years. Consequently, ages are presented as 0+, 1+, 2+, and so on. For analysis, age 0+ is classed as "young of year", 1+ as "subadult" and 2+ and older, as "adult".

Usable specimens consisted of 180 female reproductive tracts, 199 male testes pairs, and 194 bacula. Incomplete aging reduced these sample sizes for some analyses. For females, reproductive tracts were removed and frozen whole. Tracts were thawed and ovaries sliced longitudinally in 1 mm sections under a dissecting microscope. Corpora lutea were counted and the presence of developing follicles recorded. Corpora lutea regress rapidly after parturition (Rausch and Pearson 1972) and are an exact count of the number of ova shed for the most recent litter. General characteristics of uteri were noted (not bred, thickened walls, flaccid). An attempt was made to flush uterine horns for blastocysts (Hamilton and Cook 1955) but few blastocysts were recovered and the technique was abandoned. Flushing does not appear to be a reliable technique for the recovery of blastocysts as loss rate is high (Rausch and Pearson 1972, Liskop et al. 1981). In addition, carcasses were in varying stages of decomposition and the condition of the blastocysts was questionable. Uterine horns were slit longitudinally and examined for placental scars. Regression of placental scars is relatively rapid (Rausch and Pearson 1972), therefore counts are not biased by scars from previous litters. If macroscopically

pregnant, fetuses were removed, weighed and crown-rump length measured.

Females were classified as:

1. non-reproductive: no corpora lutea, no developing follicles, no placental scars.
2. pre-reproductive: developing follicles present in ovaries.
3. pregnant: corpora lutea, implantation sites or fetuses present.
4. post-partum: degenerating corpora lutea, fading scars, flaccid reproductive tract.

The relationship between mean number of fetuses and number of corpora lutea was examined for females having macroscopic embryos. Mean number of corpora lutea was calculated for each age class of females. Number of fetuses was estimated by linear interpolation between 2 data points of the known relationship between corpora lutea and fetuses using a generalized FORTRAN function (SLP). Mean numbers of corpora lutea, scars and fetuses were compared using t-tests.

Paired testes and epididymides were weighed. If only one testis was present, the weight of the pair was estimated by doubling the weight of the single testis. Carcasses were subject to varying degrees of dessication. Testes, being externally situated, were especially susceptible to drying. As degree of dessication was not consistent, weights were standardized by soaking testes in water for 24 hours. Bacula were stripped of flesh, cleaned by dermestid beetles and weighed. Maximum length was measured using dial calipers. Atypical bacula, those broken and rehealed in bent positions, were omitted. Oneway ANOVA to test for significance followed by multiple comparisons using Fisher's Modified Least Significant Difference ($p \leq 0.05$, MLSD) (Carmer and Swanson 1973) were used to compare testes weights and bacula weight and length among age classes. ANOVA was used to examine variation in mean weights of testes by age class and time of year. Means \pm 1 standard deviation are reported.

Results

Females

Young of year females were either non-reproductive (33.9%, 21/62) or pre-reproductive (66.1%) (Fig. 1.1). Of subadults, 7.4% (2/27) were pregnant. Adult females that were either pregnant or post-partum comprised 73.4% (58/79) of the age class. Of the 11.4% (9/79) of adult females that were non-reproductive, 77.8% (7/9) had no evidence of prior breeding; the oldest was 4+ years old. The remaining 15.2% (12/79) were pre-reproductive. The percent of females pregnant or post-partum was 53.3% for 2+ year olds and ranged from 86 to 93% for 3+ to 5+ year olds (Table 1.1). Of the 8 females 6+ to 11+ years old, 62.5% were reproductive.

Pregnant females were caught throughout the trapping season (Fig. 1.2), indicating implantation occurred at least as early as November. The distribution of fetus crown-rump length over time (Fig. 1.3) suggests an extended period of implantation and subsequently, parturition. A female caught on 3 March was near term; all fetuses (n=4) were fully furred and the mean weight and mean crown-rump length of fetuses was 107.7 ± 9.6 g and 112.5 ± 5.7 mm, respectively. In contrast, fetuses (n=4) of a female trapped on 15 March had a mean weight of 7.1 g and a mean crown-rump length of 53.0 mm. Of post-partum females (n=7), 1 was captured in January and 5 in February. One female captured on November 8 had placental scars but no corpora lutea, indicating either a late birth or that resorption of embryos had occurred. Developing follicles as well as regressing corpora lutea were present in ovaries of all post-partum females.

Mean number of corpora lutea for all females was 1.20 ± 1.85 (n=181). The smallest number of corpora lutea for pregnant females was 2. For 23 females with macroscopic embryos, mean number of corpora lutea ($\bar{x}=3.91 \pm 1.04$) overestimates mean number of fetuses produced (3.17 ± 0.83) (paired $t_{22}=3.87$, $p<0.001$). However, mean number of scars ($\bar{x}= 3.28 \pm 1.18$, n=18) does not differ from mean number of fetuses, ($t_{40}=0.36$, $p>0.70$). Neither counts of scars nor fetuses take into account embryos that are resorbed or young that die after birth. Of 19 litters having

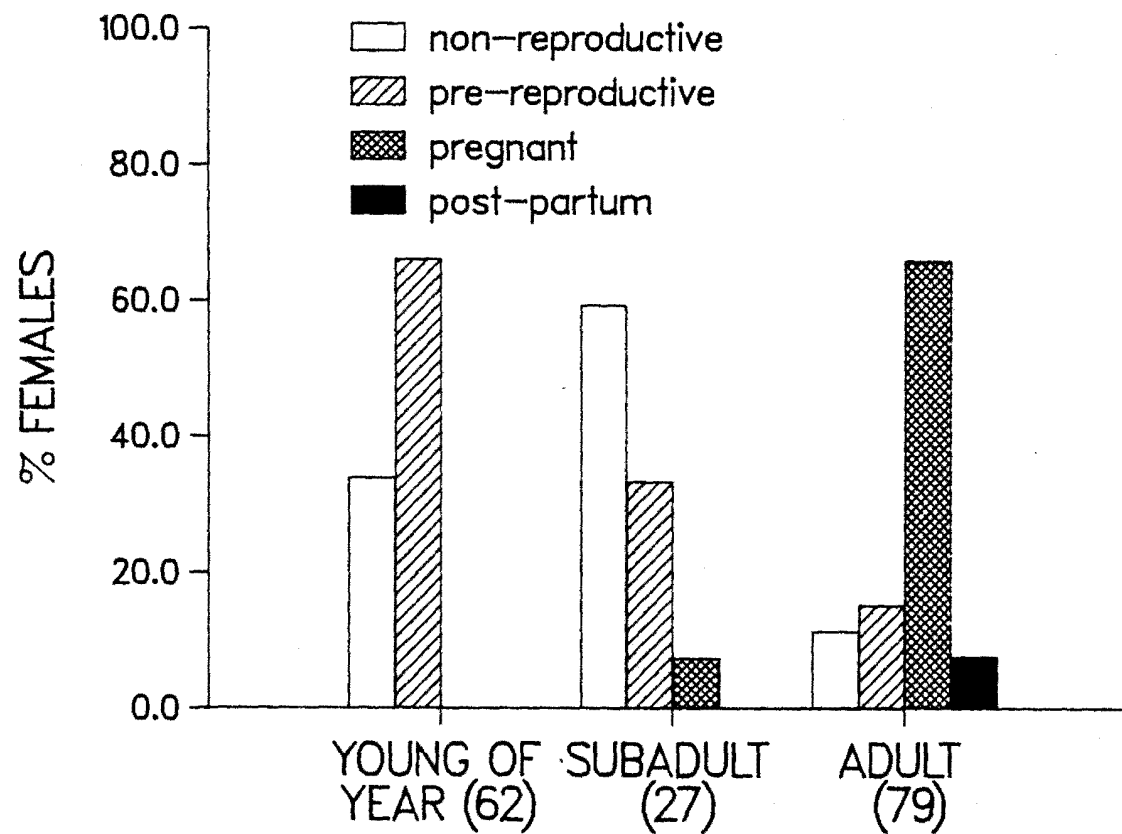


Fig. 1.1. Age classes of female wolverine in different reproductive stages, Yukon 1982-1985.

Table 1.1. Non-reproductive females in age classes of Yukon wolverine, 1982-1985.

AGE	N	% NON-REPRODUCTIVE	% PREGNANT OR POST PARTUM
0+	82	100.0	0.0
1+	27	92.6	7.4
2+	30	46.7	53.3
3+	13	7.7	92.3
4+	13	7.7	92.3
5+	7	14.3	85.7
6+-11+	8	37.5	62.5
TOTAL	180	70.6	29.4

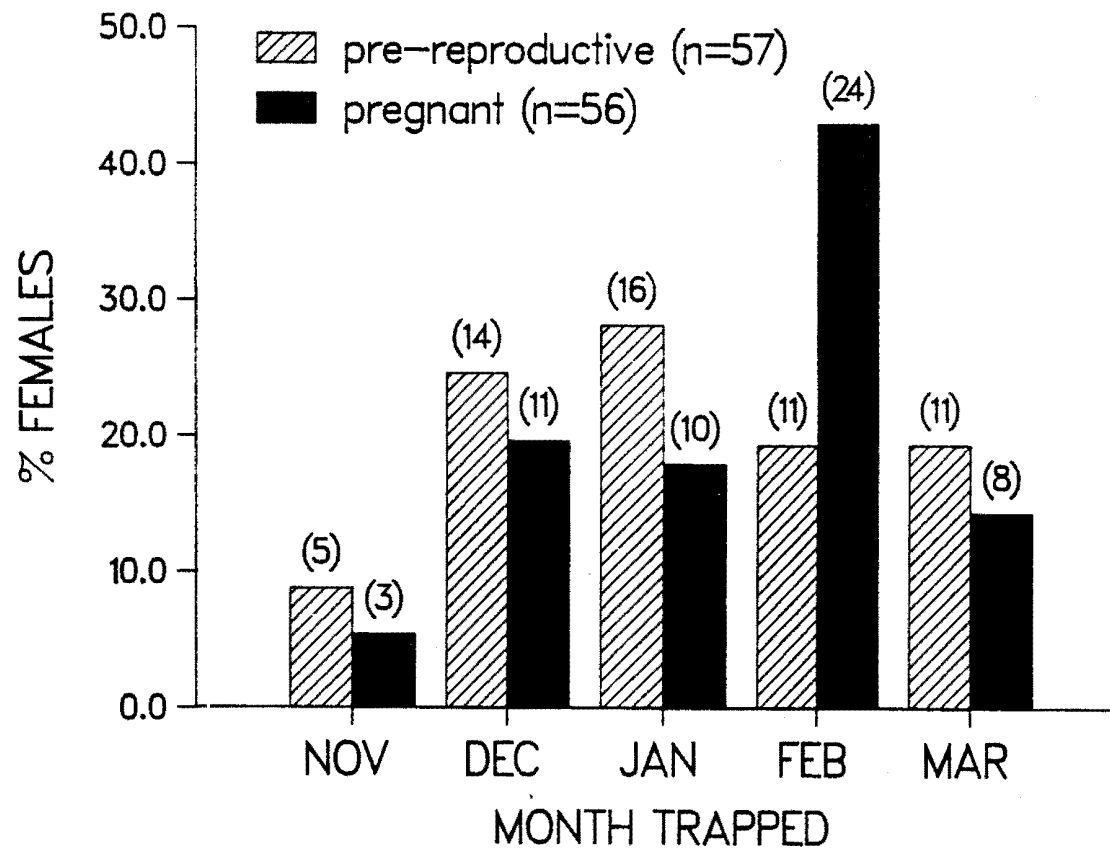


fig. 1.2. Pre-reproductive and pregnant wolverine trapped November to March, Yukon 1982-1985.

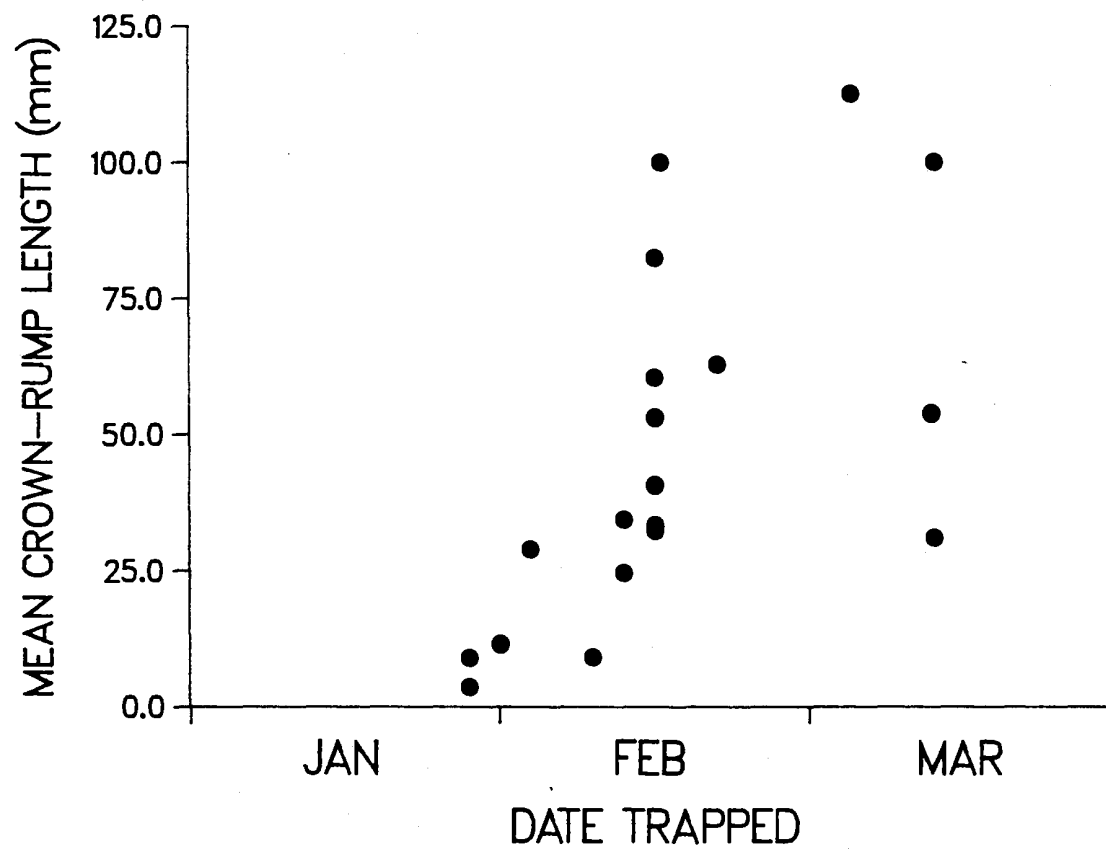


Fig. 1.3. Mean measurements for *in utero* litters of wolverine trapped January to March, Yukon 1982-1985.

measurable fetuses, 1 fetus from a litter of 3 and 1 from a litter of 4 were beginning to disintegrate in the uterus.

For 23 females with macroscopic embryos, the number of corpora lutea is related to mean number of fetuses (Fig. 1.4). Using this relationship and mean counts of corpora lutea, number of fetuses was estimated for females of each age class (Table 1.2). The following assumptions were made in these calculations:

1. A 1:1 relationship for $n \leq 2$ corpora lutea and fetuses.
2. As only a small proportion of subadults reproduce, estimated number of fetuses for this age class is the observed proportion.
3. The potential number of young a mature female is capable of producing is independent of whether or not she becomes pregnant. Thus, mean corpora lutea counts do not include those adult females which were not pregnant or post-partum.

Males

Oneway ANOVA indicated differences exist among age classes of wolverine in mean weights of testes ($F_{2, 196}=44.96$, $p<0.0001$). However, mean weights for subadults did not differ from young of year (MLSD $p>0.05$) and these age classes are considered as "immature". Age class and month trapped were significant factors in explaining variation in male testes weights (Table 1.3). Testes weights of adults increased as March approached (Fig. 1.5). Differences existed between age classes in mean length ($F_{2, 191}=39.78$, $p<0.0001$) and weight ($F_{2, 191}=61.28$, $p<0.0001$) of bacula. However, overlap indicates age classification based on characteristics of bacula is not definitive (Table 1.4).

Discussion

Females

Pre-reproductive females were trapped in all months from November through March. Sample sizes were not consistent over time; greatest numbers of wolverine were caught in the middle of the season, and few were caught in November and

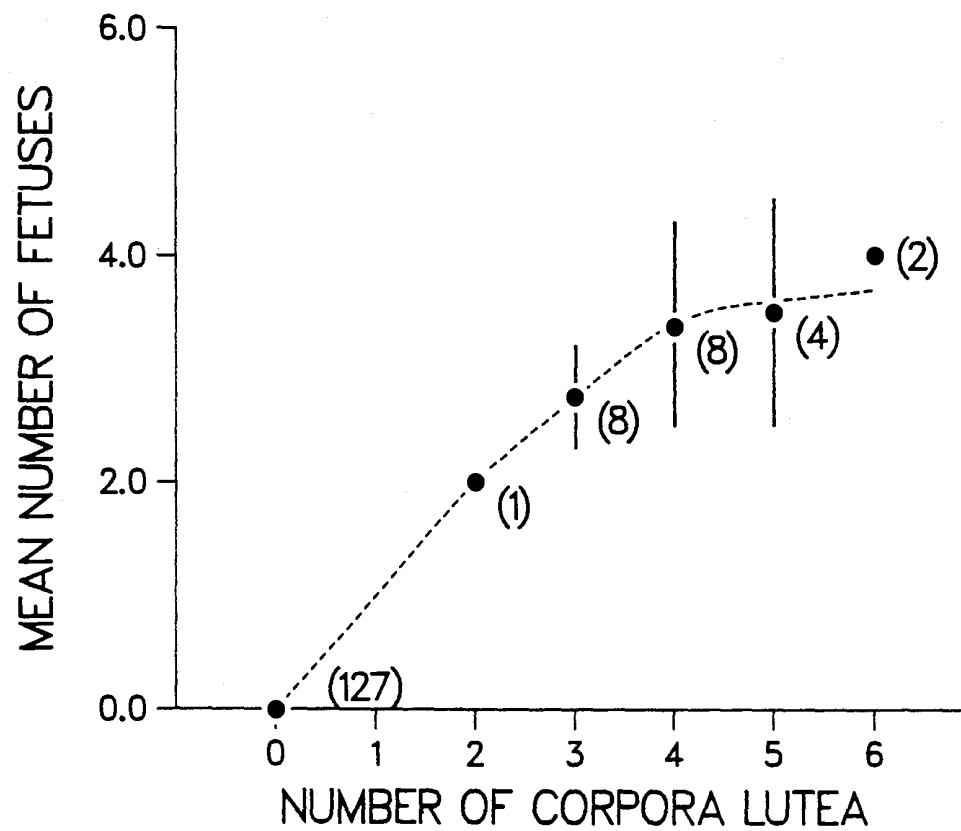


Fig. 1.4. Relationship between mean number of wolverine fetuses produced and number of ova shed, Yukon 1982-1985.

Table 1.2. Estimated age-specific productivity for female wolverine in Yukon, 1982-1985.

AGE	N	MEAN CORPORA LUTEA	SD	ESTIMATED ^a FETUSES
0+	62	0.00	0.00	0.00
1+	27	0.22	0.80	0.22
2+	15	3.13	0.83	2.83
3+	10	3.60	0.70	3.13
4+	10	4.10	0.99	3.39
5+	6	4.17	0.75	3.40
6+ - 11+	5	4.40	1.14	3.42

^aLinear interpolation using known relationship between number of corpora lutea and mean number of fetuses for females having in utero litters.

Table 1.3. ANOVA for standardized^a testes weights of Yukon wolverine, 1982-1985.

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	P
Between Groups	756.61	14	54.04	9.87	<0.001
Age Class	306.54	2	153.27	28.00	<0.001
Month Trapped	182.04	4	45.51	8.31	<0.001
Interaction	61.42	8	7.68	1.40	0.199
Within Groups	903.33	165	5.47		
Total	1659.94	179	9.27		

^aTestes were soaked in water 24 hours before weighing.

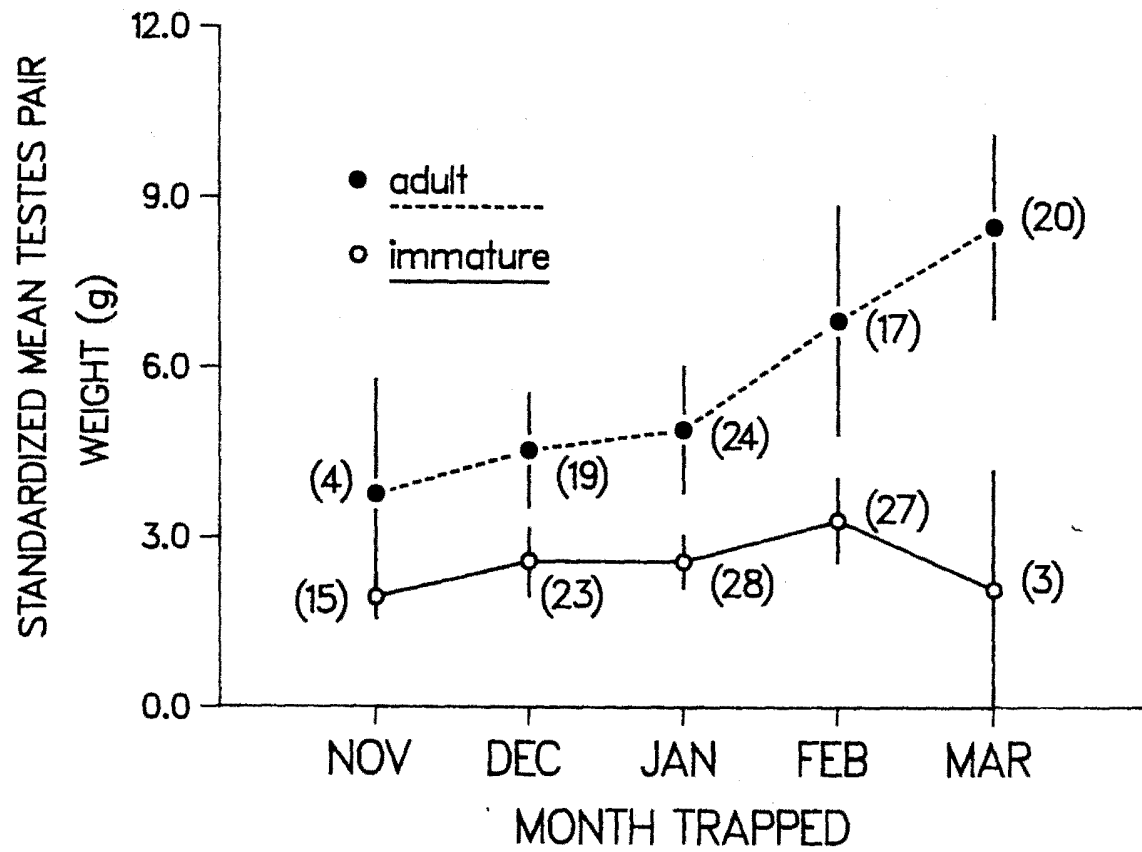


Fig. 1.5. Standardized mean weights of testes pairs for age classes of wolverine trapped November through March, Yukon 1982-1985.

Table 1.4. Mean bacula measurements for age classes of Yukon wolverine, 1982-1985.

AGE CLASS	N	MEAN	SD	MIN	MAX	95% CONFIDENCE LIMITS
LENGTH (mm)						
Young of Year	61	73.30	5.07	58.06	84.04	72.04 - 74.64
Subadult	40	76.19	6.18	62.12	88.40	74.22 - 78.17
Adult	93	81.05	5.18	56.82	91.72	79.98 - 82.12
WEIGHT (g)						
Young of Year	61	1.06	0.31	0.59	2.13	0.98 - 1.14
Subadult	40	1.28	0.50	0.63	3.13	1.12 - 1.45
Adult	93	1.96	0.62	0.82	3.35	1.83 - 2.09

March. As small sample sizes cannot be assumed to be representative, results may not accurately indicate frequency of occurrence of pregnancy or follicular development over time. Induced ovulation in mustelids is known for mink (*Mustela vison*) and ermine (*Mustela erminea*) (Martinet et al. 1984), polecat (*Mustela putorius*) and skunk (*Mephitis mephitis*) (Mead and Wright 1983), and likely occurs in wolverine as well. The prolonged estrus characteristic of induced ovulators is usually effected by growth of several follicular waves (Weir and Rowlands 1973). Because many follicles develop but only few actually ovulate (Weir and Rowlands 1973), presence of follicles in ovaries or time of development cannot be construed as evidence that estrus is pre-eminent. Thus, available information is insufficient to define a proestrus period for wolverine.

Female wolverine did not breed in their first summer, consistent with results of Rausch and Pearson (1972) and Liskop et al. (1981). Of subadults, 7.4% were pregnant, in contrast with the 50.0% (20/40) reported by Rausch and Pearson (1972) and 84.6% (11/13) reported by Liskop et al. (1981). Direct comparison with Rausch and Pearson (1972) is difficult as they classified young of year as "0-15 months" and subadults "16-28 months". Both Rausch and Pearson (1972) and Liskop et al. (1981) used cementum analysis as an aging technique. Wolverine are one of the most difficult mammals to age using this method (Banci 1982) and systematic error in reported results should be considered. However, even assuming that a proportion* of subadults were misclassified by age, pregnancy rate for subadult females in this study is the lowest reported for wolverine. Approximately 50% of the 2+ age class were pregnant. Because above studies lumped 2+ year and older females into "adults", comparisons cannot be made. Age of sexual maturity in mustelids varies with nutrition (Mead and Wright 1983). Differences in age of sexual maturity between Yukon (1982-1985) and other areas and periods may reflect differences in nutritional status. Future studies using comparative aging techniques will illucidate extent of the variation in age of sexual maturity for wolverine.

Although methodological differences make comparisons with other studies difficult, results from mature females imply that differences in reproductive rates exist among wolverine populations. The proportion of adult females pregnant

(73.4%) is less than that found in Alaska/Yukon, 91.8% (90/98) (Rausch and Pearson 1972), and in British Columbia, 88.5% (23/26) (Liskop et al. 1981). Comparison of reproductive rates of wolverine among studies using corpora lutea counts is not possible as the authors did not state whether they included ovaries with no corpora lutea in their calculations. In addition, usefulness of this statistic is limited without considering age-specific differences. Rausch and Pearson (1972) found no difference in number of ova shed between first breeders and multiparous females. My results indicated that reproductive rate increases with age, consistent with age-specific natality curves described for other mammals (Caughley 1977, p. 83). Because reproduction is age-dependent, differing age compositions of samples between studies could account for some of the differences in estimates of natality.

Wright and Rausch (1955) found unimplanted blastocysts in females killed in October, November and January; Rausch and Pearson (1972) in December; and Liskop et al. (1981) in February and March. The period of pregnancy includes all months of the trapping season and indicates that time of implantation occurs at least as early as November. The distribution of embryo size over time emphasizes the variability in timing of implantation and parturition. If a female implants in November, and the active period of pregnancy is 30 to 40 days (Rausch and Pearson 1972), birth would occur in December. This may be an inhospitable time to give birth for many northern mammals but not necessarily for wolverine. Parturition should be timed for maximum survival of young, likely the time of greatest food availability. Considering that wolverine are scavengers dependent on ungulate kills (Chap. III), food should be more plentiful in winter, and this may be the best season for wolverine reproduction.

This study is the first to comment on the presence of non-reproductive females within age classes of wolverine that are sexually mature. The proportion of non-pregnant females in age classes 2+ to 5+ years ranged from 7.7 to 46.7%. Pregnancy rate of females 6+ years and older (62.5%) may be less than that of younger adults. This finding needs to be confirmed with a larger sample size. The relatively high proportion of pregnant adults (73.4%) indicates that most females breed annually, presumably even if they have had a litter the same year. In many

mammals, ovulation occurs shortly after parturition (Weir and Rowlands 1973). The presence of follicles in ovaries of post-partum females suggests wolverine females are capable of breeding soon after having young. Reproductive characteristics and success are closely linked to food resources (Robbins 1983:167-206). However, the relationship between habitat productivity and wolverine reproduction is not clear. The oldest female in this study with no evidence of prior breeding was 4+ years. Female wolverine in arctic Alaska that inhabited an area where food was scarce bred but not all produced kits (Magoun 1985). One adult female produced no young in the 3 years she was observed (Magoun 1985). Approximately 50% of monitored females in an area having greater food resources were not pregnant (Hornocker and Hash 1981). Two of 3 radio-collared adult females in Yukon inhabiting an area apparently abundant in food did not reproduce (Chap. IV).

Newborn wolverine kits are altricial (Shilo and Tamarovskaya 1981). By 7 months of age, kits in the wild attain adult weight (Magoun 1985). Rapid growth of young emphasizes the large energy and nutrient contribution made by their mothers. Lactation is energetically very expensive, more so than gestation (Sadleir 1984). Weight loss of live wolverine imply demands placed on females with kits are extreme (Chap. IV). Even if a female with kits does breed, such demands may influence her ability to reproduce the following year. Evidence from radio-collared wolverine suggests the proportion of females pregnant determined from reproductive tracts overestimates the proportion of females in the population that will have young. Loss of young may occur before or after birth. Resorption of fetuses was observed for 2 of 19 macroscopic *in utero* litters. The proportion of non-detectable losses *in utero* is unknown but likely large, considering the low reproductive success observed in the wild. Implications are that resorption of entire litters occurs, early in pregnancy. Loss after parturition (1 kit each from 2 litters of 4) was reported by Pulliainen (1968). The relatively high proportion of adult females pregnant in this study and that found by Rausch and Pearson (1972) and Liskop et al. (1981), suggest reproductive losses occur primarily *in utero* and after implantation. Adequate food during pregnancy may be the most critical factor determining reproductive success.

Mean litter size from *in utero* fetuses found in this study (3.2) exceeds that reported for northern British Columbia (2.6) (Liskop et al. 1981) and is comparable to that reported for Alaska/Yukon, (3.5) (Rausch and Pearson 1972). The value for northern British Columbia is based on 5 females and may be inaccurate because of the small sample size. Rausch and Pearson (1972) report a range of 1 to 6 "detectable" fetuses (n=54 females). Their plot of crown-rump length over time is based on a smaller sample (n=20 fetuses) and implies "detectable" fetuses includes those that were too small to be easily measured. This range does not indicate those fetuses which are resorbed early and is an overestimate of actual number produced. *In utero* litters in this study ranged in size from 2 to 4. From 161 dens in northern Europe, Pulliainen (1968) reported a mean litter size of 2.5, litters of 2 and 4 were rare. In arctic Alaska, from 5 litters a maximum of 2 kits were observed after den abandonment (Magoun 1985). Field data necessary to estimate size of litters born and weaned are not available.

Males

Based on evidence of spermatogenesis, Liskop et al. (1981) classified males as mature if testes weighed more than 6.5 g. Using this criterion, in Yukon no subadults were sexually mature, whereas by March all adults were in breeding condition. Rausch and Pearson (1972) noted males were sexually mature at 14-15 months but some did not show evidence of spermatogenesis until 26-27 months. My results indicate most males, as most females, are not reproductively active until 2+ years of age. Rausch and Pearson (1972) reported a peak in testes weights in June, presumably also indicating the peak in breeding activity. The trend of increase in average weight of testes during early spring is apparent in my data.

Growth of bacula is stimulated by male hormones at the onset of sexual maturity (Wright 1950). Rausch and Pearson (1972) commented on the overlap in bacula weights between age classes and concluded their utility was limited to separating young of year from older animals. My results using both length and weight of bacula agree with their findings. Extent of overlap in bacula measurements between young of year and subadults supports an age at sexual

maturity of 2+ years for male wolverine. Bacula measurements should not be used as criteria of age without other evidence.

CHAPTER II

MORPHOLOGY AND CONDITION IN WINTER

The status of a wild population is not adequately determined by simply monitoring numbers of animals. Indicators of health and nutritional status are required which may be used to predict condition before environmental effects become apparent in population size (Kirkpatrick 1980). However, the condition of a population is a poorly defined concept. A suitable index should be related to an animal's chances of living or dying and be able to indicate the resilience of an individual or population (Hanks 1981). Indices which have been used to indicate nutritional status include measurements of various fat stores, skeletal attributes, body weights and blood characteristics (Kirkpatrick 1980). Unknown nutritional histories (Hanks 1981) and lack of knowledge regarding how physiological indices are related to the health of an animal makes interpretation of these indices difficult. Caughley (1977:55) suggested population condition was best illustrated by " r_s ", the age-specific rate of survival and fecundity. However, calculation of r_s requires a stable age distribution (Caughley 1977:54), an assumption rarely valid for wild populations. Additionally, the use of a single statistic to index demographic vigor does not indicate the recuperative powers of a population subject to sudden environmental stress (Hanks 1981). Hanks (1981) suggested condition was best determined by monitoring fetal development and juvenile mortality; however, he acknowledged this was seldom possible for wild populations.

For management purposes, an easily measurable and readily computed index is desirable. Riney (1955) suggested the use of a kidney fat index (KFI), computed as weight of perirenal fat/kidney weight x 100. Kidney weight is incorporated in the calculation to allow comparisons between animals of different size. KFI has been used extensively as an indicator of condition in ungulates (reviewed in Van Vuren and Coblentz 1985). The equation has recently been criticized. Kidney weight does not appear to be linearly proportional to body weight; animals of smaller size have proportionally larger kidneys (Van Vuren and Coblentz 1985). Secondly, seasonal changes in kidney weight have been documented for some species (Hanks 1981).

One objective of a larger study designed to investigate the status of Yukon wolverine (*Gulo gulo*) populations was to assess physiological condition (Intro.). Knowing condition will assist in determining when during winter wolverine are stressed and most vulnerable to trapping. Wolverine are scavengers, contending with generally unpredictable food supplies (Chap. III). As mammals store energy primarily in the form of adipose tissue (Pond 1978), body fat may be justifiably equated with usable energy stores (Lindstedt and Boyce 1985). Lindstedt and Boyce (1985) determined an allometric equation predicting fasting endurance as a function of total fat stores, ambient temperature and body size. Total body fat may thus be used to indicate resilience to food shortages. A large sample of carcasses submitted by Yukon trappers over 3 winters, 1982/83 to 1984/85, was available. I was unable to quantitatively determine total body fat of wolverine and instead recorded a subjective measure based on a visual assessment of body fat. This index was then compared to KFI. A knowledge of body size is necessary when considering differences in food habits between sexes and among age classes. The large sample permitted me to document morphological characteristics and assess the extent of sexual dimorphism in body size for wolverine.

My objectives are to:

1. Compare KFI and a subjective fat index between sexes, age classes, years and months.
2. Compare estimated fat content between reproductive (pregnant and post-partum) and non-reproductive females.
3. Determine and compare body weights and measurements for age classes and sexes of wolverine.

Materials and Methods

From 1982 to 1985, 459 carcasses were obtained. Measurements recorded were body length (tip of nose to base of tail), heart girth, and greatest neck diameter (taken above or below salivary glands). Tail length, shoulder height and hind-leg length were measured but not used because these were rarely complete on

carcasses. Body weights and measurements were compared among age classes using oneway ANOVA. Fisher's Modified Least Significant Difference ($p \leq 0.05$) was used for multiple comparisons (Carmer and Swanson 1973). Rausch and Pearson (1972) estimated that the hide and fluids lost during skinning and dessication comprised on average 25% of a wolverine's total body weight. Only skinned weights were available for wolverine in my sample and corresponding body weights of live wolverine were estimated using this assumption. Mean body weights \pm 1 standard error are reported.

The renal membrane was removed, leaving perirenal fat attached, and weighed. Kidneys were weighed without renal membranes. Kidney fat index was computed (Riney 1955). KFI's were compared between sexes and among age classes, years and months using ANOVA. Total body fat was estimated as "low", "medium" or "high", based on a visual assessment of amounts of subcutaneous, mesentery and organ fats. Frequency distributions of this subjective index within sexes, reproductive and non-reproductive females, age classes, years and months were compared using Kruskal-Wallis (K-W) tests.

Results

Estimated live weights and skinned measurements are presented in Table 2.1. Within sexes, only body weight differed among age classes; between adult and subadult females and between young of year and adult males (Table 2.2). Oneway ANOVA indicated other differences were apparent, in body length and heart girth for females and heart girth for males. These differences were slight as age classes did not differ using simultaneous multiple comparisons. Sexes differed significantly with respect to body weight and all measurements.

There was large variation in KFI. Mean KFI was $22.6 \pm$ S.D. 18.7, and ranged from 0 to 165. No main effect (sex, age class, year, month) explained this variation (ANOVA, $p > 0.40$). Most wolverine had medium estimated fat content (69.1%, 317/459), 14.6% (67/459) had low and 16.3% (75/459) high. More females (20.6%) had low estimated fat content than males (9.8%) (K-W $\chi^2 = 5.94$, $p < 0.05$,

Table 2.1. Estimated weights^a (kg) and skinned measurements (cm) for age classes of Yukon wolverine, 1982-1985.

	YOUNG OF YEAR			SUBADULT			ADULT		
	MEAN	N	95% CONFIDENCE LIMITS	MEAN	N	95% CONFIDENCE LIMITS	MEAN	N	95% CONFIDENCE LIMITS
FEMALES									
Weight	8.3	60	7.8 - 8.7	7.9	30	7.4 - 8.4	8.7	82	8.3 - 9.1
Body Length ^b	70.7	60	69.8 - 71.7	70.5	30	69.1 - 71.9	72.0	81	71.1 - 72.9
Heart Girth	31.1	60	30.4 - 31.8	31.0	30	30.0 - 31.9	32.1	81	31.5 - 32.7
Neck Diameter ^c	26.6	60	25.8 - 27.4	28.0	29	26.6 - 29.3	27.0	76	26.3 - 27.7
MALES									
Weight	11.5	59	10.9 - 12.2	11.9	44	11.1 - 12.6	12.8	111	12.3 - 13.3
Body Length ^b	78.2	59	77.0 - 79.4	78.5	43	77.2 - 79.8	79.4	109	78.6 - 80.1
Heart Girth	36.1	59	35.2 - 37.0	36.7	44	35.6 - 37.7	37.3	110	36.7 - 37.9
Neck Diameter ^c	31.0	57	30.1 - 31.8	31.7	43	30.7 - 32.8	31.7	105	31.1 - 32.3

^aAssuming pelt, blood and dessication comprise 25% of body weight.^bTip of nose to base of tail.^cGreatest diameter.

Table 2.2. Oneway ANOVA comparing mean body weights and measurements among age classes and between sexes of Yukon wolverine, 1982-1985.

	F	DF.	Groups Different ^a
FEMALES			
Weight	3.53*	2,169	subadult/adult
Body Length	2.68+	2,168	none
Heart Girth	3.16*	2,168	none
Neck Diameter	1.90	2,162	none
MALES			
Weight	4.82**	2,211	young of year/adult
Body Length	1.69	2,208	none
Heart Girth	2.71+	2,210	none
Neck Diameter	1.10	2,202	none
SEX COMPARISONS			
Weight	59.94***	5,380	all females from males
Body Length	67.71***	5,376	all females from males
Heart Girth	58.72***	5,378	all females from males
Neck Diameter	35.98***	5,364	all females from males

+ $p < 0.10$ * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$ (else not significant, $p > 0.10$).

^aFisher's Modified Least Significant Difference ($p \leq 0.05$).

Fig. 2.1). Distributions between reproductive and non-reproductive females and among age classes, years and months did not differ ($p>0.10$).

Discussion

Adult males weighed more than young of year males, but age classes did not differ in body measurements. Adult females weighed more than subadult females, but did not differ from young of year. This result may indicate a weight loss by subadult females during their initial period of independence. Sexes are highly dimorphic, differing significantly in body weight and all measurements. Mean estimated body weight for adult females was 8.7 ± 0.2 kg and 12.8 ± 0.3 kg for adult males. Weights are in general agreement with those reported for Yukon and Alaskan wolverine (Rausch and Pearson 1972). The largest adult female weighed 10.8 kg skinned and had an estimated 14.4 kg live weight. The largest adult male weighed 16.0 kg skinned and had an estimated 21.3 kg live weight. Weight of this wolverine exceeds the maximum reported by Rausch and Pearson (1972), a skinned weight of 15.4 kg and an estimated 20.4 kg live weight.

The extensive variation indicated that the KFI has limited utility as an index for predicting winter condition of wolverine. Most wolverine (85%) had either medium or high estimated fat contents. Only the subjective measure indicated differences occurred between sexes. Why more females than males had low estimated fat content is unknown. Within females, no differences were found between those that were reproductive and non-reproductive. Differences among age classes, years and months were not apparent. If strong differences in condition were present, I expect they would have been identified by at least one of the two indices. Quantitative determination of total body fat for large mammals is difficult and time consuming. Until a suitable alternative is available, a subjective measure may be a useful screening technique. However, the use of this index requires that researchers are familiar with their study animal and are able to relate a visual assessment of body fat to physiological condition.

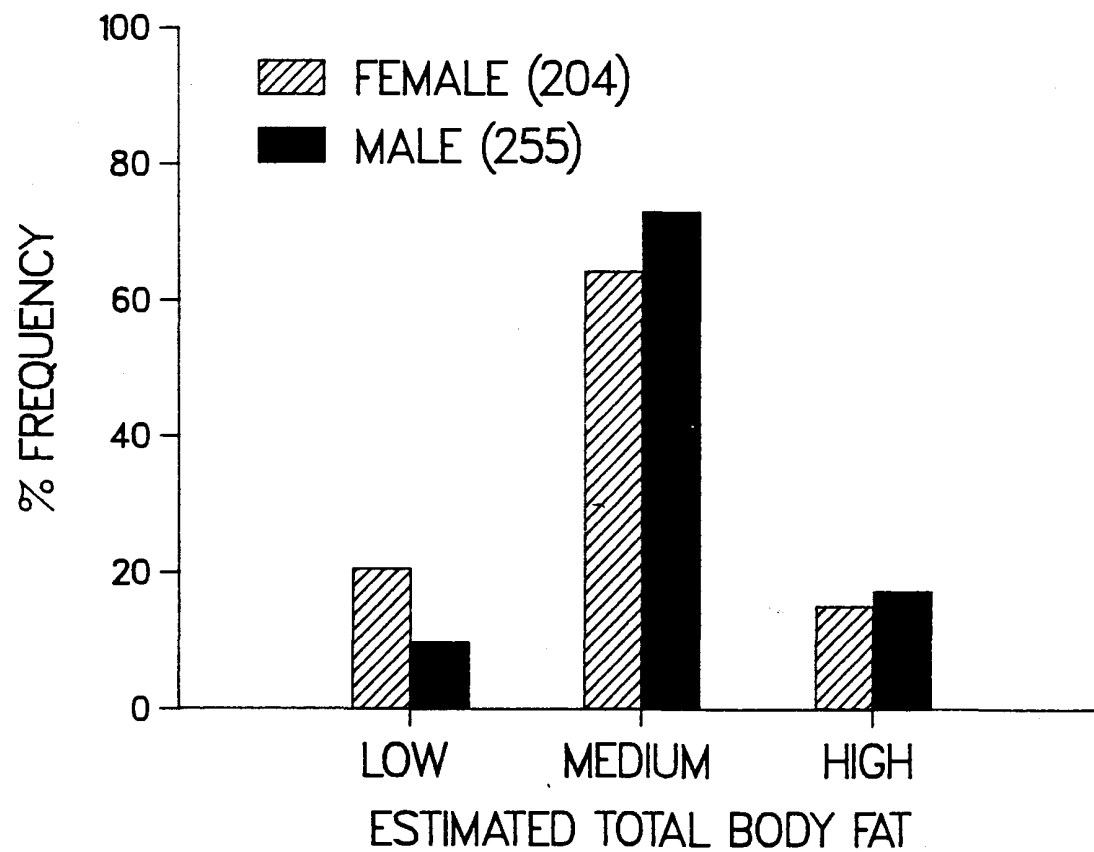


Fig. 2.1. Estimated body fat among sexes of Yukon wolverine, 1982-1985.

The length of time wolverine are able to survive without food (fasting endurance) depends on body weight as well as fat reserves, and is not reflected in the subjective fat index. Fat varies in proportion to body weight with an exponent greater than unity across mammal species, indicating the magnitude of stored fat is a greater fraction of body mass as size increases (Pitts and Bullard 1968, Calder 1984:50–51). This relationship has not been examined intra-specifically. Lindstedt and Boyce (1985) suggested that the slope is likely to be steeper than that for the inter-specific relationship. Limited data support this hypothesis for wolverine (Banci unpub. data). The strong sexual dimorphism in body weight for wolverine implies sexes differ in the amount of fat reserves they are able to maintain. Understanding the allometry of body fat and weight would allow fasting endurance to be predicted. Since adequate energy reserves are critical for a scavenging species reliant on unpredictable food supplies, a measure of fasting endurance may be the best indicator of physiological condition for wolverine.

CHAPTER III

SEASONAL FOOD HABITS

An understanding of the seasonal variability of important foods, relationship of home range and habitat use to food distribution and availability, and dietary influences on reproduction and growth is necessary to evaluate the status of wild populations and manage species effectively. Wolverine (*Gulo gulo*) are generally described as being opportunistic, primarily scavenging in winter and resorting to a more omnivorous diet in summer. However, quantitative studies are few. Winter food habits have been determined from analyses of gut contents and scats: n=20 stomachs, Alaska (Wright and Rausch 1955); n=193 stomachs, Alaska/Yukon (Rausch and Pearson 1972); n=35 colons, south-central Alaska (Gardner 1985); and n=82 scats, arctic Alaska (Magoun 1985). An aged and sexed sample of wolverine collected by Yukon trappers over 3 winters, 1982/83 to 1983/84, allowed investigation of food habits by sex, age class and time of year. The sample of stomachs (n=411) is the largest collected to date from one area over a short period.

Stomach contents may not accurately depict an animal's diet at time of capture. Time since last meal and length of time spent in traps will affect extent of digestion and amount of material retained in stomachs. Hence, proportion by weight of contents will not reflect amounts consumed and cannot be used as a criterion for evaluating importance. Rate of passage of undigested material through the gastrointestinal tract is affected by amount and temporal sequence of food eaten, food composition, level of hunger, consumption of additional prey and external cues such as daylight (Robbins 1983:315). Available information is insufficient to estimate the length of time prey or their remnants remain in wolverine stomachs. However, because of the rugose nature of the stomach lining, hair retention is prolonged. Frequencies tabulated by including these "trace" occurrences will encompass more than one meal, likely taken from more than one location, and over a period longer than a few hours. A potential bias of the described method is differential retention; the frequency of prey having low

retention of hair in stomach rugae may be underestimated. Frequencies of trace amounts for prey groups can be compared to assess their relative "detectability" in stomachs. Of the stomachs containing a prey group, the proportion that occurs in trace amounts is the detectability for that prey group. If the detectability of two prey types does not differ, the observed proportions of trace amounts will not differ either. The underlying assumption is that carcasses represent a random sample with respect to the time elapsed since the last meal and time spent in traps.

The use of stomach contents to describe food habits of a trapped species can be biased because of bait consumption. However, wolverine live-trapped in southwest Yukon, excepting recaptures (Banci, pers. obs.), and adult wolverine in Alaska (Magoun 1985) did not consume trap bait. I expect non-consumption of bait to be a general phenomenon, attributable to the stress of being trapped, assuming most wolverine are not habituated to traps. Items typically used as bait are fish, ungulate hide, flesh from discarded carcasses, domestic mammals (cow, horse), and occasionally snowshoe hare (*Lepus americanus*). All species, excepting domestic mammals, are normally present in an area, thus discriminating bait from prey cannot be based on bait type. Information about type of trap used (quick-killing or restraining) permitted the comparison of frequency and weights for typical bait items.

Wolverine have been reported feeding on cedar nuts, bracket fungi, and edible roots (Novikov 1956, Krott 1960). However, these data were collected from trapped wolverine. Vegetation may be consumed at trap sites (trap debris) or ingested incidentally with prey. Plant material occurring in stomachs of quick-killed wolverine will not be attributable to trap debris and can be used to estimate the occurrence of vegetation in diet of wolverine.

Adequate nutrition in winter is important in determining the reproductive success of female wolverine (Chap. I). Food habits may differ between sexes because of the requirements of reproduction. Wolverine are sexually dimorphic (Chap. II). The smaller body size of females implies their diet may also differ

from males because of different nutritional requirements. Differences in food habits may also occur among age classes. Adults have the benefit of experience and may be more adept than juveniles at scavenging or hunting. A difference in the foraging pattern of wolverine will be reflected in their use of habitats. The vulnerability of sex/age classes to trapping is a function of home range size and extent of movements (Chap. V). Thus, understanding differences in food habits will also assist in interpreting and predicting the sex/age composition of harvests.

Use of frequency as a measure of importance overemphasizes small prey which occur frequently and underestimates large prey which occur less often (Floyd et al. 1978). The size of prey determines nutritional content and value to wolverine. However, if actual weights of prey species are used to assess importance, the assumption is made that the entire prey was accessible. This assumption is not necessarily true for scavenging species, especially if prey consists of large herbivores. The amount of food present at ungulate kill sites depends on the efficiency of predators, the presence of other scavengers and time since the kill. Information on the availability of both live and scavenged prey is required. This information, especially for ungulate kills, is difficult to determine. However, if wolverine are opportunistic, as has been reported, observed frequencies will indicate availability, as long as food is limiting. Circumstantial evidence regarding prey distribution and abundance will be used to estimate prey availability and to support this hypothesis.

A scavenging lifestyle implies that wolverine have a varied diet. The ability to successfully hunt a variety of prey is an asset in times of low food availability. However, sex/age classes may differ in their capacity to maintain such a diet. I examine this hypothesis by comparing the distribution of the number of prey groups occurring in stomachs between sexes and among age classes. The examination of which prey groups are most commonly associated in stomachs and those which rarely occur together may assist in determining prey availability and preferences of wolverine.

My objectives are to:

1. Identify the types of prey consumed and estimate their relative contributions to the diet of wolverine.
2. Assess the detectability and extent of differential retention of prey hair.
3. Examine differences between proportions of prey groups in stomachs of wolverine caught by quick-killing and restraining traps to assess the frequency of bait in the diet.
4. Compare diets between sexes and among age classes of wolverine.
5. Compare diets among years and months.
6. Examine associations of prey groups within stomachs.
7. Compare distributions of the number of prey groups per stomach between sexes and among age classes.

Materials and Methods

For each carcass, the esophagus and duodenum were tied, stomach excised, injected with 10% formalin, wrapped in cheesecloth and preserved whole. For processing, the stomach was slit, and the contents placed in sieves lined with filter paper. The stomach lining was carefully washed with hot water to remove all hair embedded in rugae. Contents were alternatively rinsed in solutions of detergent and hot water to remove grease, then dried at 60°C for a minimum of 48 hours.

The mammal species which occur in Yukon and their distributions were determined from Youngman (1975). Identification of all mammal species was attempted. Skulls and portions thereof were classified according to Hall and Kelson (1959), Maser and Storm (1970), Banfield (1974), van Zyll de Jong (1983), and by comparison to reference collections. Impressions of hair cuticles were made in coloured acetate as described by Kennedy and Carbyn (1978) and compared to keys (Day 1966, Moore et al. 1974, Adjoran and Kolenosky 1980, Titus 1980) and impressions from known specimens.

Birds were identified to family. No attempt was made to identify fish remains to family or species. Insect pupae were identified by H. J. Tesky of the

Biosystematics Research Institute, Agriculture Canada, Ottawa. If bone did not belong to a prey species found in the stomach or formed a compact mass separate from other prey, it was classified as unidentified. Soft body parts were classified as fat/flesh if not associated with hair or prey items.

Presence and dry weight (to nearest 0.1 g) were recorded for each item in each stomach. All stomachs containing a food type were expressed as a percentage of the total number of stomachs. Percent weight was determined using total weight of all items. If dry weight was less than 1.0 g, occurrence was classified as trace. Weight will only be referred to for total stomach and prey group weights in reference to trap type.

Type of trap was known for 49.6% (204/411) of carcasses. Wolverine shot, road killed, caught by neck snare, or conibear were classified as "quick-killed" (n=45). Foot-hold or live-trapped wolverine were classified as "restrained" (n=159). Proportions of prey groups found in stomachs of wolverine caught in quick-killing and restraining traps were compared using z-tests, and total weights of stomach contents and prey groups using t-tests. Z-tests were used to compare trace occurrences of prey groups and proportions tabulated by year, sex, age class (young of year, subadult, adult), and month (November through March). The number of prey groups per stomach, disregarding vegetation and wolverine hair, were tabulated. Means \pm 1 standard deviation are reported. Distributions of the number of prey groups by sex and age class were compared using χ^2 tests. Difficulties in aging and labelling errors reduced sample sizes for some analyses.

Results

Prey Types

Where individual prey were recognized, there was never more than one occurrence in a stomach. Mean weights were highly variable, and percent weights generally low (Table 3.1). For analyses, *Sorex spp.*, Muridae and pika (*Ochotona princeps*) were grouped as "small mammals", artiodactyls as "ungulate", and those with low frequency of occurrence, beaver (*Castor canadensis*), canids, lynx (*Lynx*

Table 3.1. Prey items in stomachs of Yukon wolverine trapped winters 1982/83-1984/85.

	FREQUENCY (N=788)	% OF STOMACHS (N=411)	MEAN DRY WEIGHT (g) ^b	S.D.	% OF TOTAL DRY WEIGHT ^{a b}
INSECTIVORA					
<i>Sorex spp.</i>	3	0.7	0.4	0.59	T
LAGOMORPHA					
<i>Ochotona princeps</i>	2	0.5	T	---	T
<i>Lepus americanus</i>	76	18.5	8.4	12.41	6.7
RODENTIA					
SCIURIDAE					
<i>Eutamias minimus</i>	2	0.5	1.9	0.42	T
<i>Glaucomys sabrinus</i>	2	0.5	1.8	1.56	T
<i>Marmota caligata</i>	2	0.5	T	---	T
<i>Spermophilus parryii</i>	10	2.4	8.6	12.18	0.9
<i>Tamiasciurus hudsonicus</i>	18	4.4	3.5	10.44	0.7
unidentified	5	1.2	0.1	0.18	T
MURIDAE					
<i>Microtus xanthognathus</i>	1	0.2	4.2	---	T
<i>Lemmus sibiricus</i>	4	1.0	2.3	2.76	0.1
<i>Phenacomys intermedius</i>	5	1.2	1.3	2.43	0.1
<i>Clethrionomys rutilus</i>	7	1.7	2.4	2.16	0.2
unidentified Microtinae	10	2.4	0.7	1.00	0.1
CASTORIDAE					
<i>Castor canadensis</i>	1	0.2	T	---	T
ERETHIZONTIDAE					
<i>Erethizon dorsatum</i>	45	10.9	1.7	10.98	0.8
CARNIVORA					
MUSTELIDAE					
<i>Martes americana</i>	1	0.2	0.6	---	T
<i>Mustela vison</i>	1	0.2	2.7	---	T
<i>Mustela erminea</i>	2	0.5	4.6	6.58	0.1
<i>Gulo gulo</i>	52	12.7	4.3	9.22	2.3
CANIDAE					
<i>Canis latrans</i>	1	0.2	T	---	T
<i>Canis lupus</i>	3	0.7	2.7	4.09	0.1
unidentified Canidae	1	0.2	T	---	T
FELIDAE					
<i>Lynx canadensis</i>	1	0.2	0.4	---	T
ARTIODACTYLA					
unidentified (rumen)	3	0.7	64.2	8.56	2.0
CERVIDAE					

<i>Cervus elaphus</i>	3	0.7	20.9	16.34	0.7
<i>Odocoileus hemionus</i>	5	1.2	38.0	51.13	2.0
<i>Rangifer tarandus</i>	22	5.4	34.8	37.39	8.0
<i>Alces alces</i>	40	9.7	29.9	35.59	12.5
unidentified	64	15.6	0.2	1.52	0.1
BOVIDAE					
<i>Ovis dalli stonoi</i>	1	0.2	T	---	T
<i>Ovis dalli dalli</i>	5	1.2	24.7	30.22	1.3
<i>Oreamnos americanus</i>	4	1.0	16.5	33.00	0.7
PISCES					
unidentified	13	3.2	24.4	32.47	3.3
AVES					
CORVIDAE	1	0.2	31.2	---	0.3
STRIGIDAE	1	0.2	4.5	---	T
LARIDAE	2	0.4	12.1	17.11	0.3
TETRAONIDAE	3	0.7	2.9	2.12	0.1
unidentified	26	6.3	1.3	4.45	0.4
INSECTA					
MUSCIDAE	1	0.2	0.7	---	T
UNIDENTIFIED FOOD MATERIAL					
fat	9	2.2	35.7	49.43	3.4
flesh	36	8.8	26.6	38.45	10.0
bone	90	21.9	18.7	29.54	17.6
VEGETATIVE MATERIAL	204	49.6	11.8	14.48	25.2
EMPTY	95	23.1	---	---	---

^aTotal dry weight=9560.2 g.

^bT = Trace (weight <1.0 g).

canadensis), and mustelids other than wolverine as "other". Because of the relatively high frequency of unidentified bone, I classed it as a separate group. Similarly, wolverine hair, porcupine (*Erethizon dorsatum*), snowshoe hare and fat/flesh were classed as separate groups. Of all stomachs, 23.1% were empty and 49.6% contained vegetation, the highest contribution of any group. Of animal prey groups, greatest contributions were ungulate (35.7%), bone (21.9%), snowshoe hare (18.5%), fat/flesh (11.0%) and porcupine (10.9%) (Table 3.1). Contributions of other groups were less than 10%. Fish (3.2%) and "other" (2.7%) had the lowest contributions. Percent trace for ungulate, sciurid, bird and small mammal ranged from 56.2% to 66.7% of these food groups (Fig. 3.1). Detectability of these prey groups in wolverine stomachs did not differ (Table 3.2). Percent trace for fat/flesh (15.6%) and snowshoe hare (26.3%) were not significantly different. Along with bone (6.7%), these 3 groups had the lowest detectability. The highest trace amount (95.6%) belonged to porcupine.

Comparisons between Trap Type

Differences were not apparent ($p > 0.10$) in frequencies of empty stomachs ($z = 0.35$), wolverine hair ($z = 0.13$) and potential bait items, snowshoe hare ($z = 0.27$), ungulate ($z = 1.22$) and fat/flesh ($z = 0.37$), in stomachs of wolverine caught with restraining or quick-killing traps (Fig. 3.2). Less vegetation ($z = 2.38$, $p < 0.05$) and more bone ($z = 5.13$, $p < 0.001$) were found in stomachs of quick-killed wolverine. The mean weight for 3 occurrences of fish in stomachs of quick-killed wolverine was 35.8 ± 34.5 g. Fish in stomachs of restrained wolverine occurred once and was of trace amount. Mean total weight of stomach contents (ignoring trace weights) was greater for quick-killed ($\bar{x} = 41.4 \pm 36.9$ g, $n = 36$) than restrained wolverine ($\bar{x} = 24.2 \pm 30.0$ g, $n = 108$) ($t = 2.53$, 51.3 df, $p < 0.05$). Mean total weight for ungulate in stomachs of quick-killed wolverine ($\bar{x} = 25.8 \pm 29.5$ g, $n = 17$) was greater than for restrained ($\bar{x} = 8.4 \pm 16.2$ g, $n = 45$) ($t = 2.30$, 19.7 df, $p < 0.05$).

Of stomachs from quick-killed wolverine, 33.3% contained plant material. Of these stomachs, 6.7% contained only vegetation and all were of trace weight. For restrained wolverine, 53.5% of stomachs contained vegetation. The proportion of

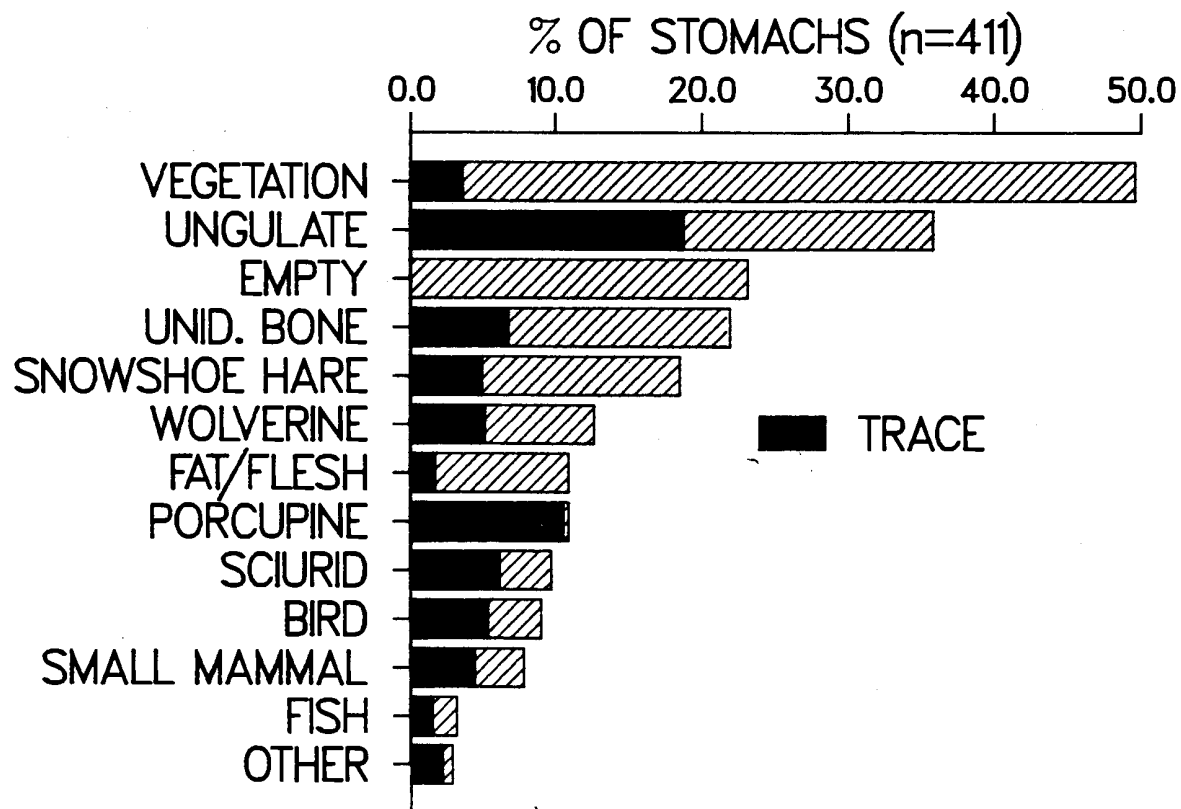


Fig. 3.1. Prey groups and trace occurrences in stomachs of Yukon wolverine trapped winters 1982/83 to 1984/85.

Table 3.2. Paired comparisons of trace proportions of prey in winter stomachs of Yukon wolverine, 1982-1985, using z-values.

	UNGULATE	BONE	SNOWSHOE HARE	FAT/FLESH	PORCUPINE	SCIURID	BIRD
BONE	7.16***						
SNOWSHOE HARE	3.72***	3.47***					
FAT/FLESH	4.36***	1.65+	1.37				
PORCUPINE	5.23***	10.12***	7.37***	7.64***			
SCIURID	1.31	7.01***	3.93***	4.57***	3.66***		
BIRD	1.49	7.03***	3.98***	4.61***	3.38***	0.23	
SMALL MAMMAL	0.40	6.06***	2.97**	3.76***	4.19***	0.67	0.86

*** $p < 0.001$ + $p < 0.10$ (else not significant, $p > 0.10$).

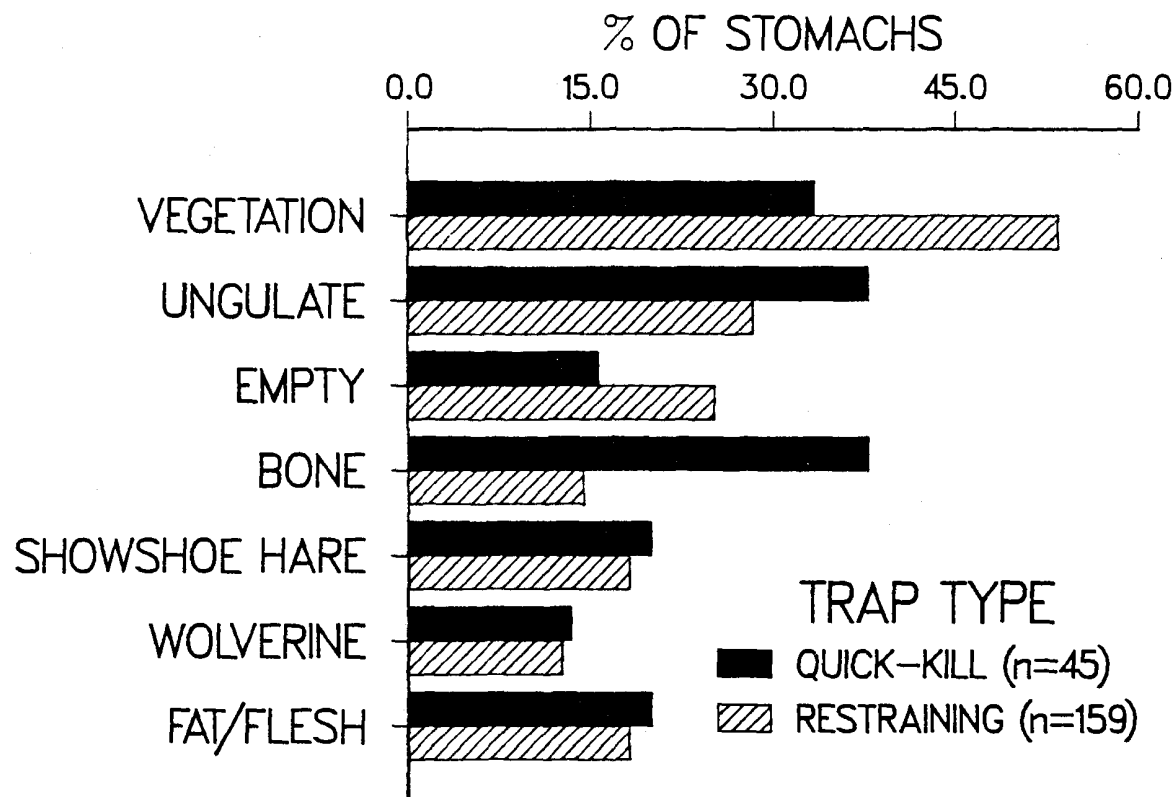


Fig. 3.2. Prey groups in winter stomachs of Yukon wolverine captured by quick-kill and restraining methods, 1982-1985.

stomachs containing only vegetation, 25.2%, was greater than for quick-killed wolverine. Only 3.1% of these stomachs contained vegetation that was of trace weight. Occurrence of vegetation with bird and all mammal prey groups (excluding sciurid, 44%) ranged from 54.5% for bird to 65.5% for small mammal.

Inter-group Comparisons

Stomachs without evidence of any prey group or having only wolverine hair and/or vegetation were treated as "empty" for the following comparisons. Proportions of empty stomachs for females (39.4%, n=165) and males (32.4%, n=188) were not different ($z=1.36$, $p>0.10$). Differences were marginally significant ($p<0.10$) for ungulate (30.3% female, 38.8% male, $z=1.68$) and bone (19.4% female, 12.2% male, $z=1.85$). Differences for other prey groups were not significant ($p>0.10$). No differences were apparent in proportions of prey groups in stomachs of subadults and adults (Table 3.3). Adult and subadult consumption of fat/flesh and adult consumption of snowshoe hare were greater than for young of year but these differences were not large. Adults consumed more ungulate and subadults more snowshoe hare than did young of year.

No differences in proportions of snowshoe hare, porcupine, sciurid and empty stomachs were apparent among years; frequencies of other prey groups were not consistent (Table 3.4). November had the lowest proportion of empty stomachs and the greatest proportions of porcupine, snowshoe hare and bone (Table 3.5). Monthly patterns for other small prey followed the same trend (Fig. 3.3). Ungulates were consumed throughout the winter.

Associations among Prey Groups

The mean number of prey groups per stomach was 1.3 ± 1.4 and ranged from 0 to 6. Distributions of the number of prey groups per stomach did not differ between sexes ($\chi^2_4=3.94$, $p>0.10$, Fig. 3.4). Distributions of the number of prey groups per stomach were not different among age classes ($\chi^2_8=7.65$, $p>0.10$, Fig. 3.5). Of stomachs containing snowshoe hare, sciurid and bird, 46–51% also contained ungulate (Fig. 3.6). Of stomachs containing small mammal, however, only

Table 3.3. Paired age class comparisons of proportions of prey in winter stomachs of Yukon wolverine, 1982-1985, using z-values.

	YOUNG OF YEAR/SUBADULT	SUBADULT/ADULT	YOUNG OF YEAR/ADULT
UNGULATE	0.65	1.10	2.26*
BONE	1.18	0.96	0.26
SNOWSHOE HARE	2.22*	0.57	1.95+
FAT/FLESH	1.83+	0.24	1.87+
PORCUPINE	1.27	0.08	1.63
SCIURID	0.49	0.01	0.65
BIRD	0.70	0.97	0.38
SMALL MAMMAL	0.52	0.38	0.16
EMPTY	0.80	0.38	1.50

* $p < 0.05$ + $p < 0.10$ (else not significant, $p > 0.10$).

Table 3.4. Paired yearly comparisons of prey in winter stomachs of Yukon wolverine, 1982-1985, using z-values.

	1982/83 - 1983/84	1983/84 - 1984/85	1982/83 - 1984/85
UNGULATE	0.30	3.35**	3.96**
BONE	2.52*	0.45	2.21*
SNOWSHOE HARE	1.00	1.28	0.37
FAT/FLESH	2.51*	0.21	2.37*
PORCUPINE	0.91	0.26	0.66
SCIURID	1.48	1.26	0.12
BIRD	1.35	2.90**	1.83+
SMALL MAMMAL	3.58***	2.10*	1.38
EMPTY	0.17	0.85	0.76

*** p<0.001 ** p<0.01 * p<0.05 +p<0.10 (else not significant, p>0.10).

Table 3.5. Paired comparisons of selected prey in stomachs of Yukon wolverine for November with December through March, 1982-1985, using z-values.

	NOV/MAR	NOV/FEB	NOV/JAN	NOV/DEC
UNGULATE	0.76	0.07	1.11	0.93
BONE	2.25*	2.94***	3.41***	3.76***
SNOWSHOE HARE	3.39***	2.61**	1.78*	2.14*
PORCUPINE	1.76+	2.56*	2.90**	2.18*
SCIURID	0.37	1.21	0.83	1.80+
BIRD		1.11	0.80	1.04
SMALL MAMMAL	1.40	0.90	0.97	1.30
EMPTY	2.38*	2.15*	1.73+	2.15*

*** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$ + $p < 0.10$ (else not significant, $p > 0.10$).

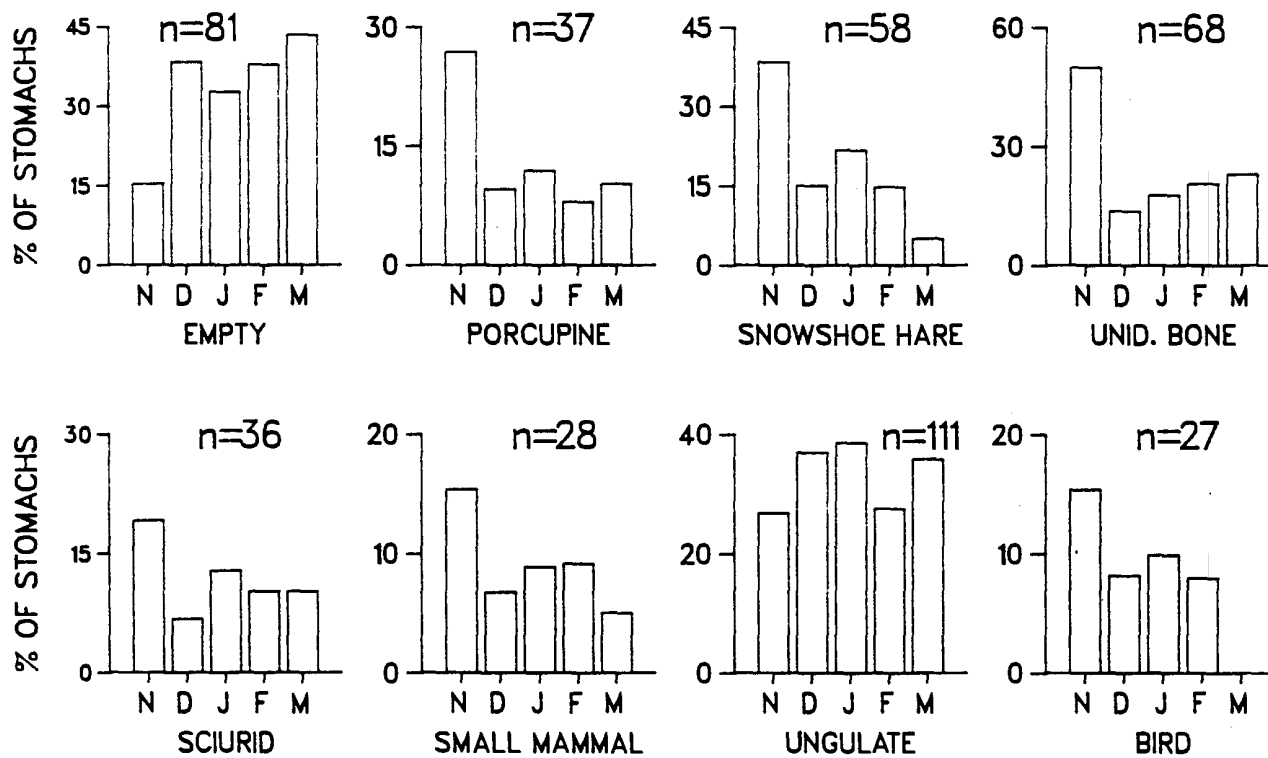


Fig. 3.3. Prey groups in stomachs of Yukon wolverine trapped in November to March, 1982–1985.

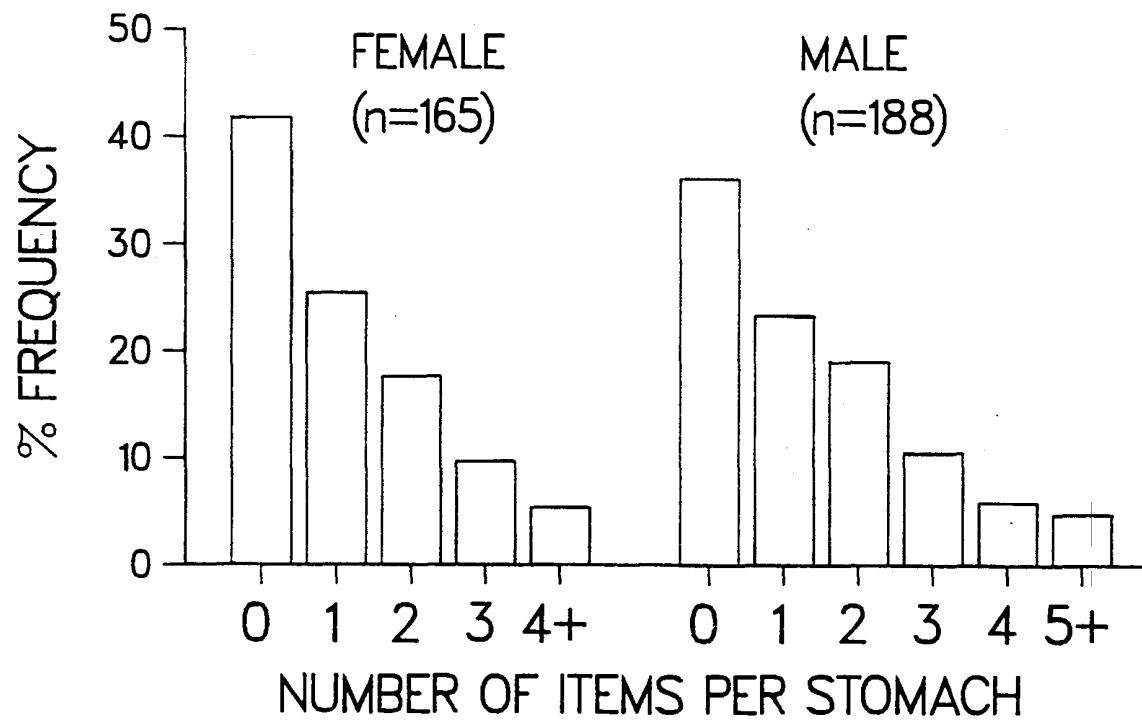


Fig. 3.4. Frequencies of number of prey groups per stomach for sexes of Yukon wolverine, winters 1982-1985.

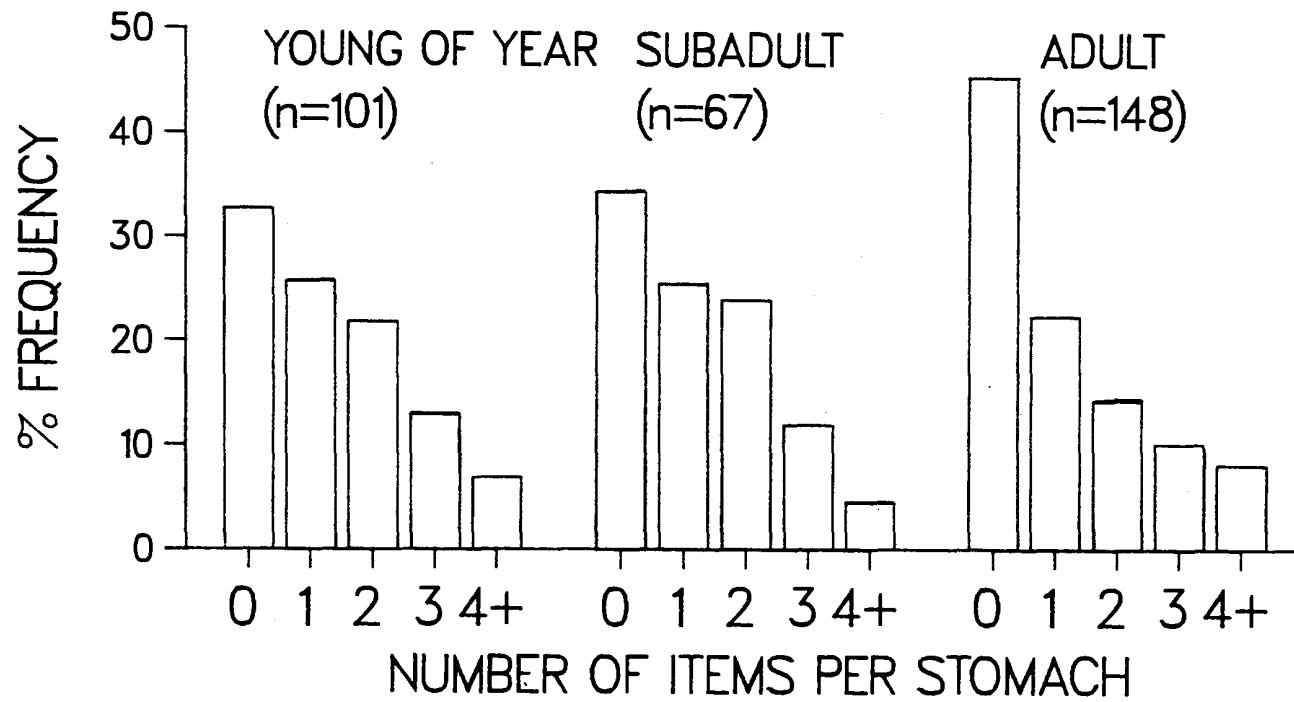


Fig. 3.5. Frequencies of number of prey groups per stomach for age classes of Yukon wolverine, winters 1982-1985.

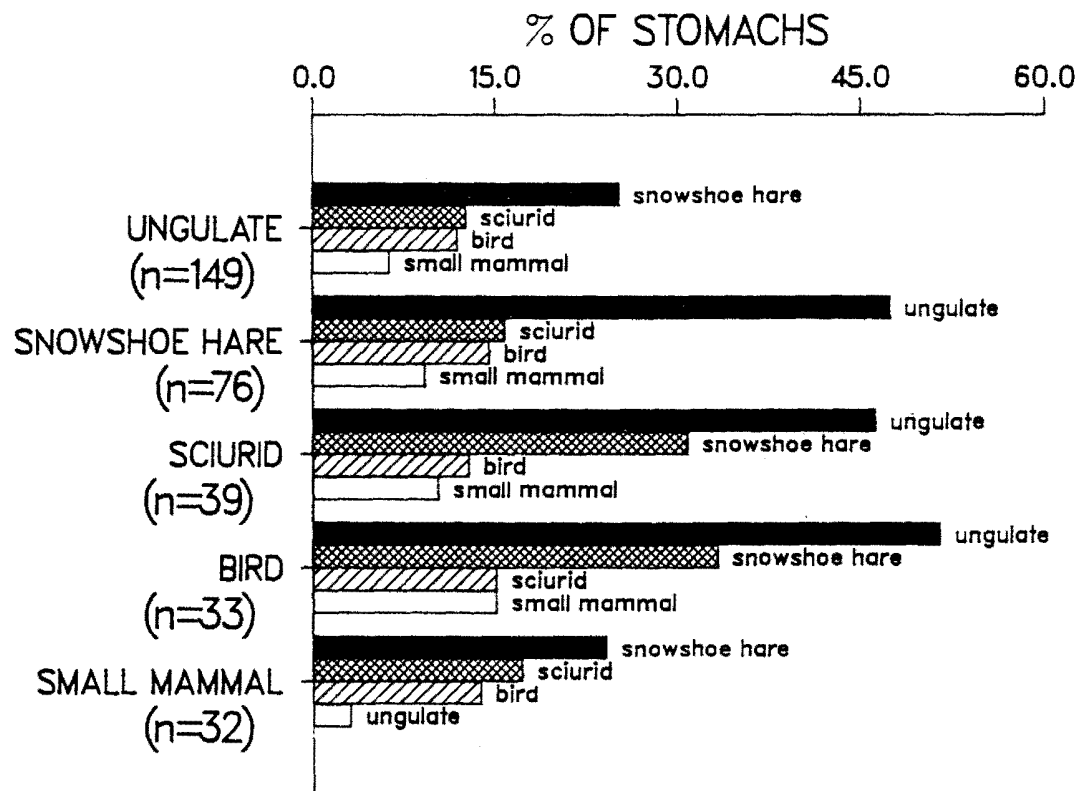


Fig. 3.6. Associations of prey groups with other prey within winter stomachs of Yukon wolverine, 1982-1985.

3% also contained ungulate. After ungulate, prey groups were associated most with snowshoe hare, 24–33%.

Discussion

Contribution of Bait to Diet

There was no difference in the occurrence of empty stomachs and consumption of fat/flesh, ungulate and snowshoe hare among restrained and quick-killed wolverine, supporting the hypothesis that consumption of trap bait is rare and not likely to bias results. Although variation was high, mean weights of typical bait items in stomachs were greater for quick-killed wolverine than for restrained wolverine. This difference may be attributable to the greater time available for digestion by restrained wolverine.

Fish in stomachs of quick-killed wolverine (n=3) is likely not bait. During winter, wolverine in southwest Yukon fed on spawned chum salmon (*Onchorhynchus keta*) frozen in river ice (Chap. IV). Locations of abundant food such as accumulations of spawned salmon may be locally important to wolverine. Evidence of domestic ungulate was not found in stomachs, further suggesting that bait did not bias food habits data. Wolverine hair in stomachs is attributable to grooming and/or self injury. Frequency of wolverine hair between trap types did not differ.

Overall Trends in Prey Consumed

The animal prey group with the greatest frequency of occurrence was ungulate (35.8%), consisting primarily of cervid species (32.6%). The largest contribution was moose (*Alces alces*, 9.7%) followed by caribou (*Rangifer tarandus*, 5.4%). Rausch and Pearson (1972) also found a higher contribution of moose (14%) than caribou (9%). Identifying cervid hair in stomachs is relatively easy due to their inflated appearance. However, identification of individual species requires a sufficient number of intact hairs so that colour and banding characteristics can be examined. A large percentage (47.8%) of cervid hair consisted only of segments. Positive identification of moose and caribou was low, hence frequencies may not indicate

relative contribution of cervid species because of differential success of identification. Elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), Stone's sheep (*Ovis dalli stonei*) and mountain goat (*Oreamnos americanus*) comprised 8.8% (13/147) of all ungulate. These species have limited distributions in Yukon, and would only be available locally. Dall's sheep (*Ovis dalli dalli*) are more widespread, however, contribution in diet was only 3.4% of all ungulate. Predation by wolves does not appear to be a significant source of Dall's sheep mortality in Yukon, possibly because of the precipitous terrain of sheep habitat (Anon. 1984). Wolverine may be more successful searching for kills of cervid species rather than attempting to find winter-killed or wolf-killed sheep on mountain slopes.

Most researchers agree that wolverine consumption of non-domestic ungulate is scavenged (Wright and Rausch 1955, Rausch and Pearson 1972, Hornocker and Hash 1981, Gardner 1985, Magoun 1985) except where fortuitous conditions permit successful predation. All these studies report the highest contribution in the diet is ungulate. In arctic Alaska, caribou was the main prey group although caribou did not occur in the study area during winter, and was only available from caches and scavenging of old kills (Magoun 1985). Banfield and Tener (1958) implied that caribou were important to wolverine and reported that the wolverine population in Labrador declined with the concomitant decline in caribou. The recent increase of caribou in Labrador is also coincident with greater sightings of wolverine (pers. comm. Tom Northcott). Availability of scavenged ungulate will depend on the ungulate rate of mortality, success of predators such as wolf in winter, and amount of material left at kill sites.

The contribution of snowshoe hare (18.5%) was the highest of all individual prey species. The winter of 1982/83 was the start of the decline phase in the hare cycle in Yukon (Boutin and Krebs 1986). Proportions of snowshoe hare in the diet of wolverine did not differ among the 3 winters of the decline (1982/83 to 1984/85). The relatively high contribution coupled with low detectability in stomachs supports the hypothesis that snowshoe hare were an important component in the winter diet of wolverine during 1982-1985, despite the decline in the hare cycle. The importance of porcupine to wolverine diet is difficult to estimate.

Most occurrences were trace as quills were readily retained in stomachs. To further complicate estimates, I do not expect much hair would be consumed. Porcupine are common throughout forested regions of Yukon and active all year. Availability is likely limited to wolverine that can successfully subdue such prey. There are no records of mortality in wolverine from ingestion of porcupine quills, although I expect perforation of internal organs would be mortal wounds. Four wolverine had quills in the abdominal cavity, mesentery or intestines, 2 of these also had quills in the kidneys. For 3 others, quills had migrated into the foramen of the lower jaw. Quills in and around the mouth was common in carcasses, even if there was no evidence of porcupine in stomachs. These quills likely indicate chance encounters or aborted attempts at predation.

Contribution of sciurids (9.5%) in the diet included every member of the family present in Yukon except woodchuck (*Marmota monax*), which is rare. Least chipmunk (*Eutamias minimus*), northern flying squirrel (*Glaucomys sabrinus*) and hoary marmot (*Marmota caligata*) comprised 15.6% of all sciurids. Distribution of these species is confined to southern Yukon. Two of these species, least chipmunk and hoary marmot, hibernate. Another hibernating species, arctic ground squirrel (*Spermophilus parryi*), comprised 25.6% of all sciurids. Magoun (1985) found that ground squirrels consumed during winter in arctic Alaska were obtained from previously cached prey. Wolverine also used caches made by red foxes (Magoun 1985). I observed "digs" on wolverine trails in southwestern Yukon although I found no evidence of cached prey. I expect caches are used in Yukon, whether made by wolverine or other carnivores, and incidences of hibernating sciurids in the winter diet of wolverine are from this source. Red squirrel (*Tamiasciurus hudsonicus*) is the most common sciurid consumed, comprising 46.1% of all sciurids. Red squirrels are widely distributed, active all year, and available all winter. Wolverine were observed excavating red squirrel middens during winter in southcentral Alaska (Gardner 1985).

Besides fish, small mammals had the smallest contribution (7.8%) to the diet. Only 2 occurrences of pika were identified. Hunting pika in mountainous terrain subject to deep snow would be energetically expensive for wolverine. As distributions are limited, most Muridae are likely to be only available locally.

Heather voles (*Phenacomys intermedius*) are known only from southern Yukon, and chestnut-cheeked voles (*Microtus xanthognathus*) only from the northern half. Tundra red-backed voles (*Clethrionomys rutilus*) are found throughout Yukon. Populations of small mammals vary annually in northern environments (Krebs and Wingate 1985) and would affect availability of small mammals to wolverine.

Most occurrences of Aves were insufficient for specific identification. Both Wright and Rausch (1955) and Rausch and Pearson (1972) documented occurrence of birds in stomach contents (trace and 1.6% respectively), however frequencies were less than that found in this study (8.0%). Field observations have documented that wolverine feed on ptarmigan (*Lagopus sp.*) in southwestern Yukon (Chap IV) and in Alaska (Gardner 1985, Magoun 1985). Prey species which were rare in the diet; beaver, lynx, mink (*Mustela vison*), ermine (*Mustela erminea*), and American marten (*Martes americana*), may have been scavenged from traplines. Canid hair may have been ingested at kill sites. The one occurrence of insect pupae, *Muscina stabulans*, was likely ingestion of infested meat (pers comm, H. J. Tesky).

The contribution of soft body parts and bone is often not addressed in food habit studies. For scavengers like wolverine, these foods form an important part of the diet. Size and structure of most unidentified bone indicated that its source was likely ungulate. Contribution of bone to the diet exceeded all prey groups except ungulate (based on hair identification). Bone in stomachs often occurred in various degrees of maceration, ranging from pieces 2–3 cm in diameter to an almost powder-like consistency, indicating extensive mastication by wolverine. Extensive mastication of bone fragments was also documented for food remains collected from wolverine dens in Norway (pers. comm. A. Suthcliffe). Wolverine in arctic Alaska have survived in winter by feeding mainly on caribou bone supplemented by cached ground squirrels (Magoun 1985). The heavy dentition and extensive neck musculature of wolverine are thought to be adaptations for consuming frozen flesh and bone (Haglund 1966, van Zyll de Jong 1975). Stomach contents categorized as fat/flesh were not associated with other prey groups and formed a separate mass in the stomach. This prey group was likely obtained by scavenging from ungulate carcasses. Both fat/flesh and bone had low detectability

in stomachs indicating relatively rapid digestion. Occurrence of scavenged prey in the diet is likely higher than that estimated from frequency of these prey groups.

Vegetation does not appear to be consumed in lieu of prey but rather incidentally with prey and at trap sites. Bird and all mammal groups excepting sciurid occurred with vegetation at least 50% of the time. Vegetation contained within ungulate rumens is associated with nutrients (Robbins 1983:255-262) that wolverine may be unable to obtain from other foods.

Inter-sex and Inter-age Comparisons

Differences in types and frequency of prey groups consumed between sexes was not observed. However, the data suggest females consumed less ungulate and more bone. As both prey groups are scavenged and information regarding availability is lacking, no conclusions can be made regarding a sex difference in foraging pattern. Food habits of females likely differ from males during denning and raising young (primarily summer) due to increased energy requirements and reduced movements. Compared with non-breeders, energy expenditure of females increases 25% during gestation and more than doubles during lactation (Moors 1980). Adequate nutrition in winter appears to be the most critical factor determining reproductive success (Chap. I). Potential impacts of food scarcity are suggested by Magoun (1985). Small litter sizes and delays in female reproduction appeared to be consequences of lack of prey.

Young wolverine grow quickly (Iversen 1972) and by 7 months have reached adult size (Magoun 1985). Immature wolverine in the harvest are as large as adults (Chap. II). Within each sex, energy requirements of different age classes are not likely to differ. Observed differences in frequencies of consumption of prey types for subadults and adults with young of year were not substantial and are confounded by yearly and monthly differences in prey availability and unequal representation of age classes by month. This bias is an important consideration when attempting to compare food habits of age classes within a sample and among samples collected under different conditions. The available information only allows a general conclusion; food habits do not appear to differ substantially among age

classes of wolverine.

Inter-year and Inter-month Comparisons

Factors contributing to food availability such as climate, small mammal population densities and ungulate mortality rates vary yearly and differences in types of prey and amounts consumed are expected. Detailed information regarding these factors for the 3 years studied is lacking and available data is insufficient to explain the differences observed. Over winter, the greatest differences in diet were found in November. This month has typically less snowfall and higher temperatures than later in winter. A trend in greater consumption of all small prey species (significant for porcupine and snowshoe hare) during November may indicate greater availability of these prey. Consumption of ungulate was consistent over winter.

Associations among Prey Groups

Food habits of mustelids are typically diverse (mink: Gilbert and Nancekivell 1982; river otter (*Lutra canadensis*): Gilbert and Nancekivell 1982, Larsen 1984; American marten: Buskirk and MacDonald 1984, Hargis and McCullough 1984; ermine: Northcott 1971, Erlinge 1981). Emphasis in food habits studies is on identifying "important" foods, those that occur with greatest frequency. The role of smaller contributions of prey in a supplemental capacity has not been addressed for opportunistic mustelids. Food habits of wolverine are not only diverse with respect to the variety of prey consumed but individual meals also are varied. The diversity of prey within stomachs of adult wolverine suggests supplemental prey are important. The prevalence of stomachs containing "0" prey groups for all age classes suggests food is generally difficult to obtain.

The diet of wolverine appears to consist primarily of ungulate supplemented by snowshoe hare, sciurid, bird and small mammal, in order of importance and coincidentally in decreasing order of body size. Although availability is expected to differ among prey groups, wolverine may select prey on the basis of size or nutritional value. Consumption of small mammals by wolverine is associated with low incidence of ungulate, suggesting small prey are used when ungulates are

unavailable.

Conclusions

It is misleading to identify only one prey group as being the most important for wolverine. The potential for a large meal at an ungulate kill site is high, and exceeds that contributed by any smaller prey. However, this benefit has a cost of uncertainty associated with it as well as a cost in time required to locate such a food source. Wolves use prey in predictable patterns according to a number of factors mostly related to ease of the hunt, and when killing is easy, prey carcasses are not as fully used as when hunting is difficult (Pimlott et al. 1969, Mech 1970). If prey are particularly vulnerable, such as during severe winters, carcasses tend to be only partially consumed by wolves (Haynes 1982). This would be an opportune environment for a scavenger such as wolverine. In addition, ungulates that die from causes other than predation are used little by wolves (Haynes 1982). As bone and hide from carcasses may be available for several months after the kill date (Haynes 1982), kill sites may remain important to wolverine long after all soft tissue has been consumed, depending on the presence of other scavengers in the area. The relatively high contribution of bone and ungulate to the diet emphasizes that scavenging is an important part of wolverine foraging. The role of other prey, particularly snowshoe hare, sciurids, bird and small mammals, appears to be supplemental. Porcupine may be an important prey for wolverine but extended retention of quills in stomachs prohibits estimating contribution to the diet.

The high incidence of empty stomachs emphasizes the unpredictable nature of northern environments. Use of food caching buffers periods of low food availability. Where local conditions and availability permit, food for wolverine may be abundant and predictable. Such a situation may occur at salmon spawning streams (Chap. IV). On the coast of the Northwest Territories, wolverine successfully prey on seal pups (pers. comm. Anne Dagg). In Scandinavia, predation on domestic reindeer (Pulliainen 1965, Haglund 1966) and sheep (Sorenson and Kvam 1985) is important.

Moors (1980) examined sexual dimorphism in feeding habits of mustelids. Such differences were suggested for wolverine by Myhre and Myrberget (1975) but were based on small samples. No differences in diets were evident for males and females in my study, however it is expected that food habits of reproducing females will differ from males in summer. As noted by Hornocker and Hash (1981), summer food habits for wolverine are not well known. Newell (1978) found small rodents (voles and lemmings) to be the most frequent prey (78%) in a sample of 15 summer scats collected in northern British Columbia. Gardner (1985) emphasized the importance of ground squirrels to wolverine diet in summer in south-central Alaska. Magoun (1985) observed wolverine in summer feeding on caribou kills, marmots, ground squirrels, microtines and ptarmigan. Late winter scats collected in southwestern Yukon contained kinnickinick berries (*Arctostaphylos uva-ursi*) (Chap. IV), suggesting wolverine are opportunistic. The summer diet is expected to be more varied than the winter diet because of the greater availability of berries, small mammals and sciurids. However, greater variety does not imply more abundant food. Ungulate mortality is greatest in winter, thus number of kills available to wolverine for scavenging will be less in summer. Wolverine have been documented frequenting areas of caribou and moose calving in Alaska (Gardner 1985) and caribou calving and sheep lambing in Yukon (Chap. IV). However, the period of birth for ungulates is short. The timing of pregnancy and parturition of wolverine in winter and early spring (Chap. I) suggests these seasons are better for wolverine in terms of more abundant food resources.

PART C
FIELD STUDIES

CHAPTER IV

HOME RANGE AND HABITAT USE

Home Range Use

The development of radio-telemetry greatly facilitated the investigation of movements and home range use for wide ranging mammals. Before 1976, field studies of wolverine (*Gulo gulo*) were conducted by snowtracking (Scandinavia: Krott 1959, Pulliainen 1963, Haglund 1966, Myhre 1967, Myrberget et al. 1969 and U.S.S.R.: Makridin 1964). In 1976, Hornocker and Hash (1981) initiated the first radio-tracking study of wolverine in North America. Radio-telemetry studies in south-central Alaska (Gardner 1985, Whitman et al. 1986) and arctic Alaska (Magoun 1985) have recently been completed. The field studies reported herein are part of a population study designed to assess the status of Yukon wolverine populations. This work is the first radio-telemetry study of wolverine in Canada.

Powell (1979) reviewed spatial distribution in Mustelidae and concluded that the basic pattern appears to be intrasexual territoriality, where only home ranges of opposite sexes overlap. Scent marking, dominance relations and food supply affect the maintenance and stability of this spacing pattern (Powell 1979). All completed studies on wolverine, including this one, were conducted in physically and ecologically distinct areas. Study areas differ with respect to habitat types, topography, prey availability and harvest pressure. It would be ambitious to claim a single study is definitive with respect to understanding spatial patterns in wolverine. Home ranges of wolverine in Montana overlapped between individuals of the same and opposite sex (Hornocker and Hash 1981). In arctic Alaska, home ranges of adult males were strictly exclusive, those of adult females overlapped only in winter (Magoun 1985). Such differences imply behavioural flexibility. Comparisons of behaviour under different conditions are needed to reveal the underlying mechanisms behind wolverine spatial distribution.

One objective of studies involved in tracking wild species is to estimate home range size. Emphasis on obtaining these estimates treat home range as a

component, albeit a mutable one, of an animal's behavioural repertoire. However, home range is more than just an area dictated by limitations of physical space or gross food available. As stated by Laundre and Keller (1984), use of an area is determined by habitat composition, physiographic make-up, food distribution (as opposed to abundance), and other factors necessary for survival. These are not adequately delineated by a simple measure of home range size. However, for species difficult to enumerate by other means, average home range size may have considerable importance. If home ranges are exclusive, mean home range size may be used to estimate the numbers of adults resident in an area of known size. This requires an understanding of how home range use varies seasonally and yearly, how it is related to changes in prey distribution and availability, and the extent of overlap among home ranges.

Knowing the stability of a spatial system is necessary if densities are to be estimated using measures of home range size. The spatial patterns exhibited by a species may exhibit considerable variation, a function of the defensibility and abundance of a food resource (Lott 1984). The opportunity to examine flexibility in the spatial strategy of wolverine arose during this study. An abundant source of food in the form of spawned chum salmon (*Oncorhynchus keta*) frozen in river ice is present in Kluane River, in southwest Yukon. This area falls in a registered trapline which has been productive for the harvest of wolverine. The sex/age composition of these harvests was available for two years, 1982/83 and 1983/84, and provided insight into the spatial patterns of wolverine resident in the area.

The use of habitats within a home range and the extent of movements are related to the reproductive and physiological status of an animal and are a function of prey distribution and availability. Reproduction (Chap. I), body size and condition (Chap. II), and winter food habits (Chap. III) have been determined using wolverine carcasses submitted by Yukon trappers. These data form the framework for interpreting the behaviour observed from radio-collared wolverine. Observations of live wolverine assisted in determining possible natural mortality factors and observations of feeding activity permitted the corroboration of food habits data determined from stomach contents.

The accuracy of home range estimates is affected by methods of analysis (Swihart and Slade 1985). The minimum convex polygon (Mohr 1947) has been used in all 3 previous North American wolverine field studies (Hornocker and Hash 1981, Magoun 1985, Whitman et al. 1986). Inclusion of extreme locations inflates the estimate of home range size and areas of intensive use are not identified. Harestad (1981) modified the above method so that home ranges may be considered as proportions of an animal's locations. All locations are represented by the 100% home range. Successive extreme points are then deleted to identify areas having intensive use.

My objectives are to:

1. determine yearly home range use
2. determine seasonal home range use
3. describe overlap and movements
4. discuss mortality factors
5. describe food habits
6. estimate density/population size

Study Area

Live trapping was carried out in a 1800 km² area located in the Kluane Game Sanctuary of southwest Yukon. The trapping area was bounded by Kluane National Park in the south, the Alaska highway to the north, Duke River to the east and tributaries of Donjek River to the west. Movements of wolverine extended this study area south and east for a total of 2300 km² (Fig. 4.1). The study area supports a wide variety of small herbivores (sciurids, lagomorphs, microtines) as well as 4 ungulate species: moose (*Alces alces*), woodland caribou (*Rangifer tarandus*), Dall's sheep (*Ovis dalli dalli*), and mountain goat (*Oreamnos americanus*). Mountain goats are rare and only known to occur on a few localized mountain ridges. Lynx (*Lynx canadensis*), red fox (*Vulpes fulva*), coyote (*Canis latrans*), wolf (*Canis lupus*), and grizzly bear (*Ursus arctos*) are common. Black bear (*Ursus americanus*) also occur but are rare. Other mustelids present are ermine (*Mustela erminea*) and American marten (*Martes americana*). Because the Kluane Game

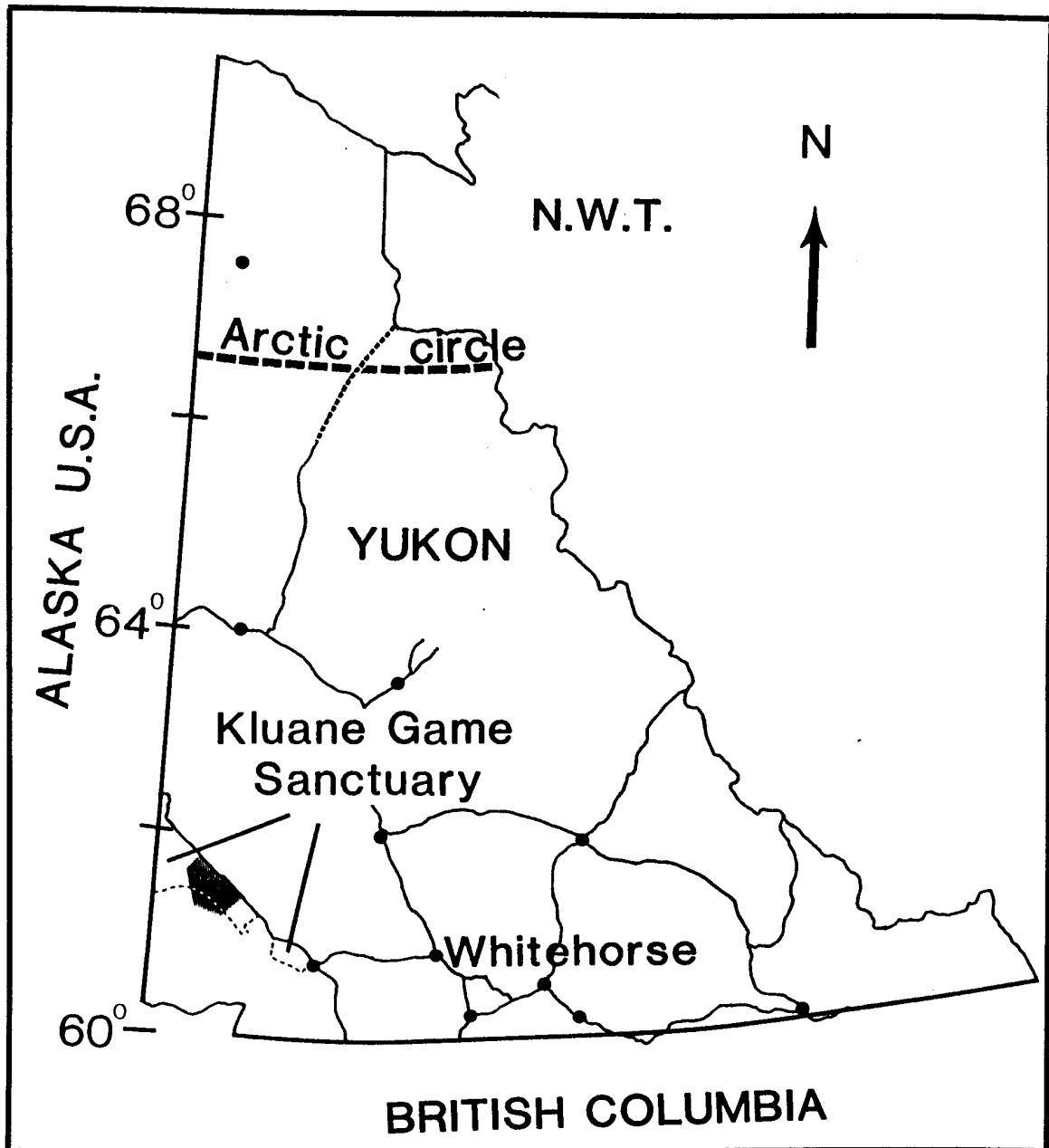


Fig. 4.1. Location of study area, communities and roads in Yukon.

Sanctuary has been closed to hunting and trapping since its establishment in 1943, the wolverine population in the study area is unharvested. Creeks are mined during summer and access is available through extensive placer mining roads. There is no human activity during winter.

Topography and Climate

The study area is in the Ruby Range Ecoregion and partly in the St. Elias Mountains Ecoregion (Oswald and Senyk 1977). The latter consists of high rugged mountains, nearly all greater than 1500 m; icefields and glaciers are prominent. Both ecoregions are in the discontinuous scattered permafrost zone (Brown 1978) and in the tundra region of Rowe (1972). Boreal forest habitat is in the B26d region of Rowe (1972) and is mostly restricted to a strip along the Alaska highway.

The Ruby Range Ecoregion contains the Kluane Ranges, Shaskwak Valley and Kluane Plateau, as designated by Bostock (1965). Topography consists of rolling to undulating hills greater than 900 m in elevation. The Kluane, Donjek, White and Nisling Rivers drain the region. Kluane Lake (396 km²), the largest lake in Yukon, occurs adjacent to the study area. Meandering streams and glacial ponds are common. Vegetation is park-like in appearance; forest stands are rarely dense and their canopies are seldom closed. Treeline occurs at 1050 m but may vary depending on local climate. The highest peak (2345 m) within the study area is Wade Mt.

The region lies in the rain-shadow of the St. Elias Mountains. Climate is typically dry and cold. Winds are common and frequently strong, especially in major valleys. Mean temperatures recorded at the Burwash Flight Station from January 1983 to March 1986 were -25°C to -8°C for January and 11°C to 12°C for July. Precipitation ranged from 6 to 14 mm for January and 43 to 121 mm for July. Summers of 1984 and 1985 and winter of 1985 had atypically high amounts of precipitation in comparison with previous years.

Habitat Use

Vegetation in the Kluane Game Sanctuary has been surveyed and classified by Oswald et al. (1981). The alpine zone contains high elevation terrain and includes areas where vegetation is low-growing, frequently prostrate and dominated by willow (*Salix spp.*), dryas (*Dryas spp.*), ericaceous shrubs and lichens. Shrubs are usually not taller than 0.5 m in height and trees are generally absent. Wet areas normally support graminoids. Vegetation is often sparse on exposed or rocky sites. Subalpine includes mountainous terrain from below alpine to large valley bottoms and plateaus. For mapping habitat types, the lower subalpine limit often follows a physiographic break between mountain slope and valley or plateau (Oswald et al. 1981). Shrub birch (*Betula glandulosa*) and willow are prevalent and extend into the alpine. Sedge and tussock fields occur on wet sites.

Below treeline, in well drained sites, white spruce (*Picea glauca*) is the climatic climax species but may share dominance with black spruce (*Picea mariana*) where permafrost is near the surface. Occurrence of balsam poplar (*Populus trichocarpa*) is sporadic. Understory species are willow, shrub birch, aspen (*Populus tremuloides*), soapberry (*Shepherdia canadensis*), alder (*Alnus incana*) and ericaceous shrubs. Waterways and associated riparian habitat are common in all zones and habitat types.

Appropriate methodology for determining whether habitat use differs from availability remains unclear (Johnson 1980, Kincaid and Bryant 1983, Alldredge and Ratti 1986). Present methods require several assumptions:

1. animals have access to and the opportunity to be observed in various habitat categories.
2. animals move independently of each other.
3. temporal spacing is independent.
4. data are collected in a random, unbiased manner.

By comparing use to availability only within a wolverine's home range, the first assumption is satisfied. In addition, wolverine do not appear to be

constrained by physiographic boundaries such as mountain ranges or large rivers (personal observation, Hornocker and Hash 1981). It is expected that movements of one individual will generally not affect those of another in time or in space, because of the wolverine's relatively low densities and use of large areas. Interactions will occur, however, during the breeding season and possibly between adults and dispersing juveniles. Short time intervals between successive locations leads to a lack of independence (autocorrelation), at least between successive points (Dunn and Gipson 1977). To rectify this difficulty, Swihart and Slade (1985) recommend a maximum of 1 to 2 observations for 24 hour period per animal. I do not expect this to be a problem with my data; locations were taken 4–11 days apart. Tracking large carnivores from the air can rarely be carried out randomly. Flights are constrained by weather, available daylight and logistics. However, by monitoring over a sufficiently long period, a representative sample of habitat use over time is obtained.

An understanding of the yearly and seasonal use of habitats is necessary to assess the capability of areas for wolverine and predict densities. Knowing what habitats are critical for a wild species is also essential to assess the impacts of human development.

My objectives are to:

1. Compare habitat use to availability for individual wolverine.
2. Compare habitat use to availability between seasons for each sex.
3. Compare use of percent forest cover, aspect, slope and elevations between seasons for individuals and for each sex.

Materials and Methods

Home Range Use

Live trapping was conducted during winters 1983/84 and 1984/85. The first 3 wolverine captured were purchased by the Yukon Department of Renewable Resources from two trappers harvesting adjacent to the Kluane Game Sanctuary. Methods of capture were 45 gallon drum and steel-box traps. Padded legholds

(#4) were also used but they were unsuccessful in holding wolverine. Initially wolverine were immobilized by securing a foreleg using a snare pull. Techniques which allowed drugs to be administered rapidly with little stress on the animal were subsequently adopted. A plunger constructed of a 1/4" plywood square, slightly smaller than the door, nailed to 2x4's was used to hold wolverine at the grill end of box traps. Wolverine in drum traps were coerced into a connecting constrainer, a 20 gallon drum of similar construction. The back end was mounted on rods and slid forward, forcing the wolverine to the grill where it was injected.

Weights were estimated and appropriate dosages selected. Aqueous ketamine hydrochloride ("Rogarsetic", Rogar/STB Ltd.) and xylazine hydrochloride ("Rompun", Haver-Lockhart) were used in 1:1 to 3:1 ratios at concentrations of 100 mg/ml (and 20 mg/ml xylazine for some wolverine). Wolverine were injected intramuscularly in the foreleg or rump area using 3.0 ml syringes and 23 gauge, 2.5 cm stainless steel needles. Immobilized wolverine were weighed, measured and an upper premolar pulled for aging. Age class (young of year, subadult, adult) was estimated based on body size, tooth wear and condition of testes/teats. Radio transmitter collars (Telonics Inc.: 148-150 mhz) and ear tags (Nasco Inc.) were attached before release.

Traps were checked daily. Tracks and sightings of mammals, ermine sized and larger, were recorded during winter 1984/85 in areas accessible by snowmachine, from Donjek River in the west to Ptarmigan Creek in the east. Regulations prohibited travelling in the park by vehicle. Tracks and sightings in inaccessible areas observed during tracking flights were recorded as well. Incidental observations were collected from local residents, miners, park personnel, pilots and other biologists. Observations collected by researchers present in the area during 1982 were also obtained. Unmarked wolverine present in the study area were monitored from June 1983 through August 1985, using snow-tracking and sightings. Sex was determined from track size, length of stride and body size, if wolverine were observed. Unmarked wolverine were classified as residents if tracks were consistently observed in an area over the duration of the study. Observations were classified as transient if tracks were seen in an area previously devoid of wolverine sign and physically distinct from areas residents were known

to inhabit, and if the occurrence was rare. Scats were collected when found. Histological examination of tissues for 1 collared female was carried out by Central Laboratory for Veterinarians in Surrey, British Columbia, through Dr. Pat Smith of Whitehorse.

A Piper super cub or Cessna 180 aircraft with a null antenna (Telonics Inc.) mounted on each wing strut was used to track wolverine. Logistics permitted monitoring flights on average once every 10 days. This interval varied depending on weather, plane availability and reliability of radio signals. If a wolverine's location could not be fixed on a flight because of poor signal, a follow-up flight was made as soon thereafter as possible. If signals of other wolverine were picked up on the follow-up, their locations were recorded. Monitoring occurred from January 1984 through March 1986. Success of ground monitoring was limited because of inaccessibility of mountainous terrain. Four ground locations were obtained for female F384 and 1 for F484. These were determined by triangulation of a minimum of 5 bearings. Home range size was calculated using "HOME" (Harestad 1981), a program that uses the minimum home range method to calculate area. Winter is designated as November through April and summer May through October. These seasons coincide with snow-present and snow-free periods, respectively.

Habitat Use

During tracking flights, locations were plotted onto 1:50,000 topographic maps and accompanied by a written description of habitat type and percent forest cover. Local descriptions (riparian, hillside, roadway, rock face, plateau, meadow) were noted. This information was crossreferenced with vegetation maps (1:100,000) of Oswald et al. (1981). Where ground knowledge differed from the vegetation maps, ground knowledge was used. Classification for analysis included 3 zones; alpine, subalpine and boreal. Within each zone occurred a maximum of 5 possible habitat types: coniferous, mixed, shrub, grass (includes graminoids) and talus/rock. For each location, slope and aspect in degrees were calculated and elevation recorded. Aspect was categorized as "N": 316-45°, "E": 46-135°, "S": 136-225°, "W":

226–315°, and "flat". Classification of percent forest cover was consistent with that of Oswald et al. (1981): <20%, sparse; 20–50%, scattered; 50–80%, open; and >80%, closed.

Habitat types were transferred from vegetation maps onto 1:50,000 topographic maps. Riparian habitat was defined as the area 0.05 km on either side of water bodies and included all streams, rivers, sand bars, deltas, and permanent glacial ponds. To determine habitat availability, grids of computer generated random locations were overlaid on each home range as described by Marcum and Loftsgaarden (1980). Habitat type for each point was recorded. Occurrence of riparian habitat was recorded independently of zone and habitat type. To obtain adequate sample sizes, this process was repeated within each home range until relative frequencies of habitat types remained constant.

Numbers of locations per habitat type (use) were compared to expected (available) using a χ^2 goodness of fit test (Neu et al. 1974). Bonferroni simultaneous confidence intervals for proportions of habitat types used were constructed ($p < 0.05$, Byers and Steinhurst 1984). The hypotheses tested using above methods are:

- H_1 : Usage occurs in proportion to availability considering all habitats simultaneously.
- H_2 : Usage occurs in proportion to availability considering each habitat separately.

Habitat use was compared to availability separately for each season for each sex. For riparian habitat, proportion used was compared to availability using standard z tests. Use of elevations, slope, aspect and percent forest cover were compared between sexes and seasons using Mann–Whitney U tests. To distinguish these results from those from standard z-tests, statistics are indicated as "MW z". Differences apparent at $0.05 < p < 0.10$ were considered as a tendency to use a habitat category more or less frequently than available.

Results

Ten wolverine, 5 males (3 adults, 1 subadult, 1 young of year) and 5 females (3 adults, 2 young of year), were captured over the 2 winters (Table 4.1). Teeth were not available for M183, F384 and F484 and age class was estimated. M183, M184 and M284 were captured by trappers. A total of 2480 trap-nights was required to capture the remaining 7 wolverine. One male was "lost" immediately and 1 female was lost after 10 months of tracking because of collar malfunctions (Table 4.2). Four of 6 mortalities were recovered, 2 were inaccessible. The remaining 2 wolverine were monitored to the end of the tracking period, March 31, 1986. The data are sufficient (minimum of 295 days on air) to analyze yearly and seasonal home range use and movements for 5 individuals: 3 adult females and 2 males, an adult and a subadult.

Yearly Home Range Use

100% home ranges are illustrated in Fig. 4.2. Home ranges containing 90% of closest locations represent 21%–66% reductions in size (Table 4.3) and indicate areas of intensive use. Females without kits, F484 and F584, had yearly home ranges of 202 km² and 343 km², respectively. If excursions are discounted, their home ranges are almost equivalent, 157 and 153 km² respectively. Yearly home range size of F384, who I believe had young, was 139 km². Her 90% home range (47 km²) was 3 times smaller than that for the other 2 females for which sightings confirmed kits had not been born. F684, a young of year female, was trapped within F384's home range during early winter of 1985 and may be her daughter.

The largest home range of all individuals, 526 km², belonged to subadult male M285. The area he used was even greater because he had left the study area and could not be relocated from November to December 1985. He returned in mid-January 1986 and remained in the area for only 3 weeks before departing again. His last location placed him north of the highway; shortly thereafter he was trapped. Home range size of adult male M385 (283 km²) was smaller than that of one of the adult females and of M285 (Table 4.3). No excursions were apparent

Table 4.1. Age, weight and measurements (cm) of live wolverine trapped in Kluane study area, Yukon 1983/84 - 1984/85.

AGE CLASS (years)		WEIGHT (kg)	BODY ^a LENGTH	TAIL LENGTH	HIND LEG ^b LENGTH	SHOULDER ^c HEIGHT	HEART GIRTH	NECK DIAMETER
MALES:								
M183	Adult	14.1						
M184	Young of Year (0+)	10.2	82.0	23.0	41.0	42.0	41.0	31.0
M284	Adult (10+)	15.0	84.0	19.0	42.0	41.5	59.0	36.0
M285	Subadult (1+)	11.8	82.0	23.0	42.0	41.0	47.0	36.0
M385	Adult (4+)	14.1	86.8	28.0	44.3	42.5	50.5	37.0
MEAN		13.0	83.7	23.2	42.3	41.7	49.4	35.0
S.D.		2.0	2.3	3.7	1.4	0.6	7.5	2.7
FEMALES:								
F384	Adult	11.0	74.0	29.0	40.0	41.2	40.0	28.0
F484	Adult	10.0	75.5	23.5	42.5	36.0	35.5	28.0
F584	Adult (3+)	8.0	75.6	20.5	41.5	34.5	40.0	31.0
F684	young of year (0+)	6.6	73.0	18.0	43.5	40.5	35.0	27.5
F185	young of year (0+)	7.8	73.5	26.0	41.0		40.0	28.0
MEAN		8.7	74.3	23.4	41.7	38.0	38.1	28.5
S.D.		1.8	1.2	4.3	1.3	3.3	2.6	1.4

^atip of nose to base of tail.

^bdistal tip of pelvis to tip of longest toe, leg extended.

^cdistal tip of scapula to tip of longest toe, leg extended.

Table 4.2. Radio-collared wolverine trapped in Kluane study area, Yukon 1983/84 - 1984/85.

IDENTIFICATION ^a	DATE TRAPPED	LAST LOCATION	DAYS ON AIR	MEAN DAYS/LOCATION	COMMENTS
M183	11/24/83	not relocated	0		collar malfunction
M184	01/01/84	08/02/84	39	6.5	possible wolf kill
M284	01/01/84	21/01/84	21	4.2	mortality - trapped
M285	12/03/85	01/02/86	326	11.0	mortality - trapped
M385	07/04/85	31/03/86	358	7.8	
F384	09/02/84				
"	12/12/84				recapture
"	28/12/84				recapture
"	14/01/85				recapture
"	16/01/85		342	8.6	mortality
F484	02/18/84	10/12/84	295	11.9	collar malfunction
F584	23/11/84	31/03/86	494	16.8	
F684	27/11/84	21/02/85	87	17.4	mortality - unknown
F185	13/02/85	16/03/85	32	6.2	mortality - unknown

^aM=male F=female.

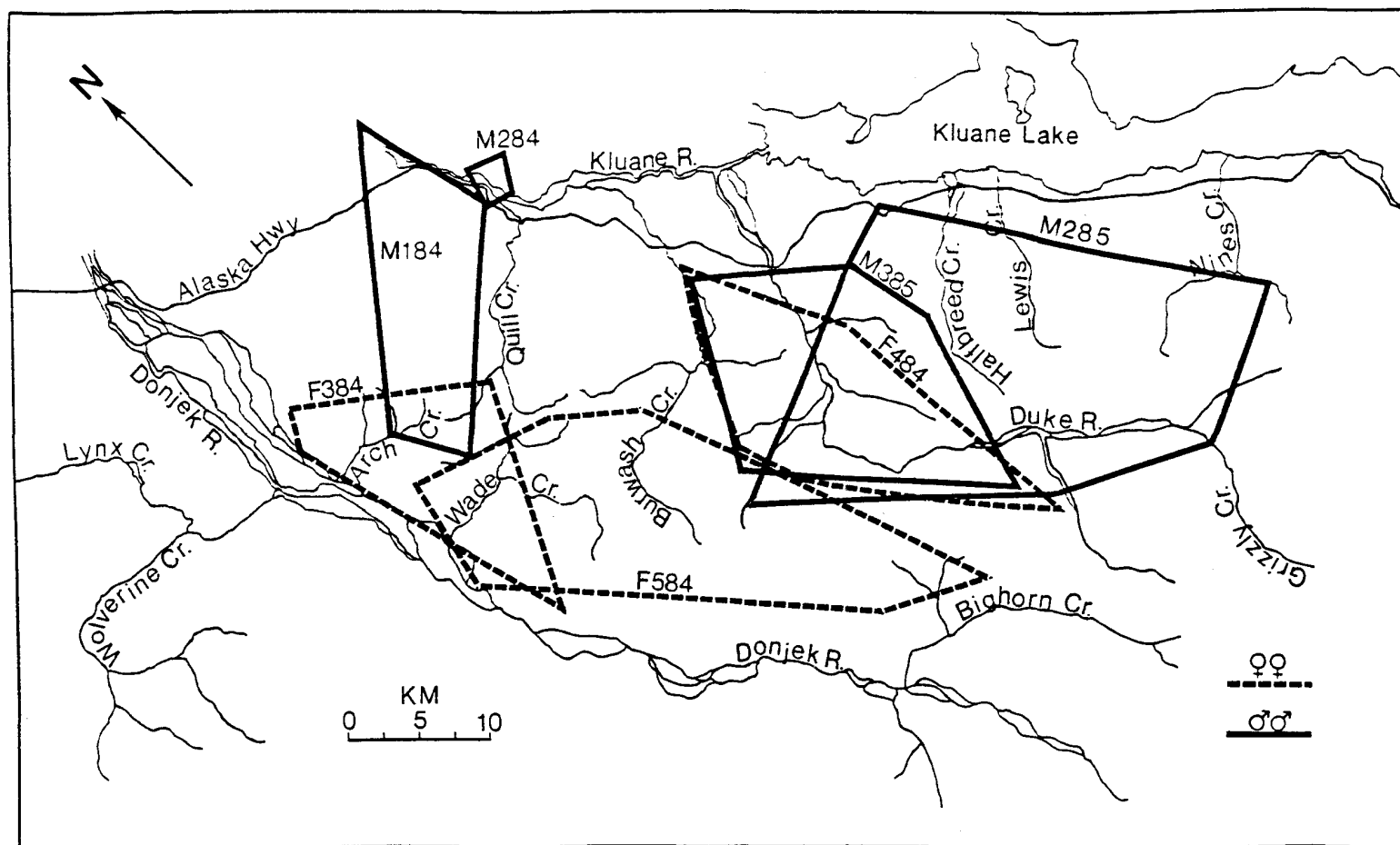


Fig. 4.2. 100% home ranges for male (M) and female (F) wolverine radio-collared in southwest Yukon, 1983-1986.

Table 4.3. Home ranges containing 90-100% of observations for 5 wolverine radio-collared in Kluane study area, Yukon 1983-1986.

	% HOME RANGE	SIZE (km ²)	N	% OF TOTAL AREA
F384	100	139	39	100
	97	76	38	55
	90	47	35	34
F484	100	202	30	100
	97	157	29	78
	90	134	27	67
F584	100	343	33	100
	97	269	32	78
	94	153	31	45
	90	128	29	37
M285	100	526	21	100
	92	412	20	78
	90	283	18	54
M385	100	238	29	100
	97	209	28	88
	90	188	26	79

for M385. During 21 days of monitoring, M284, an old adult male, used an area consisting of 4.7 km² (Fig. 4.2). This wolverine had been recaptured at least once before being killed by the resident trapper. F185 was the only wolverine captured on the west side of Donjek River, although tracks indicated another wolverine was present on Wolverine Creek. After the death of F185, monitoring of tracks in this area ceased.

Seasonal Home Range Use

Seasonal estimates of home range size do not contain all months for all individuals (Table 4.4). Accurate winter estimates of home range size are not available for F384, F484 and M285. Mean summer home range size for the 3 adult females is 156 km² (SD=48), range 118–210 km². Discounting a long distance movement reduces F384's summer home range to 62 km² from 118 km² (Table 4.4, Fig. 4.3). Her activity was limited to a 14 km² area during November through early January and her movements during this interval mainly followed my traplines. She was recaptured 3 times between December 12th and January 14th. At first recapture her body weight was 25% less than at first capture in February. She had a fresh, open wound on her lower back. Spacing of teeth marks was consistent with that of a wolf. Although it was not possible to obtain an age, heavily worn teeth indicated she was an old animal. After the last recapture, she was brought to Whitehorse and examined by a veterinarian. She died in captivity 2 days later. Histological results included protozoal cysts in diaphragmatic and skeletal muscle, parasitic pneumonia and focal interstitial nephritis.

F484's summer home range omitting her 1 excursion (110 km²) is 22% smaller than her yearly home range. She shifted use of her home range from northeast to southwest as winter ended and summer progressed (Fig. 4.4). Use of areas cannot be assumed to be consistent between seasons of different years, however locations for February to April 1984 and November to December 1984 suggest that her winter home range may not be substantially different from summer (Fig. 4.4). Her collar malfunctioned during December of 1984. Prior to signal loss, she was using an 8 km² area at 1311 m to 2073 m elevation, consisting mainly of alpine talus habitat.

Table 4.4. Seasonal home ranges containing 100% of observations for 5 wolverine radio-collared in Kluane study area, Yukon 1983-1986.

	DATES	SIZE (km ²)	N
F384	FEB-APR	30	8
	MAY-OCT	118	23
	"	62*	22
	NOV-JAN	14	8
F484	FEB-APR	61	7
	MAY-OCT	141	18
	"	110*	17
	NOV-DEC	8	5
F584	NOV-APR	119	11
	MAY-OCT	210	11
	"	82*	9
	NOV-MAR	3	11
M285	MAR-APR	116	8
	MAY-OCT	437	10
	JAN-FEB	32	3
M385	APR	27	4
	MAY-OCT	46	12
	NOV-MAR	146	13

*Less extreme locations.

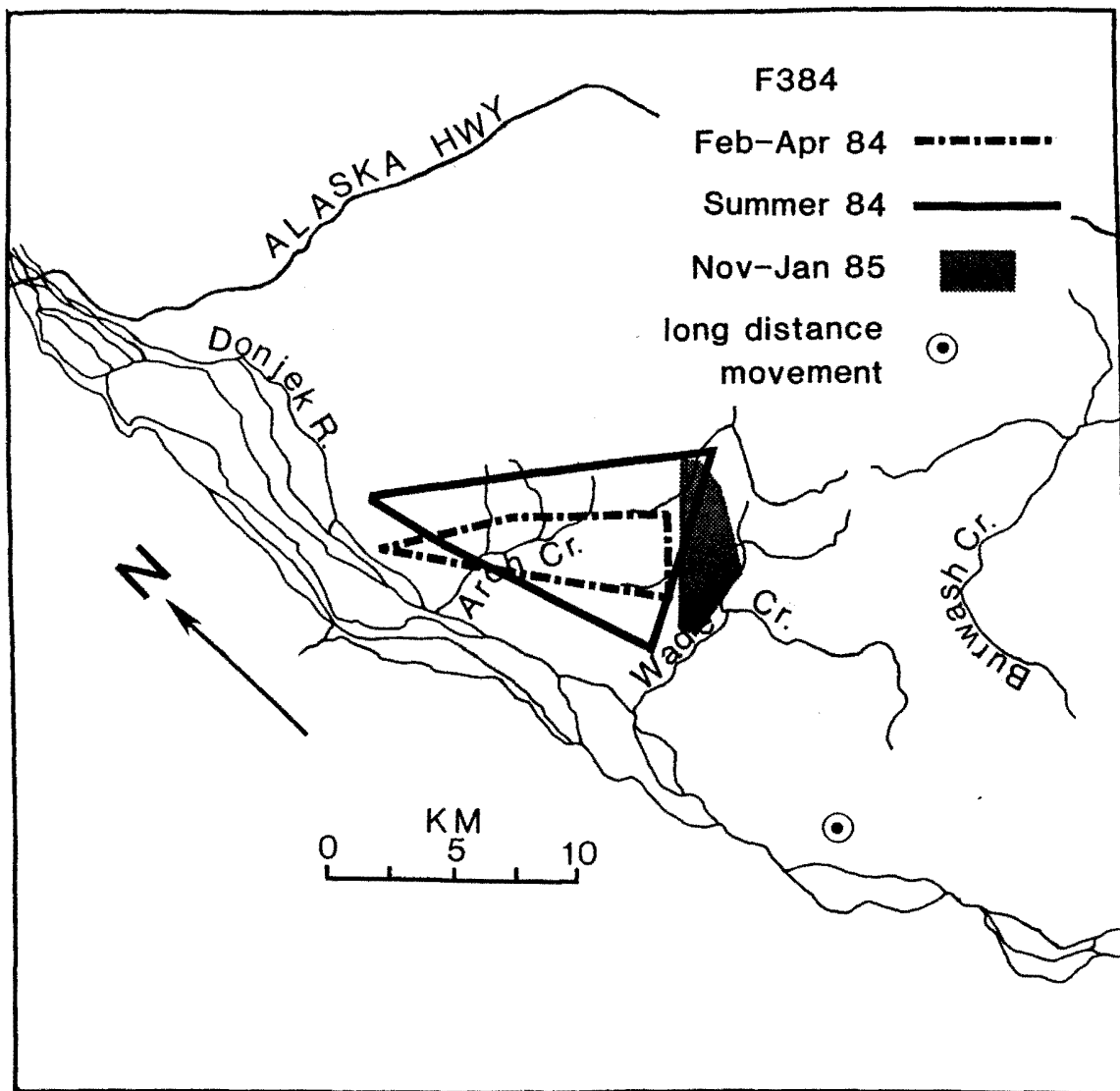


Fig. 4.3. Seasonal 100% home ranges for radio-collared wolverine female F384, Yukon 1984-1985.

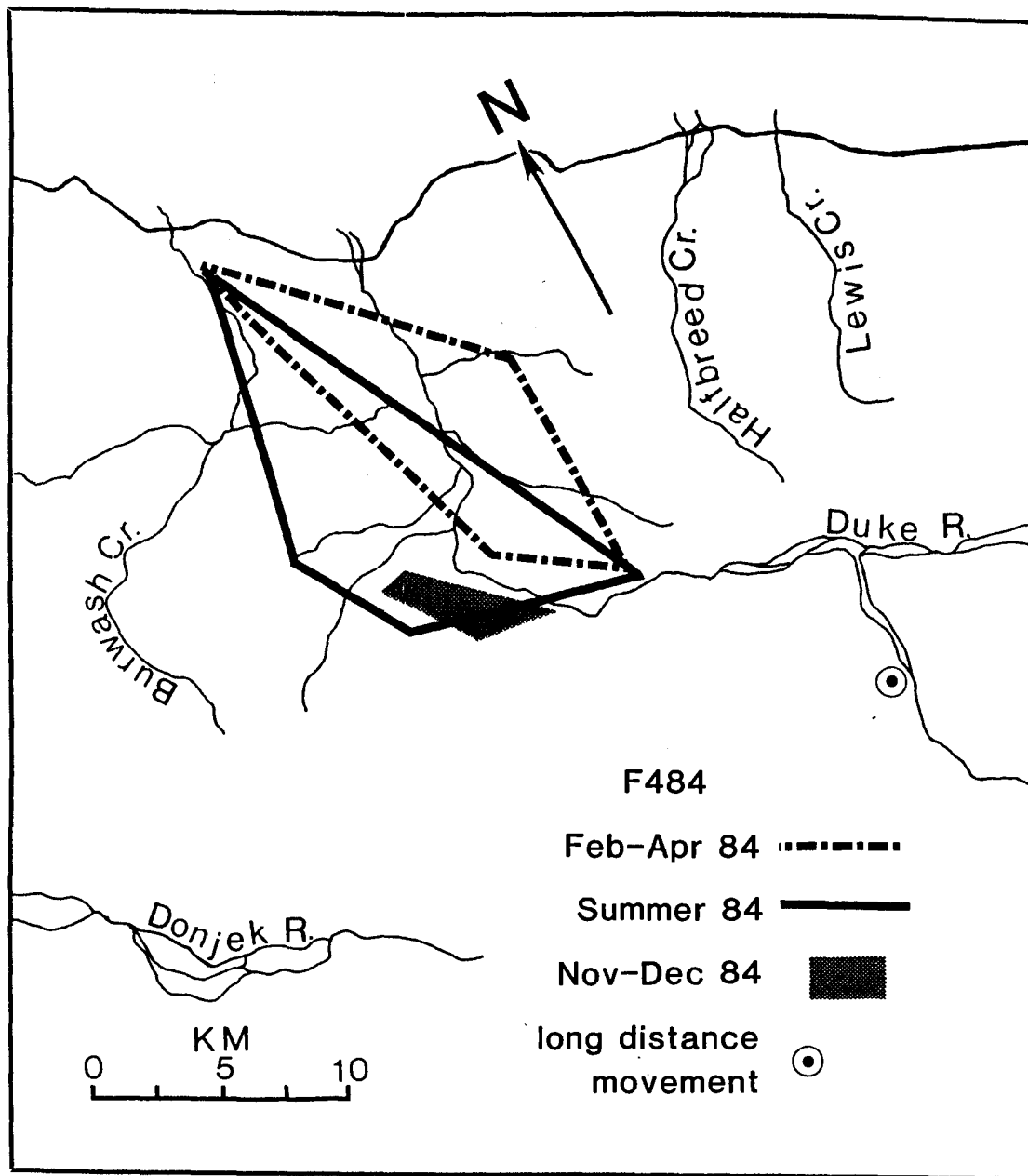


Fig. 4.4. Seasonal 100% home ranges for radio-collared wolverine female F484, Yukon 1984.

The difference in seasonal home range size for F584 (Table 4.4) was primarily attributable to 2 excursions made in July and August (Fig. 4.5). Discounting these movements, summer home range (82 km²) was smaller than winter (119 km²). Her signal was picked up 9 times in an 0.1 km² area during November and January through March 21, at 1768 m to 1828 m elevations. (Because of inclement weather, no locations were obtained in December.). Her behaviour during this period was suspect and initially I believed she had died. However, subsequent movements were observed. Her last locations, on March 23rd and 31st, were at 1920 m elevation, 2.6 km northwest from previous locations.

Summer home range for subadult male M285 (437 km²) was the largest of all individuals. Winter home range description is incomplete (Table 4.4, Fig. 4.6). M385, an adult, had a summer home range (46 km²) the smallest of all individuals. The following winter, he expanded both north and east for a winter home range three times the size of his summer home range (Fig. 4.7).

Overlap and Movements

F484's home range was completely contained within M385's, however overlap may not be as depicted in Figure 4.2 as these 2 individuals were not monitored concurrently. Information regarding extent of overlap between home ranges of F384 and F584 is minimal as F384 was alive for only 2 months after F584 was captured. * Locations of the 2 females on or near the same day were at least 6 km apart. Nonconcurrent use of the same area did occur as on December 12, F384 was recaptured in the trap used to capture F584 on November 11. However, F584 was not consistently found within F384's home range until April, 3 months after the latter's death.

F484 was lost shortly after the capture of F584 and it was not possible to determine if overlap occurred. However, I do not believe F484 died. If home ranges remained relatively constant in space, it is likely their home ranges were distinct. Overlap between home ranges of M285 and M385 was extensive. On 2 occasions, May 18 and August 9/10, the 2 males were on opposite banks of Duke River. It is not known whether any interaction occurred although direction of travel

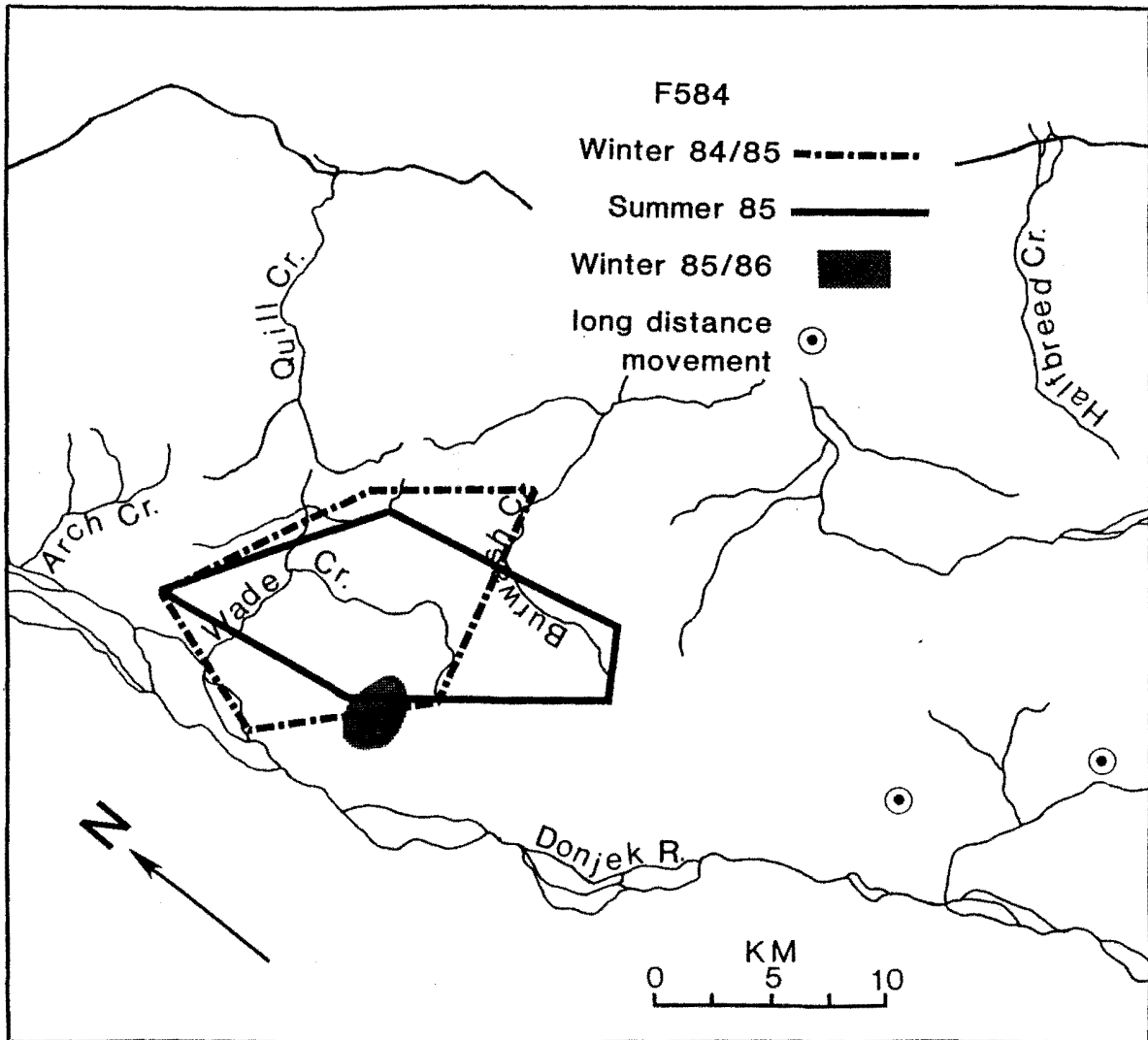


Fig. 4.5. Seasonal 100% home ranges for radio-collared wolverine female F584, Yukon 1984-1985.

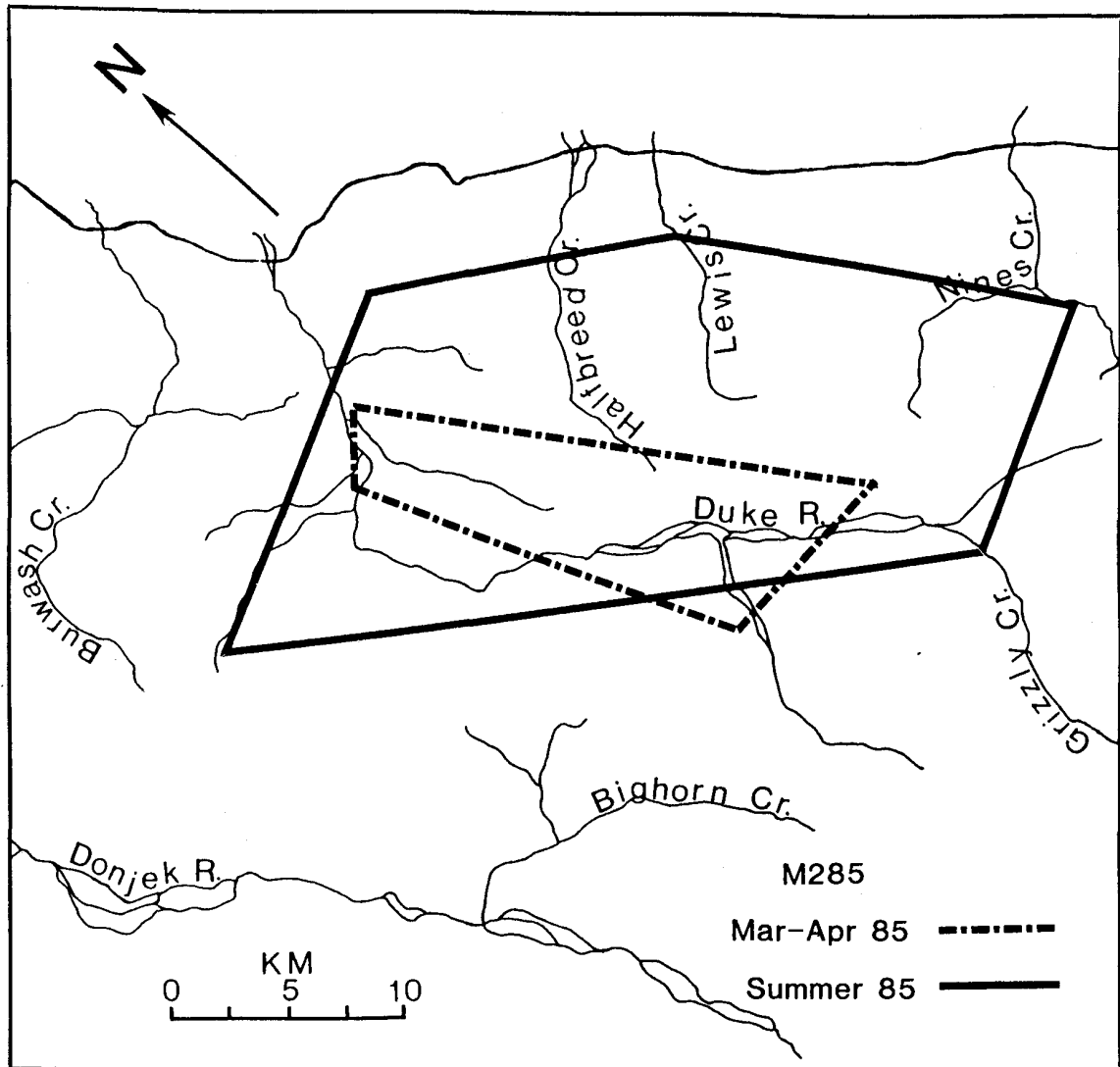


Fig. 4.6. Seasonal 100% home ranges for radio-collared subadult wolverine male M285, Yukon 1985.

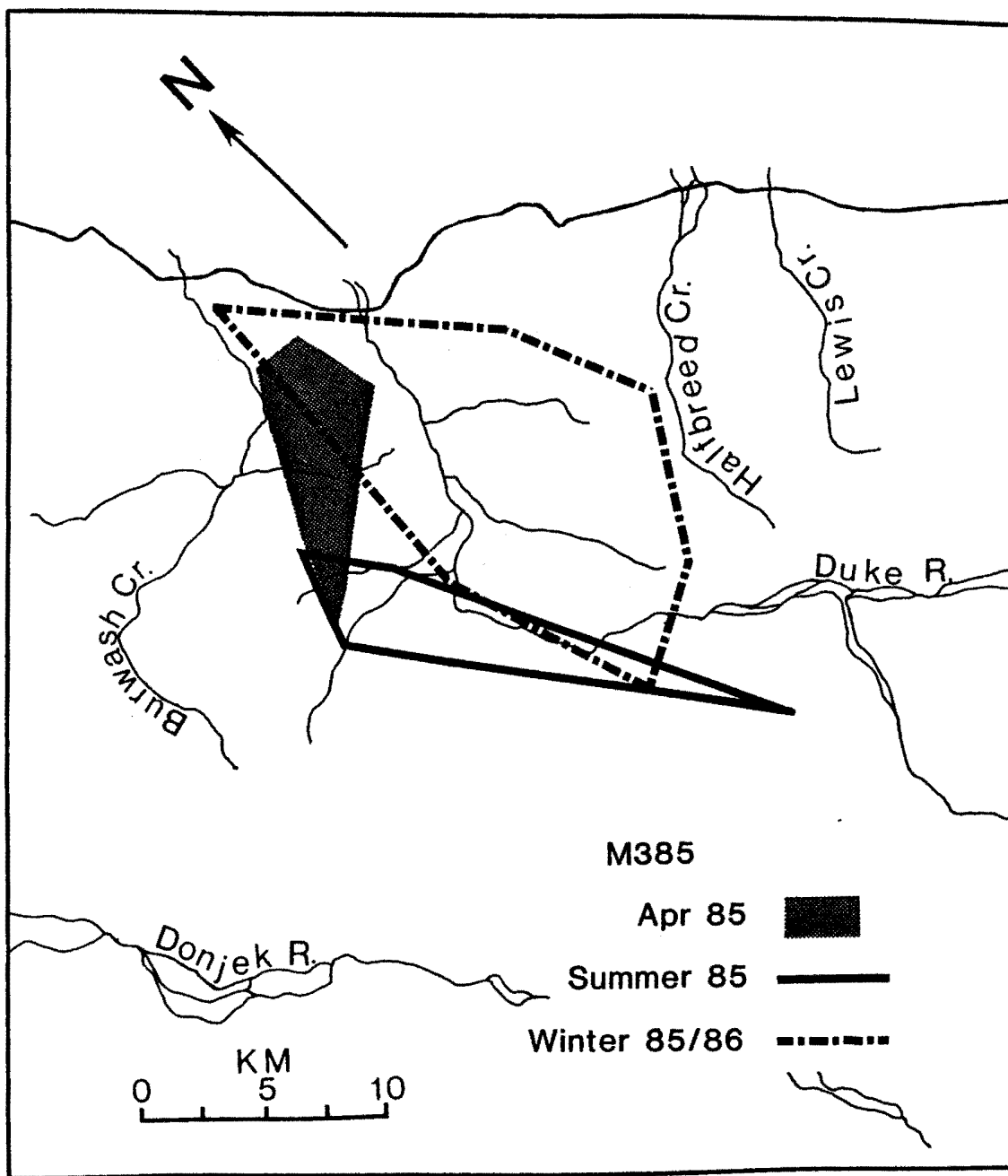


Fig. 4.7. Seasonal 100% home ranges for radio-collared adult wolverine male M385, Yukon 1985-1986.

was similar until M285 left the study area in late October.

Reduced movements of F384 and concentration of locations between April and June suggested she was denning. I was unable to locate a den by ground tracking, however, frequent aerial locations in summer indicated intensive use of one area. I believe the den was located in the north-eastern section of her home range (Arch Creek) although she made regular trips to to the west (Wade Creek).

Minimal data are available regarding movements of young of year wolverine. During his 39 days on air, M184, a young of year male, used a 139 km² area, equivalent to F384's yearly home range. He crossed the highway heading south after release during the first week of January and was recaptured in female F384's home range on 13 January. In early February, he re-crossed the highway heading north and returned to the area of first capture where he subsequently died. The 2 young of year females, F684 and F185, made movements of 10.2 km in 87 days, and 4.7 km in 32 days, respectively, before dying.

Maximum distances travelled in 1 day were 11.3 km for F384 and 17.3 km for M184. Maximum distances for all other individuals ranged from 2.9 km/day (10 days, F584) to 4.5 km/day (3 days, M285). M285 likely travelled greater distances when he left the study area but this information is not available. Distances are straight line estimates over time and do not reflect actual ground covered.

Mean distances travelled in winter by adult females (Table 4.5) were less than for summer ($t_{66}=2.21$, $p<0.05$). However, individually, only F584 showed differences in seasonal movements ($t_{13}=2.49$, $p<0.05$). Of males, only M385 travelled greater distances in winter ($t_{13}=2.42$, $p<0.05$). Variation in movements was significantly greater in summer for F384 ($F_{14\ 20}=6.97$, $p<0.001$) and F584 ($F_{20\ 10}=3.14$, $p<0.05$) and greater in winter for M285 ($F_{9\ 9}=11.36$, $p<0.001$) and M385 ($F_{15\ 11}=12.17$, $p<0.001$). No differences were apparent for F484 ($F_{10\ 16}=2.29$, $p>0.13$).

Table 4.5. Average distance travelled per day by radio-collared wolverine in Kluane study area, Yukon 1983-1986.

	YEARLY				WINTER				SUMMER			
	MEAN km/DAY	SD	RANGE	N	MEAN km/DAY	SD	RANGE	N	MEAN km/DAY	SD	RANGE	N
F384	1.4	2.2	0.0-11.3	36	0.8	1.0	0.0-3.9	15	1.8	2.7	0.1-11.3	21
F484	0.8	0.7	0.0-3.1	28	0.9	0.9	0.1-3.1	11	0.8	0.6	0.0-2.1	17
F584	0.5	0.6	0.0-2.9	33	0.3	0.4	0.0-1.8	22	0.9	0.8	0.2-2.9	11
F684					0.2	0.1	0.0-0.3	3				
F185					0.2	0.3	0.1-0.4	2				
M184					4.0	6.6	0.4-17.3	6				
M284					0.7	0.5	0.4-1.4	4				
M285	1.1	1.2	0.1-4.5	20	1.3	1.6	0.1-4.5	10	0.9	0.5	0.3-1.5	10
M385	0.9	1.1	0.0-4.4	28	1.3	1.3	0.1-4.4	16	0.4	0.4	0.0-1.3	12
FEMALES ^a	0.9	1.5	0.0-11.3	97	0.6	0.8	0.0-3.9	48	1.2	1.9	0.0-11.3	49

^aAdults.

Mortality

Two young of year females, F684 and F185, died during the study from non-human related causes. Although F684's condition appeared adequate, she had no back and gut fat reserves. Her weight at capture was 6.6 kg. In comparison, F185 of the same age and similar length weighed 7.8 kg (Table 4.1). No evidence of predators or a kill site was present at her last location and I believe she died of starvation. F185 was alive for a maximum of 31 days from time of capture. As no evidence of predators or a kill site was present, cause of death is also suspected to be starvation and/or injury.

M184 was found dead on a river bank. His right foreleg was torn off and wounds present on his body appeared to have been inflicted by one or more wolves. His internal organs were missing but otherwise he was not consumed. Besides F384 and M184, an unmarked individual appeared to have had an interaction with wolves. In April 1985 an apparently healthy adult male wolverine was found dead at a wolf kill site during an unrelated tracking flight just over the border in Alaska. A fox was observed scavenging on this wolverine (Rob Pyde, pers. comm.) but otherwise he had not been eaten.

Habitat Productivity and Food Habits

Populations of snowshoe hare (*Lepus americanus*) in Yukon crashed in 1982/83 (Boutin and Krebs 1986). Hares were sighted rarely in the study area during 1983/84 but appeared to be more plentiful in the winter of 1984/85 (Fig. 4.8). Moose were present all year, using low lying areas and river valleys in winter. Most of the Burwash caribou herd overwinter north of the highway and spend summers in the game sanctuary. Of the herd (250-300 animals), 10-30% were present in the study area during November 1981 through March 1982 (Doug Wing, biologist, Foothills Inc., pers. comm.). Calving extends from 15 May until early June in widely dispersed locations. Dall's sheep are abundant year-round and lamb in the area in spring. At least 2 wolf packs were known to be present during the study's duration. Sightings and tracks of solitary wolves as well as fox and coyote were relatively common (Fig. 4.8). It was difficult to document presence of

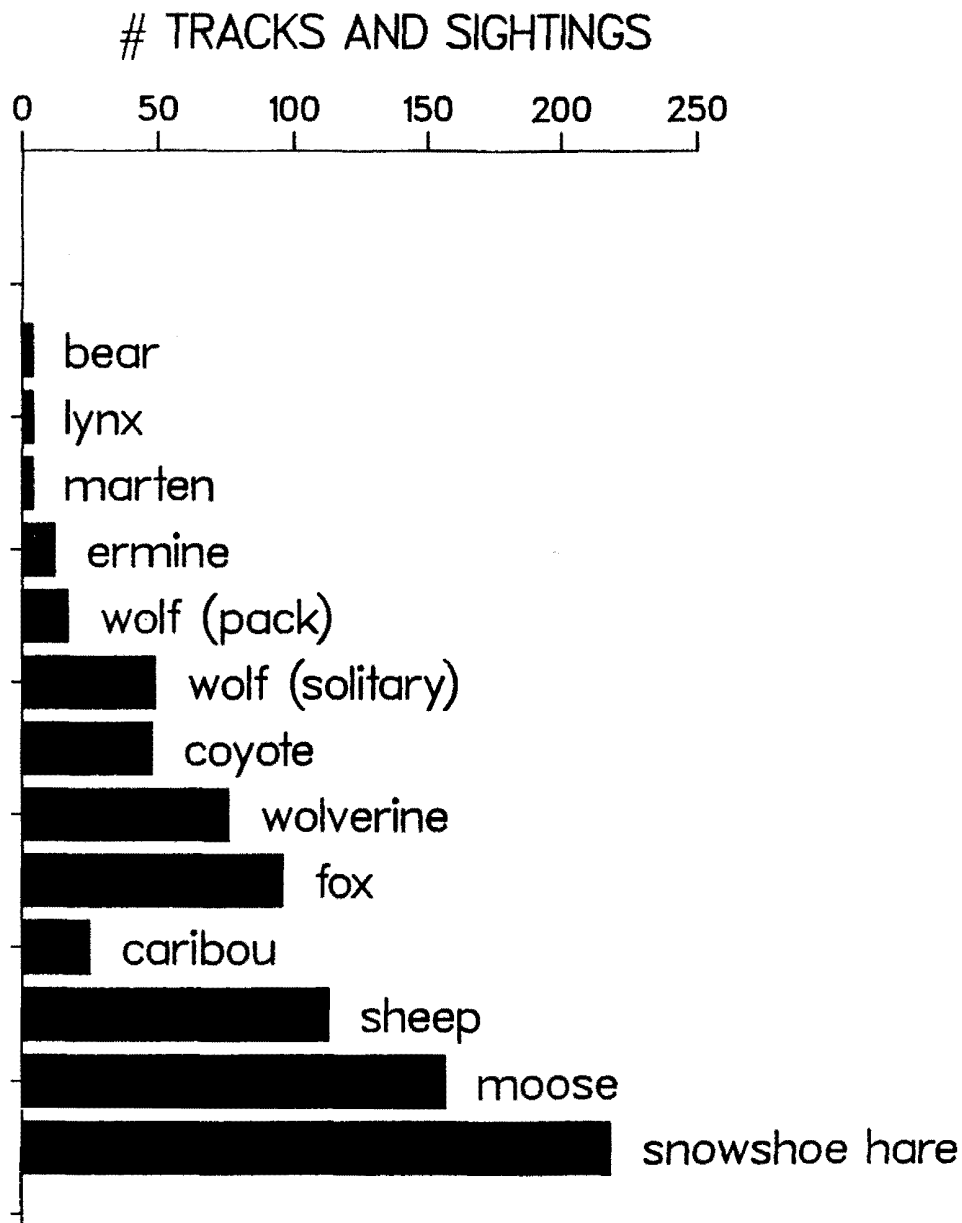


Fig. 4.8. Number of mammals observed or tracked in Kluane study area, Yukon, from November 1984 to April 1985.

kill sites because of their occurrence in subalpine coniferous forests. During 2 winters, 3 wolf kills (2 caribou, 1 sheep) were located. A moose kill was located in May, apparently killed by a grizzly bear. Evidence of wolverine feeding activity was observed at all kills except one of the caribou kills. Observations of wolverine feeding also included arctic ground squirrel (*Spermophilus parryi*) and ptarmigan (*Lagopus sp.*) (Table 4.6). Winter scats (n=12) collected in the study area contained snowshoe hare, red-backed vole (*Clethrionomys rutilus*), pika (*Ochotona princeps*), moose, red squirrel (*Tamiasciurus hudsonicus*), and arctic ground squirrel. As well, 5 of these scats collected in March and 1 in February contained kinnickinick berries (*Arctostaphylos uva-ursi*).

Sites of capture for M184 and M284, and site of death for M184 were located on the banks of Kluane River, in areas where spawned chum salmon become frozen in river ice. This salmon run typically consists of 5000–6000 fish and spawning occurs from mid-October to November in spawning beds 16 to 24 km long (John Burdik, Fisheries and Oceans, pers. comm.). Salmon remnants were still available when I visited this site in March and evidence of other carnivore feeding activity (fox, coyote) and wolf tracks were present. The resident trapper informed me that his success at catching wolverine was attributable to setting traps at this food source. This area falls in registered trapline (RTL) 177 which tends to be productive in terms of wolverine captured. For 11 seasons between 1951/52 and 1982/83 when wolverine were trapped, mean number caught was 3.2 (SD=1.5) per season, range 1–6. A limited amount of sex/age data obtained from submitted carcasses are available for RTL 177 and adjoining RTL 176, to the west. RTL 176 contains a smaller salmon spawning population present in the Donjek River. For the 2 winters 1982/83 and 1983/84, harvest of adult wolverine for RTL 177 consisted of 2/7 males (1 male is M284) and 5/8 females. For RTL 176, 4/6 males were adult and 0/2 females. One wolverine was not submitted and its age/sex class is unknown. The 2 traplines are similar in size, 954 km² for RTL 176 and 898 km² for RTL 177. Salmon also spawn in Duke River, however, no evidence of salmon frozen in river ice was found for this waterway.

Table 4.6. Observations of wolverine feeding activity in the Kluane Game Sanctuary, Yukon 1982-1985.

DATE	AGE/SEX CLASS	OBSERVATION	LOCATION	HABITAT
1982 JUNE	Adult	Ground squirrel in mouth.	Burwash Uplands	Alpine shrub
1982- 1985 WINTER	Various	Feeding on spawned salmon frozen in river ice.	Kluane R.	Boreal coniferous
1984 FEBRUARY	Young of year male (M284)	Recaptured on sheep kill.	Arch Cr.	Subalpine coniferous
1984 7 MAY	Adult female (F585)	Feeding on garbage at miner's cabin.	Wade Cr.	Subalpine coniferous
1984 15 MAY	Adult male (M1) ^a	Chasing ground squirrels.	Nickel Cr.	Subalpine shrub
94 1984 23 MAY		With caribou cow and newborn calf (outcome unknown).	Tatamagouche Cr.	Subalpine shrub
1984 31 MAY	Adult male (M2) ^a	On fresh moose kill.	Burwash Uplands	Alpine shrub
1984 DECEMBER		Chasing ptarmigan (from tracks).	Arch Cr.	Subalpine shrub
1985 APR/MAY		In sheep lambing area (outcome unknown).	Sheep Mt. ^b	Subalpine/Alpine

^aunmarked resident males.

^bKluane National Park.

Population Characteristics and Scent-Marking

A total of 94 observations of unmarked wolverine were obtained for March and August 1982 (6), July 1983 (2), February–May 1984 (20), August 1984 (2), and November–April 1984 (64). Nine were sightings and the rest were trails. Observations were scarce for summer because of difficulties in locating tracks during this season. Unmarked wolverine identified as residents consisted of 3 females (number of trails and sightings), F1 (5), F2 (12), F3 (9), and 2 males M1 (10), M2 (9). M1, F1, and F2 were captured in padded legholds but escaped. All wolverine were sighted at least once except for F3. Large size for both males indicated they were adults. Age class of females is unknown but as all 3 were present in the area a minimum of 2 years, they would have become adults by the end of the study. Home ranges for all residents are shown in Figure 4.9. Ranges of unmarked wolverine are estimated and indicate observed locations.

Five transients were identified although it is likely that more passed through the area. One track, recorded once, was distinctive as only 4 toes were present on one foot. Scent marking was frequently observed when snow-tracking wolverine. These scent marks consisted of urine and/or musk deposits at the base of spruce trees or willow clumps. Wolverine usually scratched the snow in the marked area and occasionally claw marks on tree trunks were observed. Although my success at snow-tracking wolverine was restricted to their use of trails, roads and low lying areas, tracks of transients were not associated with scent-marking. Wolverine signs did not occur throughout the study area. Tracks were conspicuously absent on Donjek River and in forested areas between Quill and Burwash Creeks, and Quill Creek and Donjek River.

Habitat Use

Habitat use did not differ from availability for females F384 and F584 (Table 4.7). Subalpine mixed and boreal shrub habitats occurred infrequently in female F584's home range. No locations in these habitat types were noted, and for analysis, availability was lumped into "other". Female F484 used alpine shrub habitat less than available (Table 4.7). When the data were combined for all

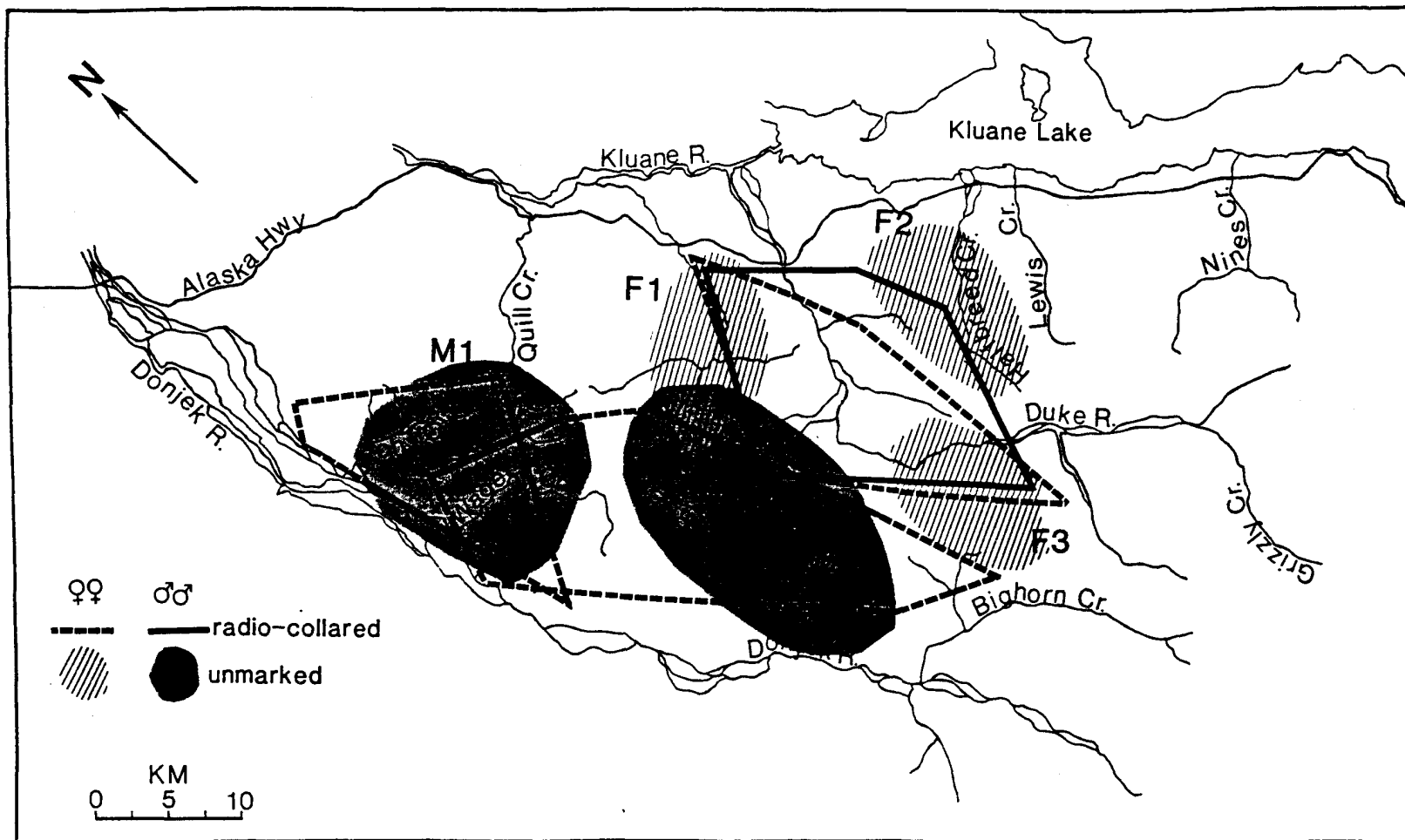


Fig. 4.9. Home ranges of radio-collared and unmarked adult wolverine resident in Kluane study area, Yukon 1983 - 1986.

Table 4.7. Yearly use of habitat types by 3 radio collared adult female wolverine in Kluane study area, Yukon 1984-1986.

HABITAT TYPE		PROPORTION AVAILABLE	N OBSERVED	PROPORTION USED	95% CONFIDENCE LIMITS	
F384:						
Alpine	shrub	0.29	9	0.23	$0.05 \leq p_i \leq 0.41$	$\chi^2_3 = 6.17$
Subalpine	shrub	0.27	8	0.20	$0.03 \leq p_i \leq 0.38$	
	grass	0.05	0	0.00	$p_i = 0.00$	
	coniferous	0.24	14	0.36	$0.15 \leq p_i \leq 0.57$	
	mixed	0.08	4	0.10	$0.00 \leq p_i \leq 0.23$	
Boreal	coniferous	0.07	4	0.10	$0.00 \leq p_i \leq 0.23$	
F484:						
Alpine	talus	0.21	10	0.34	$0.11 \leq p_i \leq 0.58$	$\chi^2_3 = 11.07^*$
	shrub	0.18	1	0.03*	$0.00 \leq p_i \leq 0.12$	
	grass	0.01	0	0.00	$p_i = 0.00$	
Subalpine	shrub	0.41	14	0.48	$0.24 \leq p_i \leq 0.73$	
	coniferous	0.19	3	0.10	$0.00 \leq p_i \leq 0.25$	
Boreal	coniferous	0.01	1	0.03	$0.00 \leq p_i \leq 0.12$	
F584:						
Alpine	talus	0.27	8	0.24	$0.04 \leq p_i \leq 0.45$	$\chi^2_3 = 11.46$
	shrub	0.30	11	0.33	$0.11 \leq p_i \leq 0.56$	
	icefields	0.08	0	0.00	$p_i = 0.00$	
Subalpine	shrub	0.19	5	0.15	$0.00 \leq p_i \leq 0.32$	
	grass	0.02	3	0.09	$0.00 \leq p_i \leq 0.23$	
	coniferous	0.09	4	0.12	$0.00 \leq p_i \leq 0.28$	
Boreal	coniferous	0.03	2	0.06	$0.00 \leq p_i \leq 0.17$	
Other ^a		0.01	0	0.00	$p_i = 0.00$	

^aSubalpine mixed, Boreal shrub.

*use not in proportion to available ($p < 0.05$).

females, seasonal use of habitat types did not differ from availability (Fig. 4.10).

Both males used less alpine talus and more subalpine coniferous habitats than expected if use was proportional to availability (Table 4.8). Alpine grass, icefields, subalpine grass and boreal coniferous habitats occurred infrequently in male M285's home range. As above, availability was lumped into "other". Males used more subalpine coniferous habitat in winter and less alpine talus habitat in summer than were available (Fig. 4.11). Use of riparian habitat did not differ from availability for all individuals of both sexes (z-test, $p > 0.20$).

Seasonal use of percent forest cover types, aspects, slopes and elevations was not consistent among individuals of the same sex (Table 4.9). M285 and F484 had no seasonal differences with respect to all habitat parameters. Differences in use of forest cover types were apparent only for female F584. She used habitats with sparse cover more in winter (66.7% of observations) than in summer (45.4%) ($p < 0.05$). Elevations used by all individuals ranged from 762 m to 2088 m and comprised the range of elevations occurring in the study area. Differences were not apparent for use of aspects ($p > 0.15$) and not great for use of elevations. Higher elevation terrain (> 1500 m) tended to be used more in summer and below treeline habitat more in winter by female F384 and male M385. Female F384 used steeper slopes ($> 61^\circ$) more in summer and flatter areas ($0-20^\circ$) more in winter.

When the data were combined by sex, seasonal use of percent forest cover types, aspects and elevations did not differ (Table 4.9). Both sexes appeared to use sparse habitats more than other cover types in winter and closed habitats less than other cover types in summer but these trends were not significant ($p > 0.10$). Females used steeper slopes ($> 61^\circ$) to a greater extent in summer (Table 4.9), however, this was attributable to F384 as no differences were apparent for the other females. A distinct altitudinal shift between seasons did not occur for either sex.

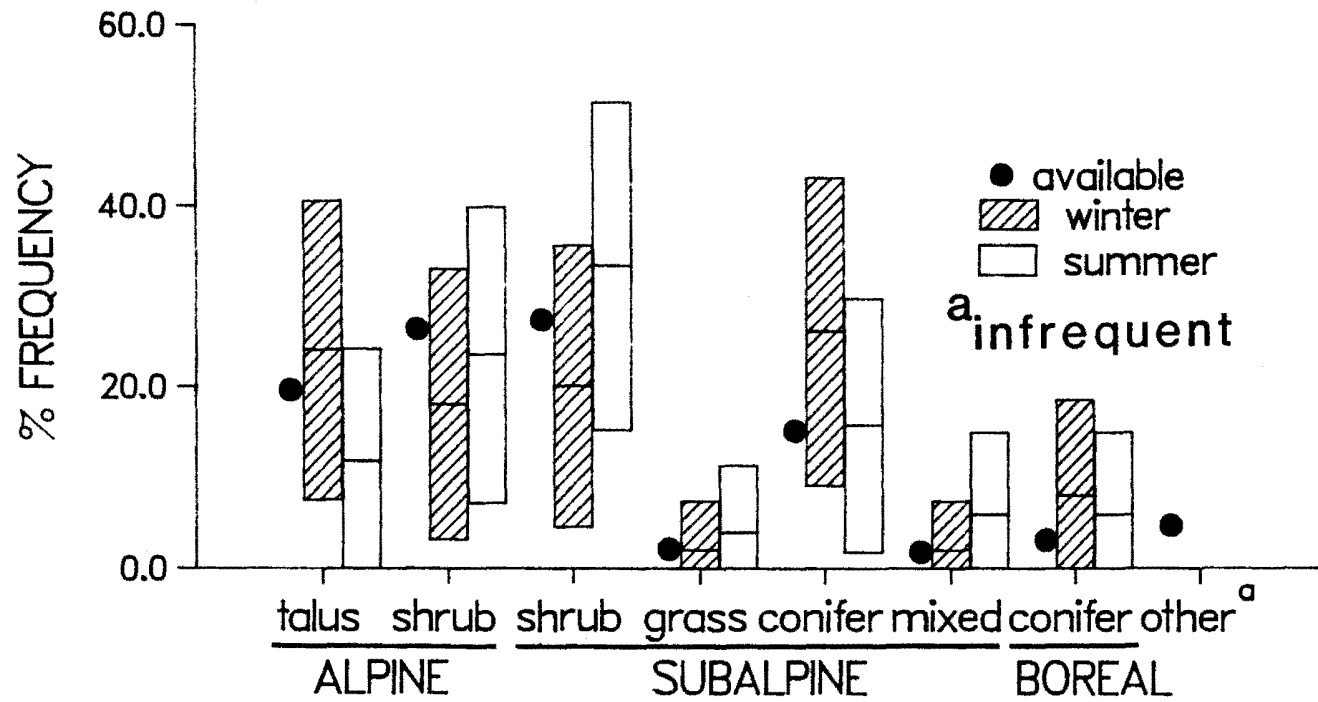


Fig. 4.10. Seasonal use and availability of habitat types for 3 adult female wolverine in Kluane study area, Yukon 1984-1986. Horizontal lines indicate means and bars, 95% Bonferroni confidence intervals.

Table 4.8. Yearly use of habitat types by 2 radio-collared male wolverine in Kluane study area, Yukon 1984-1986.

HABITAT TYPE	PROPORTION AVAILABLE	N OBSERVED	PROPORTION USED	95% CONFIDENCE LIMITS	
M285:					
Alpine talus	0.49	5	0.24*	$0.00 \leq p_1 \leq 0.47$	$\chi^2_4 = 9.49^*$
Alpine shrub	0.14	1	0.05	$0.00 \leq p_1 \leq 0.17$	
Subalpine shrub	0.18	5	0.24	$0.00 \leq p_1 \leq 0.47$	
Other ^a coniferous	0.12	10	0.48*	$0.19 \leq p_1 \leq 0.76$	$\chi^2_4 = 16.40^*$
	0.07	0	0.00	$p_1 = 0.00$	
M385:					
Alpine talus	0.19	1	0.03*	$0.00 \leq p_1 \leq 0.12$	$\chi^2_4 = 16.40^*$
Alpine shrub	0.21	4	0.14	$0.00 \leq p_1 \leq 0.30$	
Alpine grass	0.02	0	0.00	$p_1 = 0.00$	
Subalpine shrub	0.39	11	0.38	$0.15 \leq p_1 \leq 0.61$	$0.21 \leq p_1 \leq 0.69$
Subalpine coniferous	0.18	13	0.45*		

^aicefields, Alpine graminoid, Boreal shrub.

*use not in proportion to available ($p < 0.05$).

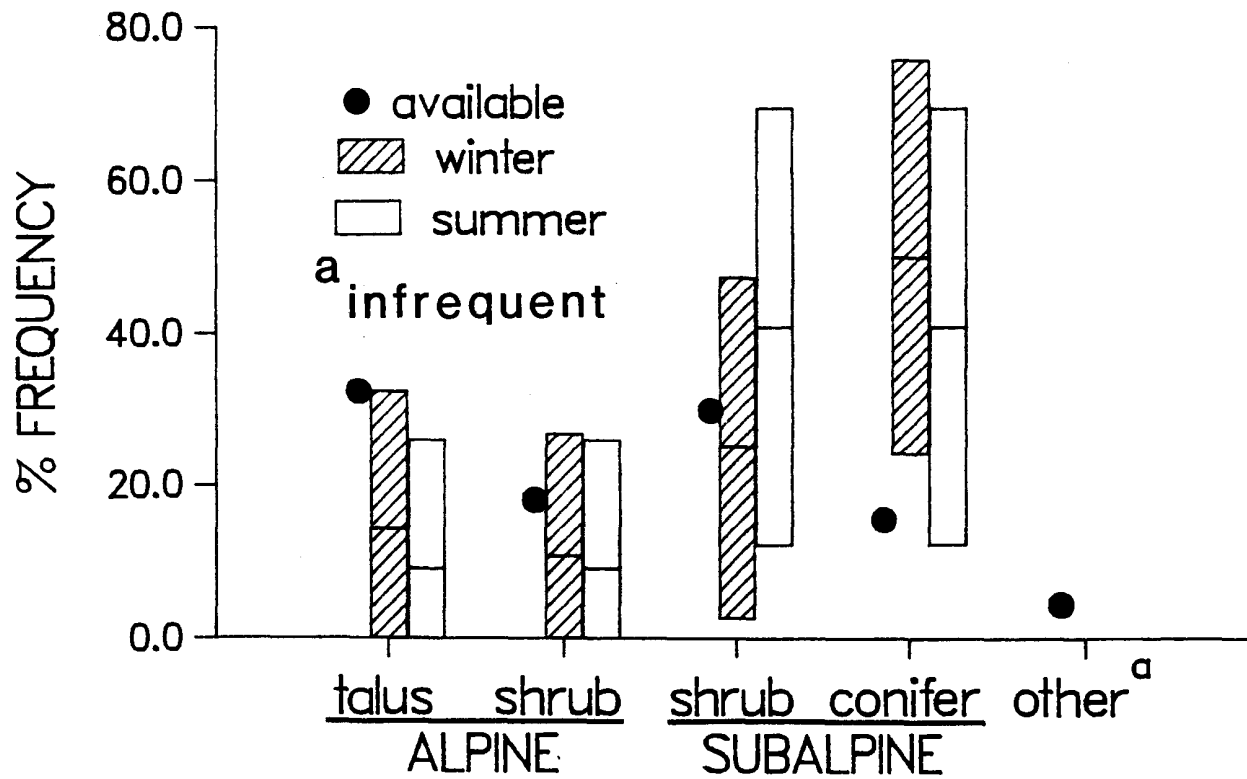


Fig. 4.11. Seasonal use and availability of habitat types for 2 male wolverine in Kluane study area, Yukon 1985–1986. Horizontal lines indicate means and bars, 95% Bonferroni confidence intervals.

Table 4.9. A comparison between seasons of the use of forest cover types, aspects, slopes and elevations for individual wolverine and sexes in Kluane study area, Yukon 1984-1986^a.

	% COVER	ASPECT	SLOPE	ELEVATION	N(WINTER) ^b	N(SUMMER) ^c
F384	0.20	0.29	2.68**	1.87 ⁺	16	23
F484	0.87	0.50	0.27	0.00	12	17
F584	1.66 ⁺	0.52	0.60	1.39	21	11
M285	1.37	1.32	0.83	1.20	10	10
M385	0.47	0.07	1.06	1.88 ⁺	17	11
FEMALES	1.61	0.90	2.36*	0.27	49	51
MALES	1.44	0.94	0.23	0.62	27	21

⁺p<0.10 * p<0.05 ** p<0.01 (else nonsignificant, p>0.10).

^aResults are z-values for Mann-Whitney U tests.

^bNovember-April.

^cMay-October.

Discussion

Yearly and Seasonal Home Range Use

Sample sizes are small, especially for seasonal home range use and my results should be regarded as preliminary until habitat relationships can be examined further. Direct comparison of home range size to other studies is difficult because of differences in data collection and analysis. Magoun (1985) notes her yearly home ranges may be under-estimated because of paucity of winter data. Whitman et al. (1986) estimated yearly home ranges using logarithmic curve projections. Hornocker and Hash (1981) combined data from more than one year. All studies include excursions in their calculations of yearly home range size. The possibility of misinterpretation because of the latter is readily apparent. F584's 100% home range is 2.4 times larger than that of F484. However, if long distance movements are excluded, home range sizes are almost equivalent.

Yearly home range size of the female with young was one half the size of home ranges for the 2 females without kits. Lactating females and those with kits in Montana had reduced yearly home ranges, 100 km² each for 2 females (Hornocker and Hash 1981); a mean of 105 km² in south-central Alaska (Whitman et al. 1986); and a mean of 70 km² in arctic Alaska (Magoun 1985). Adult female home ranges in summer appear larger than in winter because of long distance movements made in the former season. Excursions were not apparent in winter. If excursions are discounted, summer home ranges are smaller than or the same size as winter home ranges. Monitoring time was insufficient to determine whether these movements occurred yearly and terminated in the same area each time. The purpose of these excursions is unknown, however, there is no reason to assume home ranges are static from year to year. Wolverine may visit previous kill sites or other areas of known food availability. As not all resident wolverine were collared, it is not possible to determine whether excursions extended into home ranges of other wolverine. Excursions were observed frequently by both sexes of wolverine in Montana (Hornocker and Hash 1981), although season of occurrence was not reported. Winter home ranges for all adult wolverine overlapped with summer

home ranges but also included areas not used in summer. These differences are likely because of differences in prey distribution and availability between seasons. Although winter data between years are incomplete for most individuals, it does not appear that seasonal home range use is consistent from year to year.

F584's use of a small, isolated area during winter of 1985/86 is believed to be a result of fortuitous conditions creating an area of high food abundance. Such conditions would only arise through the presence of one or more ungulate kills. At the elevations she was located, 1768–1920 m, the only ungulate prey species present is Dall's sheep. As the population of sheep is unharvested, old sheep are likely common. Young and old sheep are the most affected by winter mortality; death may occur by predators or as a result of accidents such as avalanches or falling from cliffs (Burles and Hoefs 1984). It is possible F584 had come upon such a find. F484 similarly used a localized area at high elevations in winter. Restriction of movements because of the presence of ungulate kills was also observed for wolverine in south-central Alaska (Gardner 1985).

Yearly home range for the adult male (238 km²) is smaller than home ranges of adult males in Montana (a mean of 422 km², Hornocker and Hash 1981), arctic Alaska (a mean of 666 km², range 488–917 km², Magoun 1985), and south-central Alaska (an estimated 535 km², Whitman et al. 1986). At 14.1 kg, M385 was healthy and similar in weight to adult males in other studies. His summer home range (46 km²) was one third of that used in winter, and smaller than all 3 female summer home ranges. Male reproductive data (Rausch and Pearson 1972, Chap. I) and observations (Magoun and Valkenburg 1983, Krott and Gardner 1985) indicate that breeding in wolverine extends from early spring until at least August, and peaks in June. Studies have reported that home ranges of adult male wolverine expand in spring and summer, apparently because of breeding activity (Hornocker and Hash 1981, Magoun 1985). An adult male in Montana had a spring home range of 481 km², a summer home range of 190 km² and a winter home range of 97 km² (Hornocker and Hash 1981). Magoun (1985) reported a mean summer home range size of 626 km², range 488–898 km², for adult males in arctic Alaska, all larger than winter ranges.

Adult males have two basic requirements, access to females and food. Assuming F484 was alive at the same time M385 was being monitored, M385 had access to at least 3 females. As females are not reproductively active until at least 2 years of age (Chap. I), juvenile females in the area need not be considered. The reduced summer home range for M385 suggests both food and access to females were sufficient to meet his requirements. Magoun (1985) suggested that estrus is dependent on female condition, is prolonged and ovulation is induced. Sokolov and Rozhnov (1983) found no difference in duration of sniffing of urine of females in estrus and anestrus by male polecats (*Mustela putorius*) and mink (*Mustela vison*), although chemical composition of urine differed considerably. Males attempted to mate with females regardless of their condition but a female refused matings unless she was in estrus (Sokolov and Rozhnov 1983). If wolverine exhibit similar behaviour, males would need to monitor female condition to assure matings. Movements of females do not appear to be influenced by breeding activity but by the availability and distribution of food (Hornocker and Hash 1981, Magoun 1985). Adult females did not increase their movements or home range size during the breeding season in this study. The lack of activity for M385 during breeding implies females in his area also restricted their range, suggesting resources (food) were sufficient for both sexes. These results also suggest that the increased activity of males during spring and summer observed in other areas is not only attributable to breeding activity but may also be a function of changes in prey distribution.

Juvenile males undergo extensive movements (Hornocker and Hash 1981, Gardner 1985, Magoun 1985), a function of post-natal dispersal. Movements of M285 were strongly indicative of search for a home range. Magoun (1985) found that wolverine do not necessarily disperse in their first winter. Snow-tracking data prior to his capture suggested M285 was born within the study area. His residency within the area until his second summer is consistent with Magoun's (1985) results. Although data are limited, extensive movements of the young of year male, M184, appear to be dispersal movements. Gardner (1985) suggested food abundance had little to do with dispersal of juvenile males. My results tend to support this

hypothesis. However, as juveniles have dispersed as young of year and subadults, food availability may affect the timing of dispersal.

Overlap and Movements

Consistent with spatial patterns observed in other mustelids (Powell 1979), home ranges of adult female and male wolverine overlap (Hornocker and Hash 1981, Magoun 1985, Whitman et al. 1986, this study). Adult female home ranges did not overlap during summer in arctic Alaska (Magoun 1985). My data were insufficient to determine seasonal overlap within adult sexes as wolverine were not always monitored concurrently. Overlap was determined during early winter for 2 females. However, use of F384's home range by F584 was extensive only after the former's death. Adult American marten (Powell 1979) and river otters (*Lutra lutra*) (Erlinge 1968) expand into unoccupied areas when a resident disappears. I suspect a transient or a juvenile would eventually assume part of F384's home range but evidence of other wolverine was not present during the last winter I was in the area. F684 was captured within F384's home range and is believed to be her offspring. This supposition is supported by Magoun's (1985) finding that juvenile female home ranges approximate their mother's. This behaviour is similar to that documented for other mustelids. In ermine (Erlinge 1977) and mink (Gerell 1970), juvenile females reside near the natal area while juvenile males are forced into peripheral habitats.

The only case of overlap noted between males in Alaska was between juveniles and adults (Gardner 1985, Magoun 1985). Extensive overlap was present between home ranges of adult M385 and subadult M285. The presence of a resident adult male likely affected the behaviour of M285 and possibly contributed to his leaving the area for 2 months. A physical interaction was not observed, however, their proximity on at least 2 occasions made such an interaction possible. Wounds inflicted by wolverine on other wolverine have been recorded (Hornocker and Hash 1981, Magoun 1985). A researcher at the Arctic Institute of North America, at Kluane Lake, reported evidence of an altercation between what appeared to be an adult male and a young male wolverine during early winter of 1982

(Richard Ward, pers. comm.).

Movements of adult wolverine in this study are less than those documented for Montana (Hornocker and Hash 1981) and arctic Alaska (Magoun 1985). Adult males travelled greater distances than females in Montana and Alaska (Hornocker and Hash 1981, Gardner 1985, Magoun 1985), and distances travelled in summer exceeded those in winter for both sexes in Montana (Hornocker and Hash 1981). My results are not consistent with these findings. Only 1 adult female travelled greater distances in summer and the adult male travelled greater distances in winter. Variation in movements differed seasonally for females mainly because of excursions in summer. The female for which variability of movements did not differ between seasons had the smallest excursion. Her home range was completely overlapped by that of the adult male, supporting the above premise that high food availability within his area of use made extensive movements unnecessary for females. For both males, variability in movements was greatest in winter.

Home Range Size and Spatial Strategies

A general definition of home range as the area traversed in an animal's day to day activities (Burt 1943) is commonly accepted. There is no such consensus regarding a definition of territory. Territorial behaviour is linked to the acquisition of resources. Priority access is maintained by defence, through advertisement, threat or attack (Kaufmann 1983). However, there are continuums in the degree of exclusion and intensity of behaviour needed to achieve priority access (Kaufmann 1983). Such complexity has hampered attempts to arrive at a generally acceptable definition. Furthermore, priority use must be established by social interaction and cannot simply be a function of low densities. An inability to document social interactions of wolverine precludes attempts to equate noncontiguous home ranges with territories. However, densities of wolverine are relatively low throughout areas of study and variation in spatial patterns exist, from no overlap of adult male ranges with adult females overlapping only in summer (Magoun 1985), to overlap of both sexes in all seasons (Hornocker and Hash 1981). Whether one chooses to call an area of exclusive use a home range or a territory is of little consequence in

understanding why such patterns occur in wolverine spatial behaviour.

McNab (1963) demonstrated that size of home range is a function of an animal's body weight. Carnivores have larger home ranges than similarly sized herbivores because of the greater energy expenditure of predation and patchiness of prey (Harestad and Bunnell 1979). Within a trophic class, animals in habitats of high productivity will have a smaller home range than animals in habitats of low productivity (Harestad and Bunnell 1979). Harestad and Bunnell (1979) demonstrated a tendency of home ranges to be larger at higher latitudes, as increasing latitude is broadly associated with decreasing primary production. Heterogeneity of habitat also affects home range size. Macdonald's (1983) resource dispersion hypothesis predicts that for a given patch richness, the minimum sized territory will be smaller where food patches are not dispersed. Localized high food availability and small home ranges supports this hypothesis for wolverine in the Kluane Game Sanctuary. During the study in arctic Alaska, levels of food were particularly low because of the absence of overwintering caribou (Magoun 1985), and home ranges of wolverine are larger than all others reported.

Lockie (1966) predicted that individual ranges of a given species would vary in exclusiveness according to the concentration of resources in different seasons or habitats. Mustelids exhibit a wide range of intra-specific variation in spatial strategies. Social organization of river otters ranges from strict territoriality to mutual avoidance (reviewed in King 1983). River otters will establish a territory on streams and lakes but have an undefended home range on sea coasts (Erlinge 1967, 1968, Kruuk and Hewson 1978). Space use patterns in American marten and in pine marten (*M. martes*) includes partial to no overlap of home ranges within sexes (Pulliainen 1981). King (1975) reported that male resident ermine shared a common area but never occupied this region of overlap at the same time. She suggested this overlap zone was an important and necessary part of each home range, serving as a centre of information exchange through scent marking.

The functions of scent-marking in mustelids are not well known. Pulliainen (1984) suggested scent marks of marten are not used for territorial defence but

rather as a means of transferring information among individuals. He reported observations of 3 to 4 individuals of pine marten feeding on the same cervid-sized carcass in one night (Pulliainen 1981) and suggested non-defence allows animals to temporarily share abundant food sources (Pulliainen 1984). As well as a means of information transfer, scent marking could also function as a subtle form of defence. The functions of scent-marking need not be constant but may vary depending on the status of a limited resource such as food. The reliance on a scavenging lifestyle by wolverine suggests that the abundance and availability of food are unpredictable. If the environment changes rapidly and frequently, a variable social system might be favoured (Lott 1984). The distribution and abundance of food, level of competition, predation, population density, and habitat saturation are correlates of intra-specific variation observed in avian and mammalian social systems (Lott 1984). A species will manifest territoriality when economically justified and physically possible but will shift to other strategies when either of these conditions does not hold (Lott 1984). Flexibility in spatial behaviour indicates that the method by which territorial boundaries are delineated, possibly by scent-marking in mustelids, likely has more than one function.

Wolverine display variation in spatial patterns which does not fit in with the general context of intrasexual territoriality. Researchers have observed up to 5 wolverine feeding on moose kills at Rose Lake, southwest of Whitehorse (Bob Hayes, pers. comm.). My familiarity with an abundant food source used by wolverine, the salmon of the Kluane and Donjek Rivers, allowed me to examine the sex and age class of similar wolverine groupings. These situations are unique in that not only is food of high quality but availability is predictable as fish are present all winter. The linear and extended nature of spawning beds implies defence of this food source is not possible. Six (5 females, 1 male) of 15 wolverine harvested over 2 years were adult in RTL 177 and 4/8 (0 females, 4 males) in RTL 176. Composition of the harvests suggests these traplines supported more adult wolverine of the same sex than would be expected if home ranges were exclusive. King (1975) noted that a stable but low food supply may allow short-tailed weasels to establish territories whereas a large but more variable food

supply may not. Similarly, an inability to defend a large food supply may preclude the establishment of territories. As home range patterns of the harvested wolverine are unknown, results are insufficient to infer a breakdown of territoriality. However, indications are that in areas containing abundant and predictable sources of food which are not easily defended, mutual tolerance of adults within the same sex occurs. The difference in the adult sex ratio between the 2 traplines may simply be a function of one trapline containing the overlap area of a number of adults of the same sex. This spatial arrangement would allow maintenance of individual home ranges while permitting residents to share a productive food source. Hornocker and Hash (1981) attributed the fluid state of the wolverine population in their area to the effects of human predation removing individuals before they established tenure, thus contributing to behavioural instability. Although food availability was high in their area, it is possible food was not localized nor predictable. If this was the case, home ranges would not be physically nor economically defensible, allowing extensive overlap to occur.

Mortality

The deterioration of F384 cannot be explained solely on the basis of low food availability. Although she was recaptured on three instances, she did not eat the bait or food left for her. I believe the demands of providing for her young weakened her and contributed to deterioration by parasitic infestation. As comparative data are not available, the effects of pneumonia, kidney infection and parasite load on F384 cannot be evaluated. F684's poor condition may have been a factor of her mother's (F384) condition. No information is available regarding the condition of F185 and reasons behind her suspected starvation. Starvation was also the cause of death for 2 wolverine in Montana, one very old and the other a young of year (Hornocker and Hash 1981). Coincidentally, both my area and that in Montana is reported to have high food availability. Inexperienced and old wolverine may not be efficient at securing food even if availability is high.

Interactions between wolverine and wolves have been documented in this study. Burkholder (1962) noted wolverine were occasionally killed by wolves in

Alaska. Hornocker and Hash (1981) reported golden eagles (*Aquila chrysaetos*), mountain lions (*Felis concolor*) and bears (*Ursus spp.*) were capable of killing wolverine, especially those that were young and inexperienced. An attack by a wolf does not necessarily mean death to a wolverine. By her third recapture, F384's wound had healed completely. The contribution of natural mortality factors, even in unharvested furbearer populations, is difficult to estimate. King (1983) concluded that mortality in opportunistic mustelids is affected almost solely by food. Wolverine, as scavengers, are attracted to kill sites and traps. Starvation, wolf attacks and trapping as mortality factors are consistent with the above conclusion.

Food Habits and Reproductive Success

I believe food consumed in winter was primarily scavenged from kills, although I had difficulty in locating kill sites. The occurrence of moose in scats supports winter scavenging by wolverine. Stomach content analysis of Yukon wolverine indicated that ungulate species occur most frequently in the diet but are supplemented by snowshoe hare, sciurids and small mammals (Chap. III). Red squirrel is the most common sciurid in the study area. Three species of small mammals are abundant in the Kluane area, deer mouse (*Peromyscus maniculatus*), red-backed vole and meadow vole (*Microtus pennsylvanicus*) (Krebs and Wingate 1985). The incidence of ground squirrel and pika in scats is likely from caches as ground squirrels hibernate and pikas would be difficult to obtain in winter because of their use of snow covered talus slopes. Extensive caching of prey in summer for use in winter was documented for wolverine in arctic Alaska (Magoun 1985). Observations of wolverine preying on ptarmigan is consistent with winter stomach analyses (Chap. III). Two of the collared females had porcupine quills (*Erethizon dorsatum*) embedded in their muzzles. Incidence of porcupine in stomachs of Yukon wolverine was relatively high, however, the retention of quills prohibited estimating actual contribution (Chap. III).

The incidence of kinnickinick berries in scats of late winter is consistent with the opportunistic diet described for Yukon wolverine in Chap. III. Berries are from

the previous fall crop and become exposed in late winter and early spring by melting snow. Grizzly bear scats examined in early spring also contained kinnickinick berries. Wolverine were observed in caribou calving and sheep lambing areas in spring, however, their success at predation is unknown. Feeding on arctic ground squirrels was observed in summer, however, the intensive use by wolverine of areas containing large populations of arctic ground squirrels in south-central Alaska (Gardner 1985) was not apparent. Wolverine use ungulate kill sites for long periods, consuming bone and hide (Magoun 1985), but feed predominately on small mammals if ungulates are not available (Chap. III). I (Chap. III) showed that overall diversity in diet is important, indicating the necessity for an adequate and varied prey base.

Magoun (1985) reported that adult females breed yearly but do not necessarily produce young every year. Annual breeding is supported by relatively high pregnancy rates for adult females in Yukon (Chap. I). However, in this study, 2 of 3 adult females did not reproduce although food resources appeared adequate. Not all females in Montana produced young every year, nor every second year (Hornocker and Hash 1981), possibly because food was insufficient. I suggested (Chap. I) that adequate food during pregnancy was the most critical factor governing reproductive success. The dependence of reproduction on food supply is not unique to wolverine. Productivity is apparently food-dependent in ermine and pine marten (King 1983). Observations on live wolverine suggest that demands of raising young reduce the probability that a female wolverine will successfully reproduce the next year. F384, prior to having young, weighed 11.0 kg, compared to 10.0 and 8.0 kg for the other 2 adult females. Adequate weight before parturition is important considering F384 lost 25% of her original body weight after rearing kits. As timing of implantation is variable and extended, females may not implant unless they are in sufficiently good condition to maintain pregnancy (Chap. I). Females also have the option of resorbing embryos (Chap. I).

Population Characteristics and Density

If scent marking is involved in territorial defence, resident adults are expected to participate more frequently than juveniles or transients in this behaviour. Scent marking was observed by all resident wolverine, throughout their area of travel, and has also been described by Pulliainen and Ovaskainen (1975), Koehler et al. (1980), and Magoun (1985). In this study, limited observations indicated that transients marked less frequently than residents. Erlinge et al. (1982) noted that dominant male and female ermines marked more than did subordinates. Although I expect that juvenile wolverine are subordinate to adults, it is unknown whether or not all transients are juveniles. The age composition of transients and their marking behaviour has not been well addressed for mustelids because of difficulties in identifying and tracking these individuals. It is a topic for future study.

Within the 1590 km² that was monitored, 3 adult males and 6 adult females were known to be present throughout 3 summers and 2 winters of the study. This corresponds to a density of 1 female/265 km², and 1 male/530 km², or 1 resident wolverine/177 km². Assuming that home ranges of adults are exclusive within sexes, by using a mean home range of 157 km² for females and 238 km² for males, 10 female and 7 male residents may be supported within the same area. This corresponds to a density of 1 resident wolverine/93 km². This estimate ignores areas that wolverine do not use and suggests a maximum number that may be supported. As the entire study area is not equal in habitat quality, and habitat saturation by wolverine is unlikely, this density will probably not be realized.

Van Horne (1983) cautioned against the use of density as an indicator of habitat quality and noted that quality should be defined in terms of survival and production characteristics, as well as density. As noted in this study, wolverine may not reproduce or may be subject to starvation even if abundance and quality of food is apparently high. Mortality of prey, particularly ungulates, is mediated by winter severity and adequate forage production in summer. Food availability, especially for scavengers such as wolverine, will vary from year to year and is likely unpredictable. The salmon present in the Kluane and Donjek Rivers are an

exception and were not used by wolverine within the study area. I believe the study area represented high capability habitat for wolverine. However, even for an area having diverse and apparently abundant prey, wolverine densities are relatively low. Data regarding survival of young and recruitment are necessary to assess habitat quality. However, such information is difficult to collect in field studies and not presently available for wolverine populations.

A summary of past attempts to estimate density of wolverine populations is meagre and inconsistent in methodology. Quick (1953) estimated a density of 1 resident wolverine per 207 km² for a northern British Columbia trapline. Hornocker and Hash (1981) estimated a density of 1 wolverine/65 km² in their study area in Montana. As this density was based on all wolverine they believed were present in their area, it may have included juveniles. Whitman and Ballard (1983) provided a density of 1/209 km², including kits but not juveniles, for the Susitna River Basin in southcentral Alaska. They assumed the home range observed for 1 adult male (627 km²) in their study area was characteristic of all adult males, but acknowledged that this assumption was likely invalid. Magoun (1985) estimated densities of 1/48 km² to 1/139 km² for a resident fall population in arctic Alaska, including adults, daughters which settled next to the natal area, and kits. She notes these are conservative estimates subject to error.

Four major areas of difficulty involved in estimating density of wolverine may be identified:

1. Use of mean home ranges.
 - a. Field studies have provided detailed information on only a few wolverine. Mean home range sizes based on small samples are not valid estimates of home range size for all wolverine.
 - b. Wolverine do not use all habitats within an area. Avoidance is not unique to this species; short-tailed weasels and ermines totally avoid some habitats that lack food and cover (King 1975, Erlinge 1977). Use of mean home ranges in calculations will overestimate densities.
2. Size of home range varies depending on habitat productivity. Typically, the density within a highly diverse area such as a province, territory or state is

required. Variation in home range size on this scale is likely to be large. Attempting to extrapolate results from a single study site to a considerably more diverse region may introduce error.

3. Persistent and high quality food in an area supports more wolverine than typically unpredictable environments. Such situations may maintain regional populations which are unstable and do not exhibit exclusive home ranges. Use of home range sizes to estimate density is not applicable.
4. Information regarding the size of litters successfully weaned, success of juveniles in establishing home ranges, proportion of transients in the population, and rates of mortality is unavailable. Thus, recruitment and population size cannot be accurately estimated.

I have outlined a formidable problem. However, the pressing necessity for density estimates in management of this harvested furbearer precludes deciding attempts are futile. These concerns have been further addressed in an analysis of productivity of Yukon ecoregions (Chap. VI).

Habitat Use

Generally, habitat use for females was proportional to availability. Use of infrequent habitat types was not observed for both sexes but may have been undetected because of small sample sizes and limited monitoring time. Results for males are alike because of extensive overlap of home ranges and similarity of movements. I believe the greater use of subalpine coniferous habitats in winter by the 2 males is attributable to the presence of ungulate kills in this area. Tracks of snowshoe hare were noted frequently in this habitat type as well. The incidence of boreal forest in the study area is low. The preference for mature to intermediate forest found in Montana (Hornocker and Hash 1981) was not apparent in Yukon, nor was the reluctance of wolverine to cross openings. However, the area in Montana was logged and contained clear-cuts (Hornocker and Hash 1981). Alteration by humans may influence habitat use by wolverine.

Individual variation in use of forest cover types, aspects, slopes and elevations was apparent. The frequent use of sparse cover types in winter for

F584 was attributable to her localization at high altitudes for an extended period. The trend towards use of higher elevations in summer and lower elevations in winter found in Montana (Hornocker and Hash 1981) was observed for only the denning female and the adult male. The distinct difference in elevational use reported for wolverine in south-central Alaska (Whitman et al. 1986) was not evident. Gardner (1985) hypothesized that the elevational shift between seasons was attributable to concentrations of ground squirrels in alpine areas. However, in the Kluane Game Sanctuary, non-ungulate prey in alpine habitats during summer consists of little besides pika and microtines. Wolverine did feed on ground squirrels in the study area, but this prey species occurred primarily in subalpine habitats.

Kelsall (1981), in his status report of wolverine, wrote "Habitat is probably best defined in terms of adequate year-round food supplies in large, sparsely inhabited wilderness areas, rather than in terms of particular types of topography or plant association". Results to date are consistent with this suggestion. Similar to home range use, habitat use is likely determined by prey distribution and availability. As food resources are not consistent among areas nor over time, patterns of habitat use are expected to vary seasonally and locally.

PART D
HARVEST TRENDS

CHAPTER V

HARVEST VULNERABILITY PATTERNS

Harvest rates are a function of the abundance of animals, trapping vulnerability and effort expended by trappers. A trapper may discriminate among species by using different trap types, sizes, sets and trap locations but cannot be selective with respect to sex or age, particularly for terrestrial furbearers. Thus, observed harvest patterns are not solely a function of selection by trappers. The probability of trapping a certain sex/age class is a function of home range size and extent of movements. Behaviour known to influence movements can be used to identify which classes will be most vulnerable to trapping and at what time of year these vulnerabilities will be apparent. Understanding how vulnerabilities are reflected in harvest patterns is a necessary requirement for setting trapping seasons and for identifying critical periods for sex/age classes.

Home range use and movements of wolverine (*Gulo gulo*) have been determined using radio-telemetry (Hornocker and Hash 1981, Gardner 1985, Magoun 1985, Chap. IV). Males have larger home ranges than females. Young of year males undertake extensive dispersal movements in fall and early winter. Males may also disperse as subadults, however, the frequency and timing of this dispersal is unknown (Magoun 1985, Chap. IV). Females do not undergo the extensive dispersal seen for males but establish home ranges near the natal area (Magoun 1985). Home range expansion and increased movements in early spring and summer have been documented for adult males in Montana and Alaska, and attributed to breeding behaviour (Hornocker and Hash 1981, Magoun 1985). Such behaviour was not observed in southwest Yukon (Chap. IV). The main factor influencing female movements appears to be reproduction. Food dispersion and availability influence movements and home range size of both sexes.

The effect of trapper effort on harvest vulnerability of wolverine is not understood and isolating this effect in harvest patterns is not simple. The trapping season for wolverine in Yukon extends from 1 November to 31 March. Activity of trappers, however, is influenced by climatic patterns and economic conditions.

Insufficient snow early in the season limits travel by snow machine and will dampen trapper activity. An early spring with higher than normal temperatures makes travel on waterways dangerous, effectively shortening the trapping season. Prevailing pelt prices affect the decision to trap, which furbearers to trap and when to trap. Quantification of effort involves knowing the numbers of trappers working per month and the division of emphasis according to species. Limited data regarding climatic patterns and allocation of effort over time were available for 3 trapping seasons, 1982/83 to 1984/85. Average prices of wolverine pelts sold during the 3 years were similar, \$212, \$208 and \$221, respectively.

Between 1982 and 1985, the Yukon Department of Renewable Resources maintained a submission program for wolverine. Trappers received a \$25 incentive payment per carcass. Numbers of wolverine submitted for the 3 years were 213, 112 and 123, respectively. An additional 13 wolverine were submitted by trappers of Northwest Territories for a total of 461. Total Yukon harvests for the same periods were 408, 245 and 249. As submission rates per year were high, I assumed that the sex and age composition of samples was an accurate representation of the entire harvest. Trappers were required to supply the date on which the wolverine was trapped, location and method of trapping. Because of inconsistencies in reports and difficulties in aging (lack of teeth or skulls), usable sample sizes were less than total numbers submitted. The sample is representative of all ecoregions in Yukon (Oswald and Senyk 1977) where trapping of wolverine occurs, except for Ecoregion 15 (Werneck Mountains) (Fig. 5.1). Harvest from this ecoregion, from 1951/52 to 1981/82, generally has been low.

The 3 years differed with respect to climatic patterns, prey availability and trapper effort. Yukon is a diverse area and snowfall varies considerably across the territory. Generally, however, 1983/84 was characterized by a late winter and early spring. Deep snowfalls occurred in 1984/85, throughout the winter. Of snowfall compiled from monthly totals collected at 40 weather stations across Yukon (Atmospheric Environment Service, 1982-1985), 26% was attributed to 1982/83, 28% to 1983/84, and 46% to 1984/85 (Fig. 5.2). Evidence suggests 1982/83 was atypical in regards to movements and harvest of furbearers. Snowshoe hare (*Lepus*

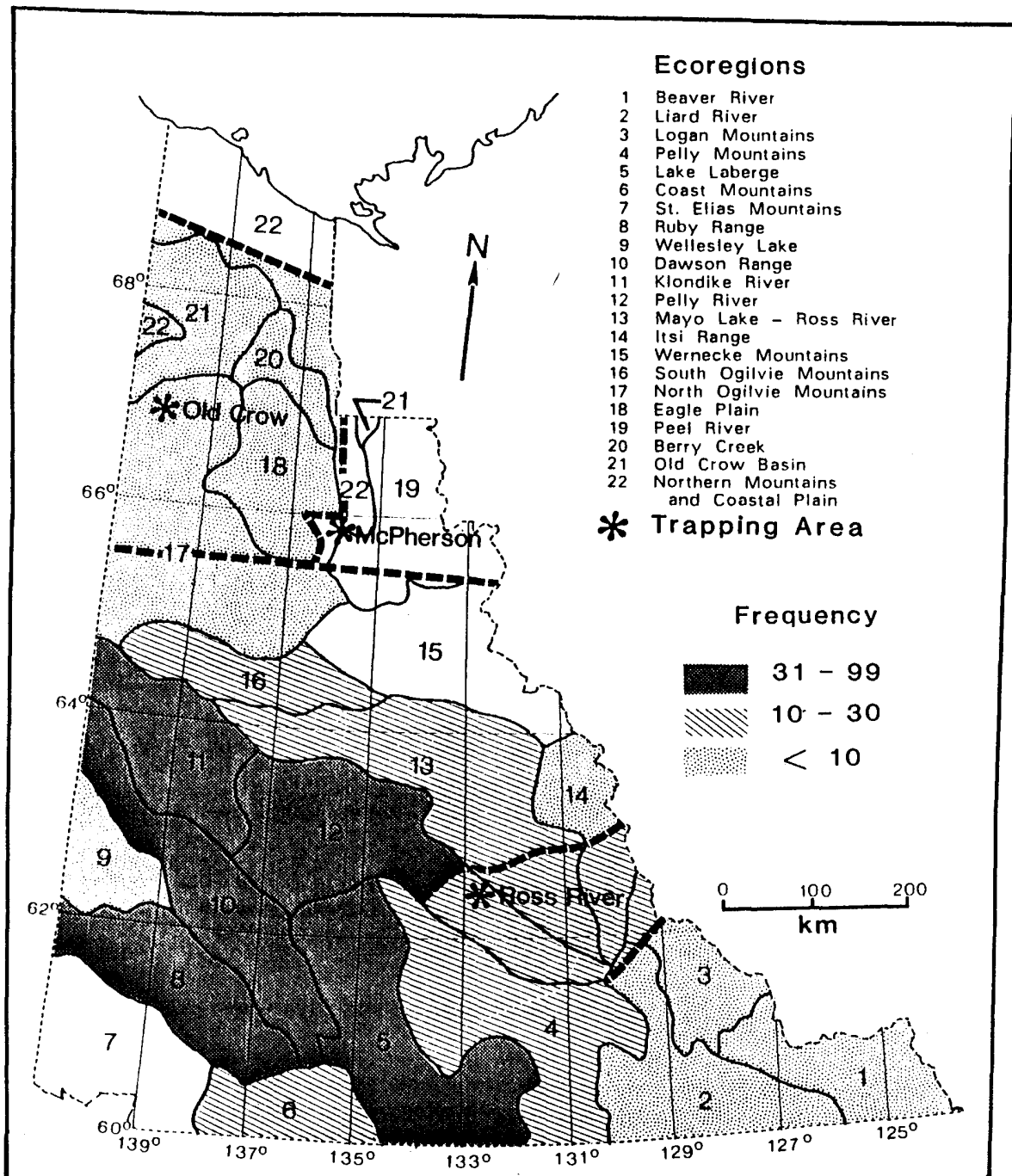


Fig. 5.1. Locations of trapped wolverine submitted by Yukon trappers during winters 1982-1985. Dashed lines are boundaries of trapping areas.

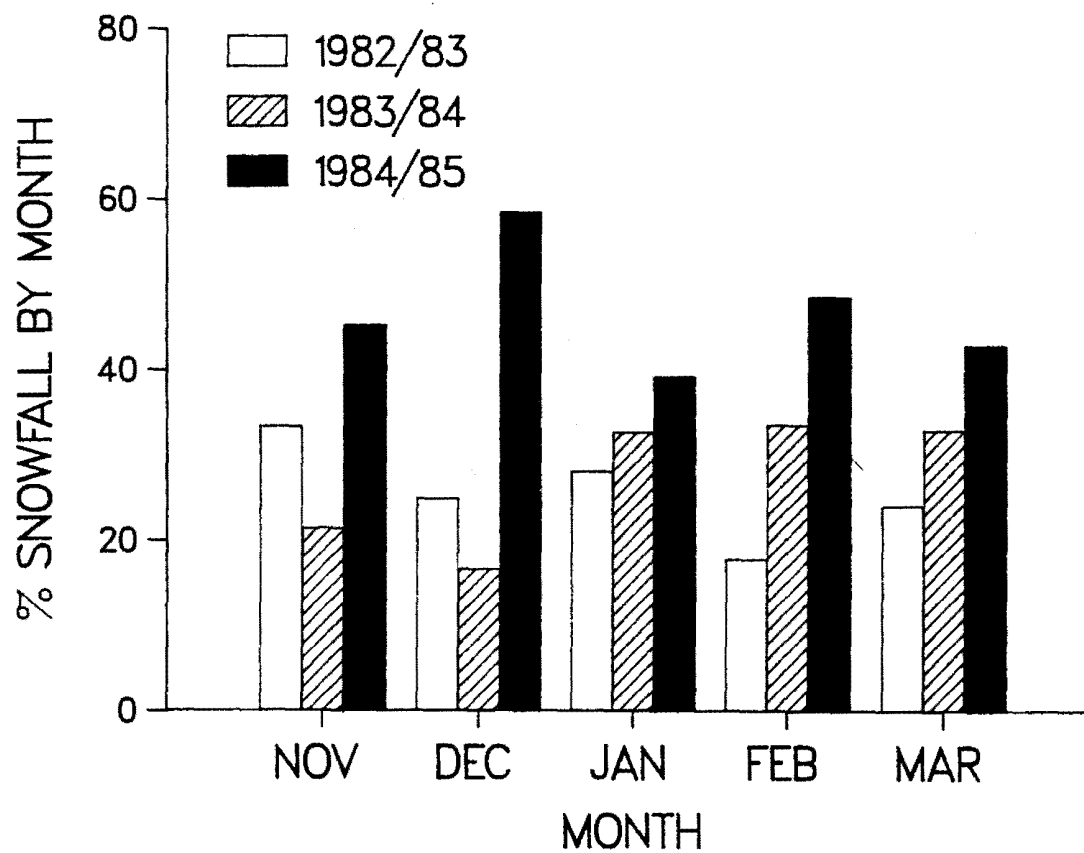


Fig. 5.2. Monthly snowfall in Yukon during winters 1982/83 to 1984/85. Results were compiled from monthly totals of precipitation (snow in mm) collected at 40 weather stations across Yukon (Atmospheric Environment Service 1982-1985).

americanus) populations crashed this year (Boutin and Krebs 1986), and arctic ground squirrels (*Spermophilus parryi*) and other small mammals were not as abundant as in previous years (B. Slough, furbearer biologist, pers. comm.). Harvests of most furbearers were higher than normal and the prevailing opinion was that this was due to a changing prey base.

Behavioural data suggest the vulnerability of a sex/age class may not be independent of that of other classes. For instance, Hornocker and Hash (1981) and Chap. IV indicated that adult males may influence dispersal movements of young of year and subadult males. Additionally, trapper effort is not likely to be consistent among years. An examination of harvest statistics for wolverine must account for differences in trapper effort, seasonal differences, differential vulnerabilities and possible interactions. Such data may be presented as a multidimensional contingency table where observations are classified by year, month, sex and age class. A class of models analagous to those used in analysis of variance, termed log-linear models, have been used to analyze multi-contingency data under a variety of different objectives (Feinberg 1970). Two statistics, marginal and partial association, indicate the magnitude of change when an effect is included in or deleted from a model (Brown 1976). Log-linear models were used to examine observed harvest trends of Yukon wolverine and assess the importance of factors and interactions.

In an ideal situation, a wildlife manager is able to extract all required information from a minimum of data. The simplest method of summarizing harvests is to present sex and age ratios. The ability of these ratios to reflect differential vulnerabilities is examined. Differences in vulnerabilities which may be attributed to changes in time, monthly and yearly, are then examined and discussed.

My objectives are to:

1. Determine and compare observed sex and age ratios in wolverine harvest from Yukon during 1982/83 to 1984/85.
2. Assess the significance of sex, age class, year, month trapped, and their interactions in explaining vulnerability patterns of wolverine.

3. Discuss observed and expected vulnerability patterns with respect to wolverine behaviour.

Materials and Methods

Ages were estimated using cementum analysis in conjunction with skull characteristics (Chap. I). Based on reproductive data, wolverine aged 0–1 years were classed as "young of year", 1–2 as "subadult", and 2 and older as "adult" (Chap. I). Sex ratios were compared to an expected of 1:1 using Fisher's Exact Probability test. Sex and age ratios among years and age ratios within sexes were compared using the Kruskal–Wallis (K–W) test. Mann–Whitney (M–W) tests compared ratios between sexes. The contingency table formed from sex, age class, month trapped and year was analyzed using log–linear models (Fienberg 1970, Brown 1976) as implemented by the BMDP4R® computer package (Brown 1983). Tests of marginal and partial association were used to determine significance of interactions (Brown 1976). Models were evaluated for goodness of fit by computing the difference between likelihood–ratio chi–square values (χ^2_d) (Brown 1976) and used to generate expected probabilities for sex/age classes.

Results

Although sex ratios (male:female) were biased towards males in all years, 1.2:1 (116:100), 1.4:1 (69:49) and 1.3:1 (73:55), respectively, only for 1983/84 was the sex ratio different from 1:1 ($\chi^2_1=3.39$) at $p<0.10$. Sex ratios were not different among years (K–W $\chi^2=3.71$, $p>0.10$). Sex ratio for the total sample, 1.3:1 (258:204) was significantly different from 1:1 ($\chi^2_1=6.31$, $p<0.05$). For each year, age ratios did not differ between sexes (Table 5.1). Age ratios disregarding sex did not differ among years (K–W $\chi^2=2.62$, $p>0.20$). The total harvest was comprised of 213 juveniles (young of year and subadults) and 200 adults.

In tests of marginal and partial association, all main factors were significant (Table 5.2). Results have the following implications:

Table 5.1. Frequencies of wolverine age classes harvested 1982/83 to 1984/85 in Yukon and Mann-Whitney (M-W) comparisons between sexes.

SEASON	SEX	% YOUNG OF YEAR	% SUBADULT	% ADULT	N	M-W
1982/83	FEMALE	41.7	12.5	45.8	96	z=0.22 p>0.80
	MALE	33.6	19.6	46.7	107	
	TOTAL	37.4	16.3	46.3	203	
1983/84	FEMALE	37.5	14.6	47.9	48	z=0.65 p>0.50
	MALE	31.8	22.7	45.5	66	
	TOTAL	34.2	19.3	46.5	114	
1984/85	FEMALE	20.5	28.2	51.3	39	z=0.65 p>0.50
	MALE	26.3	15.8	57.9	57	
	TOTAL	24.0	20.8	55.2	96	
TOTAL		33.4	18.2	48.4	413	

Table 5.2. Tests of marginal and partial association in log-linear model for wolverine harvested in Yukon from 1982/83 to 1984/85.

EFFECT	PARTIAL ASSOCIATION			MARGINAL ASSOCIATION		
	D.F.	CHI-SQUARE	PROB.	D.F.	CHI-SQUARE	PROB.
SEX (S)	1	5.94	*			
AGE CLASS (C)	2	50.89	***			
MONTH (M)	4	47.87	***			
YEAR (Y)	2	39.43	***			
MC	8	36.08	***	8	33.24	***
MY	8	22.04	**	8	19.56	*
MS	4	2.44	0.66	4	1.76	0.78
CS	2	1.44	0.49	2	1.01	0.60
CY	4	4.68	0.32	4	2.45	0.65
MCS	9	20.34	*	10	19.47	*
MCY	16	27.90	*	17	25.36	0.09
MSY	8	7.50	0.48	8	6.24	0.62
CSY	4	6.54	0.16	4	6.48	0.17
MCSY	14	22.17	0.07			

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

1. Significant:
 - a. Month by Age Class: Vulnerabilities of the 3 age classes differ over time.
 - b. Month by Year: Month trapped and year are not independent.
 - c. Month by Age Class by Sex (MCS): Vulnerabilities differ with respect to sex of wolverine as well as age class.
2. Non-significant:
 - a. Sex by Month, Year and Age Class: Overall sex ratios are independent of month trapped, year and age classes.
 - b. Age Class with Year: Age class ratios are independent of year.
3. Month by Age Class by Year (MCY): The significant partial association and non-significant marginal association suggests this interaction may be important in explaining observed trends.

To evaluate the importance of the 3-way interactions, three models were fitted. The first contained only main effects and significant 2-way interactions, the second included MCS, the third MCY. The fit of the model which included MCS was significant ($\chi^2_d=17.77$, 16 d.f., $p<0.05$). The model which also included MCY was marginally significant ($\chi^2_d=30.13$, 20 d.f., $p<0.10$). Expected values were computed using this last model and are displayed in Figure 5.3 for males and Figure 5.4 for females.

Discussion

The consistent bias in the harvest towards males is attributable to their larger home ranges and greater movements, although sex ratios were not significantly different from equality within years. The significant bias towards males in the total sample (1.3:1) indicates males are generally more vulnerable to trapping. The independence of sex and age ratios from year trapped in Kruskal-Wallis comparisons was supported by the log-linear models. Under the harvesting regimes in effect, differences among years in monthly vulnerabilities were not apparent in overall sex and age ratios. Thus examination of age and sex ratios in a harvest is unlikely to reveal differences in vulnerabilities of age classes. Young of year

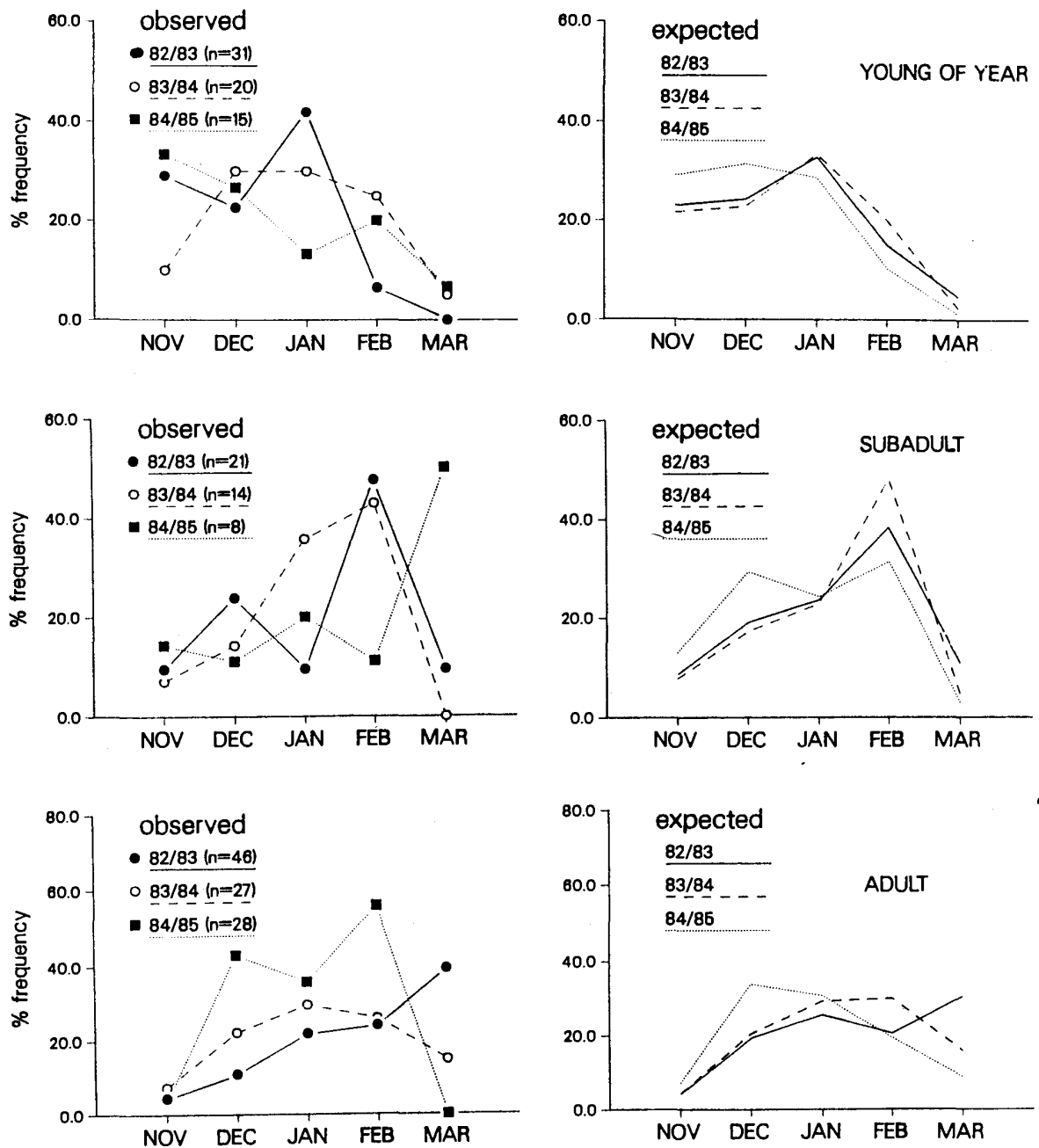


Fig. 5.3. Observed and expected monthly harvests for age classes of male wolverine trapped in Yukon, 1982/83 to 1984/85. Expected values were calculated using a log-linear model.

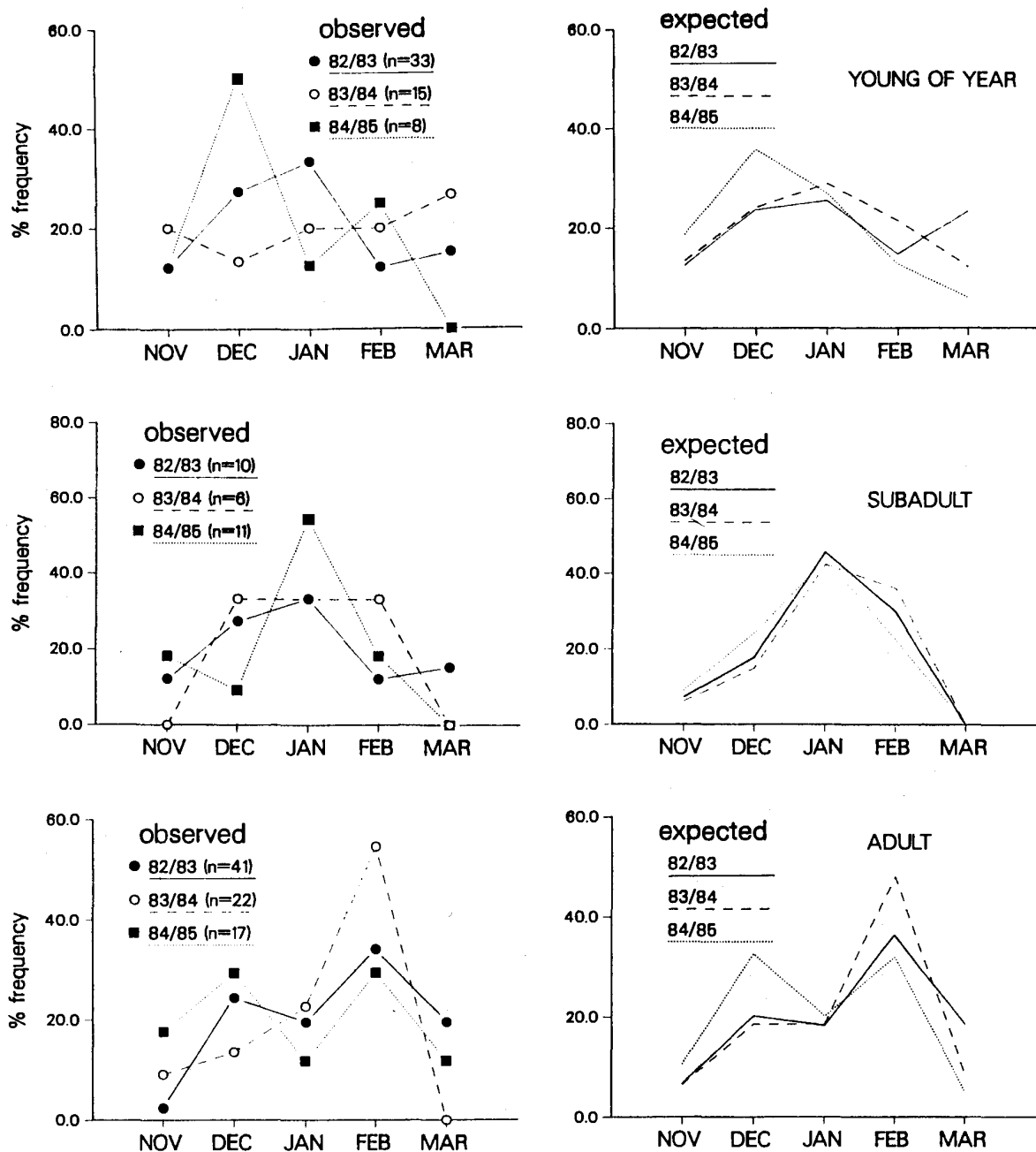


Fig. 5.4. Observed and expected monthly harvests for age classes of female wolverine trapped in Yukon, 1982/83 to 1984/85. Expected values were calculated using a log-linear model.

wolverine were the most prominent age captured and overall, juveniles (young of year and subadults) comprised 50% of the harvest.

The degree to which vulnerabilities were apparent in harvests differed among age classes. Harvest of young of year males was high from November through January, for all years. No other class demonstrated this tendency to be captured early in the trapping season. This period coincides with dispersal of young of year males. Subadult males had a peak in harvest in February, as opposed to January for young of year males. February may indicate time of dispersal for subadult males, possibly related to interactions with adult males before the start of the breeding season. Subadults have the lowest sample sizes for both sexes and additional information is necessary to understand the underlying behavioural mechanisms affecting their vulnerabilities. Only for 1982/83 was there an increase in adult male harvest in March. This may be attributable to breeding activity, however, such a tendency would be expected in all years. March may be too early for breeding activity to significantly increase movements of adult males. The atypical nature of 1982/83 in regards to prey abundance and wolverine movements likely was a factor in this increased harvest for adult males.

Young of year females did not exhibit a tendency to be captured early in the season as did young of year males. This is consistent with Magoun's (1985) findings that young females establish home ranges next to their natal area and do not undergo the extensive dispersal seen for young of year males. The expected curves for this age class are remarkably similar to those of adult males, including an increase in harvest for March of 1982/83. Sex/age classes not subject to strong behavioural influences during the trapping season are expected to demonstrate similar vulnerability patterns. Observations of radio-collared wolverine suggest neither young of year females nor adult males are subject to influences which may increase movements in winter other than prey abundance and availability (Chap. IV).

Harvest patterns of adult females are similar to those of subadult males. However, it is unlikely similar behavioural mechanisms within these classes are

responsible. Although pregnant females within this sample were trapped during January through March, most were harvested in February (Chap. I). The increased nutritional requirements of pregnancy and subsequent increase in movements should influence trapping vulnerability and may explain the increased harvest of adult females observed for February. Among years, capture of age classes of both sexes earlier in the season was generally higher for 1984/85. Increased access by trappers because of abundant snow at the beginning of 1984/85 may have contributed to vulnerability of wolverine.

The degree to which behavioural patterns of wolverine are apparent in harvests examined over time is dependent on the extent to which movements are affected. The strongest pattern evident was the tendency for young of year males to be captured predominately in early winter, November to January, a result of extensive post-natal dispersal. As wolverine have small litter sizes and reproduction is dependent on food supply (Chap. I), emphasis should be placed on identifying when during the year females are most vulnerable. Young of year females do not undergo extensive post-natal dispersal and are caught throughout the season. Observed harvest of classes not subject to strong behavioural influences is primarily a function of trapper effort. More adult females were captured in February, possibly attributable to increased nutritional requirements and subsequent increase of movements during pregnancy. Yearly differences in trapper effort because of differing snow conditions may alter expected harvest patterns. The greater these differences, the more evident they should be in the harvest. Prey distribution and availability affect vulnerabilities of all age classes and their effects are not predictable. Quantifying the relationship between trapper effort and harvest patterns is necessary to separate this effect from those attributable to behaviour of wolverine and is a prerequisite for forecasting future patterns.

CHAPTER VI

PRODUCTIVITY OF ECOREGIONS AND DENSITY

Fur harvest statistics are routinely collected by managers. The wealth of information produced often obscures the fact that in many cases, such data do not indicate population status or trends. Harvest rates are a function of animal abundance, effort expended by trappers and trapping vulnerability. Independent estimates of natural mortality and population size are required but are rarely available. Allocation of effort by trappers and success of harvest are functions of climate and economics as well as population levels. Harvest vulnerabilities interact with trapper effort in a manner that has not been quantified nor is predictable, further confounding interpretation. However, harvest statistics provide useful information even if they do not indicate population trends. The wolverine (*Gulo gulo*) is an economically important furbearer in Yukon, however, an assessment of the quality of habitats within the territory for this species is not available. My first objective is to describe the derivation of an index to productivity for Yukon, using extensive harvest data. Yukon may be divided into topographically distinct units or ecoregions (Oswald and Senyk 1977), often also serving as wildlife management areas. The ecoregion was chosen as the unit of area to compare productivity because of the low densities of wolverine and their requirement for large tracts of relatively undisturbed wilderness (Chap. IV).

Home ranges are generally exclusive within adult sexes of wolverine and average home range size has been used to estimate density (Hornocker and Hash 1981, Whitman and Ballard 1983, Magoun 1985). However, means based on small samples, avoidance of habitats by wolverine and dependence of home range size on habitat productivity preclude attempts to extend results directly from one study site to a considerably more diverse area (Chap. IV). I commented on the difficulties inherent in estimating density of wolverine and the pressing need for a suitable procedure (Chap. IV). I reasoned that, if an independent estimate of density for at least one ecoregion was available, relative productivity could be used as a scaling factor to estimate a population size for Yukon. My second objective is to propose

a means of estimating population size for Yukon wolverine using harvest statistics and a density estimate obtained from radio-collared wolverine in southwest Yukon (Chap. IV).

Beginning in 1951, with the registration of traplines, the Yukon Department of Renewable Resources monitored fur harvest using trapper declarations. In 1976 a fur inventory was established using fur export permits and fur trader records. Furs sold privately and those retained in Yukon are not accounted for. The fur inventory since 1976 is believed to account for 90-95% of the harvest (B. Slough, pers. comm.). Because of errors on fur dealer forms, harvest by registered trapline is less than 90-95% complete (B. Slough, pers. comm.). As harvest statistics are used for comparative purposes only, inaccuracies are unlikely to affect results, assuming omissions are constant across areas.

For each ecoregion and furbearer, the number of trappers operating, number of seasons trapped, number of traplines, and size of areas trapped are known. Harvest within ecoregions is related to effort (number of trappers, number of years), density of wolverine (a function of habitat quality), and possibly size of areas. The "best" index should reflect differences in habitat quality among ecoregions. Thus, relationships between harvest and effort, and harvest and size of area must be accounted for. In an analysis of the sex/age composition of wolverine harvested in Yukon over three seasons, 1982/83 to 1984/85, I have shown that harvest patterns may be explained using qualitative information regarding prey distribution and availability, snow conditions and activity of trappers (Chap. V). Thus, it is valid to assume that within a season, differential harvest vulnerabilities, economic conditions, climatic conditions and monthly allocations of trapper effort are more or less constant. In relative comparisons among ecoregions, these confounding variables will cancel.

As wolverine have large home ranges containing diverse habitats, the suitability of ecoregions for wolverine should also be related to the suitability for other species having more specific requirements. Species used in comparisons were other mustelids and furbearers occupying similar habitats; American marten

(*Martes americana*), mink (*Mustela vison*), ermine (*Mustela erminea*), wolf (*Canis lupus*), and red squirrel (*Tamiasciurus hudsonicus*). Wolves were included because of the reliance of wolverine on winter kills (Chap. III), and red squirrels because their distribution in Yukon is widespread (Youngman 1975). Coyote (*Canis latrans*), fisher (*Martes pennanti*), fox (*Vulpes vulpes*, *Alopex lagopus*), lynx (*Lynx canadensis*), American marten, mink, and ermine were classed as "terrestrial carnivores" to compare wolverine productivity to that of a diverse group occupying most habitats in Yukon.

I estimated an adult density of 1 female/265 km² and 1 male/530 km² for a study area in the Kluane Game Sanctuary of southwest Yukon (Chap. IV), in Ecoregions 7 and 8. This estimate is assumed to be representative of Ecoregion 8. Ecoregion 7 contains Kluane National Park and is not trapped. Differences in productivity among ecoregions will reflect differences in density of wolverine. Productivity of ecoregions relative to that of Ecoregion 8 are used as scaling factors to estimate densities of wolverine.

My objectives are to:

1. Compare productivity indices for ecoregions of Yukon between wolverine and other furbearers harvested 1951/52 to 1981/82.
2. Determine and compare productivity of wolverine among ecoregions.
3. Estimate densities and population sizes of wolverine within ecoregions of Yukon.

Materials and Methods

The number of wolverine harvested, the number of active trappers and size of area (km²) trapped were compiled for each registered trapline by trapping season, from 1951/52 through 1981/82. Three traplines consist of group areas which extend over a number of ecoregions. These areas (Old Crow, McPherson and Ross River) were treated as separate units. As it is unknown whether traplines reporting no harvest of furbearers represent a lack of effort or unsuccessful trapping, these traplines were excluded from analyses on a species and seasonal basis. For each

ecoregion, the number of trappers, the number of seasons, the numbers of each species that were harvested, mean trapline size and total area were tabulated. Total area represents the sum of trapline areas harvested over all seasons. Each data point represents an ecoregion, thus the data are independent. Relationships between variables were investigated using least squares regression.

For each furbearer and the group of terrestrial carnivores, the number of trappers was regressed on the number of seasons; numbers harvested on number of trappers; numbers harvested on number of seasons; numbers harvested, number of trappers and number of seasons on the total area trapped; and numbers harvested, number of trappers and number of seasons on mean trapline size. For each ecoregion, by species, a measure of effort, "trapper-years", was computed as (number of trappers) x (number of years). Trapper-years/harvest was calculated for species and mean values compared using oneway ANOVA. Fisher's Modified Least Significant Difference ($p \leq 0.05$, MLSD) was used for multiple comparisons (Carmer and Swanson 1973). Means \pm 1 standard deviation are reported. An index to productivity computed as (total area/trapper-year/wolverine) was used to rank ecoregions.

For each ecoregion, a scaling factor was computed as $\log(\text{productivity}/\text{productivity of Ecoregion 8})$. Density ($\text{km}^2/\text{wolverine}$) was calculated as (scaling factor) x (density of Ecoregion 8). The logarithmic transformation of the scaling factor was necessary because untransformed relative productivities produced unreasonably large estimates of density. Numbers of residents of each sex were estimated as $(\text{area of ecoregion (km}^2\text{)})/(\text{density})$. Densities for Ecoregions 3, and 12-14 were calculated disregarding Ross River Trapping Area. Densities do not include areas that were not trapped, Kluane National Park (Ecoregion 7), McPherson Trapping Area (Ecoregion 19) and the North Slope (Ecoregion 22).

Results

Ecoregions varied with respect to number of traplines, mean trapline size, number of trappers and mean number of trapping seasons (Table 6.1). Some harvest of wolverine was reported by ecoregions for all 32 seasons except by Ecoregion 1 (19 seasons), Ecoregion 17 (16 seasons), Old Crow Trapping Area (8 seasons), and Ross River Trapping Area (9 seasons). No wolverine were reported harvested from McPherson Trapping Area. Most traplines within ecoregions reported nil harvests of wolverine (76% to 94%, Table 6.2).

The relationships between number of trappers and number of seasons were linear and similar for all furbearer species. Slopes ranged from 1.42 to 1.53 (SE 0.02 to 0.05) and r^2 values ranged from 0.98 to 0.99 ($p < 0.0001$). The relationships of harvest with number of trappers and harvest with number of seasons were all increasing and significant but differed among species in the degree of linearity and goodness of fit. Results are shown for wolverine (Fig. 6.1). For all species, number of animals harvested, number of trappers, and number of seasons were not related to total area trapped. The relationship of harvest to mean trapline size for wolverine (Fig. 6.2a) was similar to that for other species. More furbearers were harvested from ecoregions having smaller traplines. Both number of trappers ($\log(\hat{Y}) = 7.27 - 1.85 \log(x)$, $r^2 = 0.78$, $p < 0.001$) and number of seasons ($\log(\hat{Y}) = 6.69 - 1.70 \log(x)$, $r^2 = 0.77$, $p < 0.0001$) were related to mean trapline size. If traplines are small, a greater number may be supported within an ecoregion (Fig. 6.2b) and consequently effort in the form of trappers and seasons is greater. Harvest of terrestrial carnivores was positively related to total area ($\log(\hat{Y}) = 0.81 \log(x)$, $r^2 = 0.99$, $p < 0.0001$) and productivity of ecoregions was compared only for individual species.

The relationship of wolverine harvest to trapper-years does not indicate how harvest of wolverine varies with effort expended but is a comparison among ecoregions. The greatest number of trapper-years was identified for Ecoregion 5 (Fig. 6.3). However, in Ecoregion 8, 30% less effort produced 16% more wolverine. The statistic trapper-year/harvest varied considerably within and among species.

Table 6.1. Traplines harvesting wolverine in Yukon ecoregions during 1951/52 through 1981/82.

ECOREGION	NUMBER OF RTL ^a	MEAN SIZE OF RTL (km ²)	S.D.	MEAN NUMBER OF TRAPPERS	S.D.	MEAN NUMBER OF SEASONS	S.D.
1	12	1323.4	717.8	7.6	3.5	7.0	3.4
2	30	652.5	397.3	13.0	8.3	10.1	7.3
3	7	1507.5	276.0	30.6	6.9	26.9	5.4
4	40	725.2	314.4	22.8	8.6	20.5	8.7
5	74	443.9	291.1	26.7	11.3	22.4	9.3
6	18	569.0	330.7	29.9	13.5	23.2	9.8
8	32	460.7	333.1	31.3	9.3	26.5	7.2
9	10	763.7	320.7	33.4	6.6	28.5	4.1
10	32	899.3	531.7	31.5	8.3	26.4	5.7
11	25	845.2	533.4	28.4	11.0	22.9	7.4
12	44	527.3	284.7	27.8	7.5	24.7	6.2
13	22	1058.1	665.2	24.4	5.8	22.8	5.5
14	3	2038.7	648.7	24.3	5.1	23.7	4.0
15	13	2122.3	665.7	9.8	10.6	9.7	10.6
16	13	1511.2	712.2	19.5	9.3	17.8	8.9
17	8	2400.3	1215.8	5.6	4.0	5.2	3.6
OLD CROW	1	62393.0		27.0		8.0	
McPHERSON	1	20641.0		14.0		4.0	
ROSS RIVER	1	34599.0		23.0		9.0	

^aRegistered trapline.

Table 6.2. Mean number of traplines per season that reported no harvest of wolverine and the percent of all traplines that reported no harvest over all seasons from 1951/52 to 1981/82 in Yukon ecoregions.

ECOREGION	MEAN RTL ^a	S.D.	PERCENT
1	3.8	3.4	86.9
2	8.5	8.6	90.1
3	5.2	1.5	87.8
4	23.4	4.9	91.1
5	46.1	7.9	88.8
6	10.4	2.3	79.9
8	21.9	5.4	82.6
9	7.7	2.0	86.0
10	22.7	4.3	85.9
11	14.5	3.6	81.5
12	31.1	5.2	91.5
13	14.1	3.3	90.0
14	1.9	0.9	85.9
15	3.7	2.1	94.4
16	6.5	1.7	90.0
17	2.0	1.7	76.2

^aRegistered trapline.

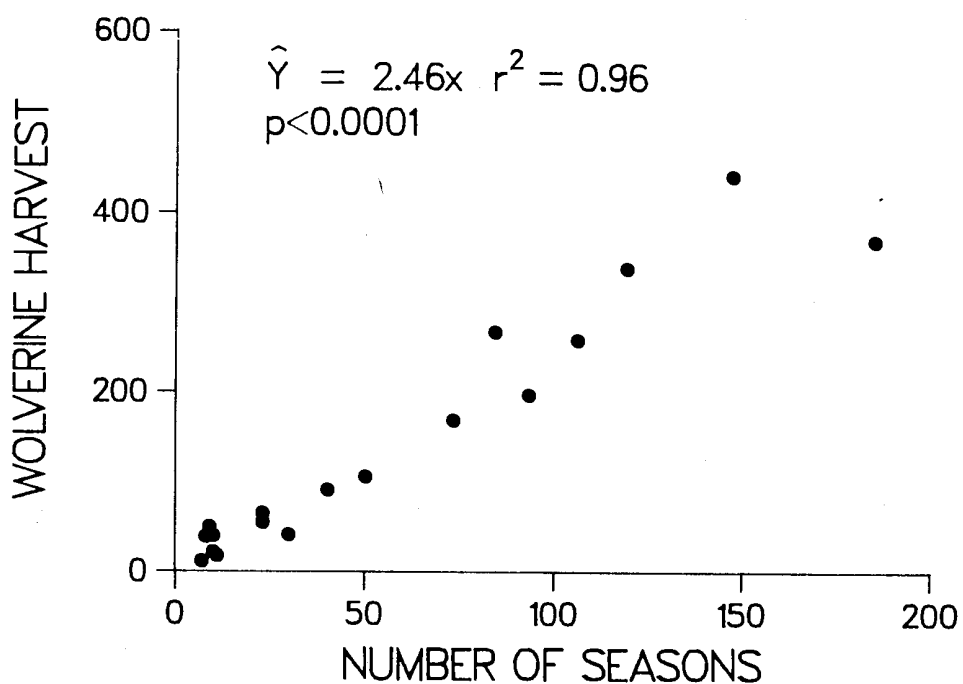
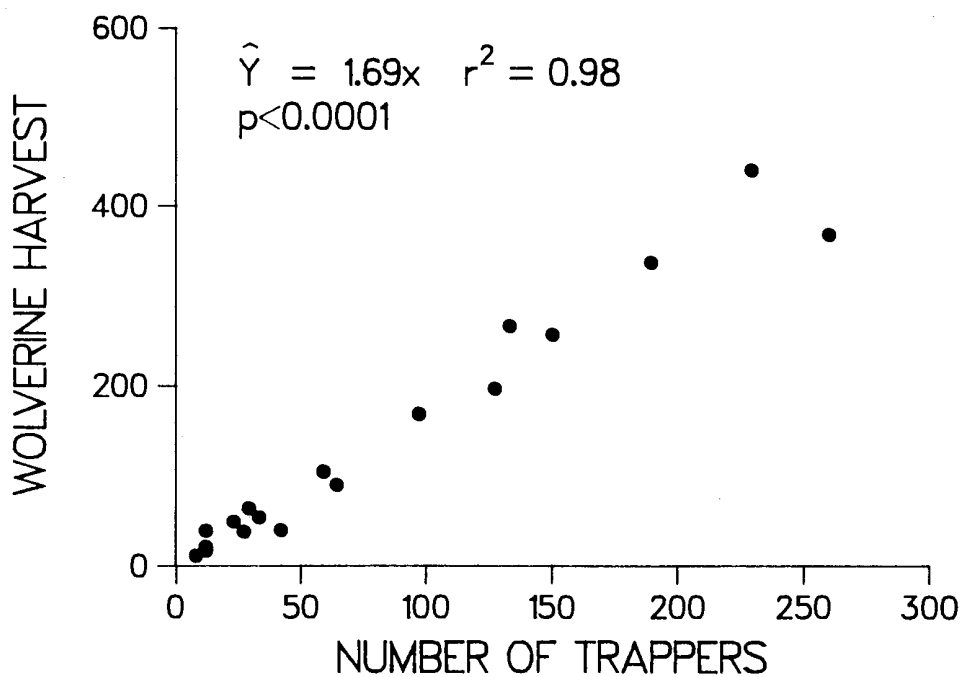


Fig. 6.1. Linear regressions of the number of wolverine harvested on the number of trappers and number of seasons for Yukon ecoregions during 1951/52 to 1981/82. Each point represents one ecoregion and points are independent.

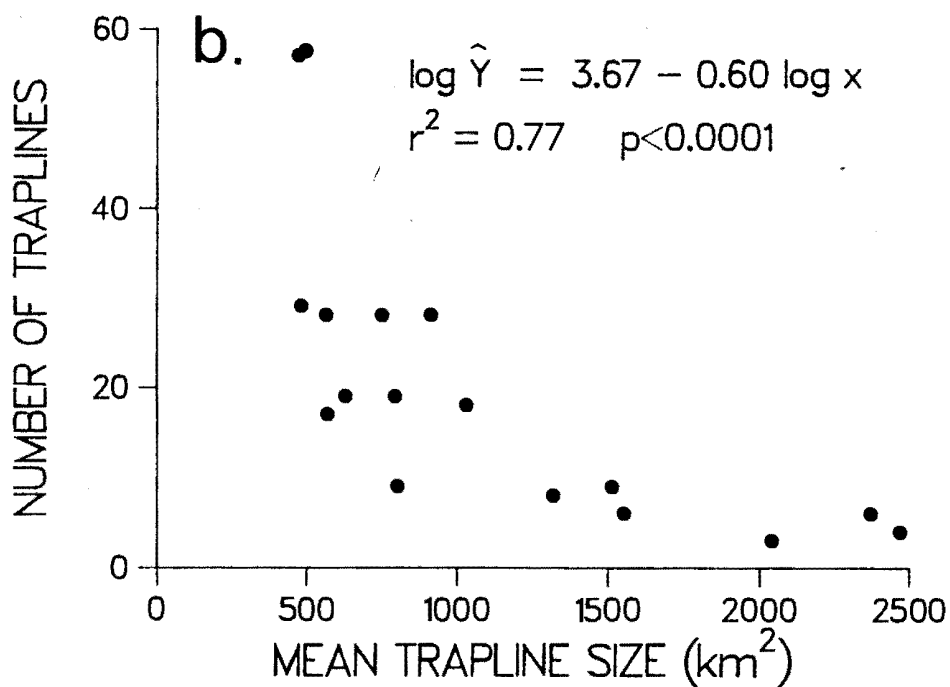
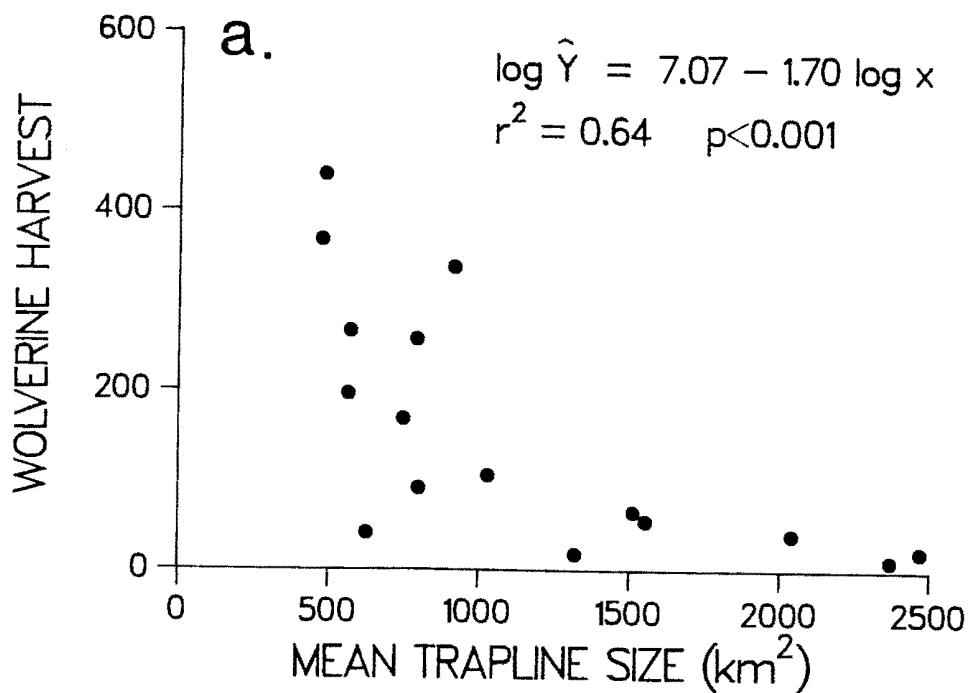


Fig. 6.2. Linear regressions of the number of wolverine harvested (6.2a) and number of traplines (6.2b) on mean trapline size for Yukon ecoregions during 1951/52 to 1981/82. Each point represents one ecoregion and points are independent.

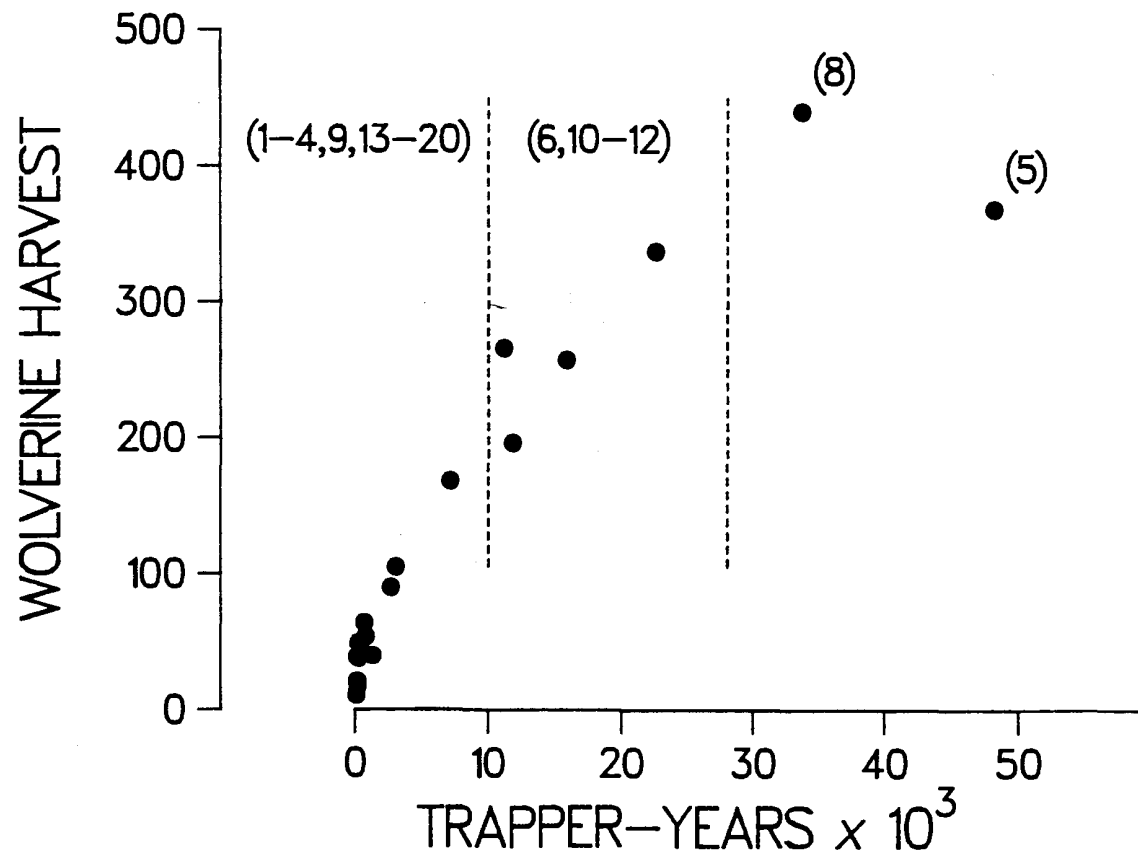


Fig. 6.3. A comparison of the number of wolverine harvested to effort (trapper-years) for the seasons 1951/52 to 1981/82 within ecoregions of Yukon. The numbers in brackets represent ecoregions.

The higher the value, the lower the harvest per unit of effort. Wolverine had the highest mean value (34.5 ± 34.3) and red squirrel the lowest (1.3 ± 1.2). Mean statistics among species were significantly different ($F_{5, 106}=6.99$, $p<0.0001$). The mean value for wolverine differed significantly (MLSD) from that for red squirrel, American marten and ermine. Other species that differed were wolf and red squirrel. The relationships between the statistic for wolverine with those of other species were positive and significant (Table 6.3). Differences in overall numbers harvested were apparent from the slopes.

Productivity relative to the greatest value (Ecoregion 8) suggests ecoregions may be grouped with respect to their suitability for wolverine. Ecoregions most similar in productivity were not necessarily contiguous. The highest productivity was attributed to southwest Yukon (Fig. 6.4). Productivity decreased both north and east, and was lowest in Ecoregion 15. As most of the northern Yukon is trapped by one group (Old Crow), total area used in computations overestimates actual area trapped and productivity is likely underestimated.

The estimated adult population size for trapped ecoregions of Yukon was 2503 resident wolverine (Table 6.4). Births were calculated using the following observations and assumptions. Of 3 radio-collared adult females in southwest Yukon, 1 had young (Chap. IV); 1 of 3 adult females are assumed to reproduce yearly. Estimated number of fetuses for age classes of Yukon females ranged from 2.8 to 3.4 (Chap. I). This range does not account for *in-utero* and pre-weaning losses (Chap. I), and a survival to weaning of 2 young per female is assumed. If females produce 1112 young ($1668 \times 1/3 \text{ reproductive} \times 2 \text{ young/female}$) and half as many subadults and transients are present, 4171 wolverine is an estimated fall population size. Harvests during 1982/83 to 1984/85 represent 6% to 10% of this estimated trapped population.

Table 6.3. Linear regressions^a of the productivity (trapper-year/harvest) of Yukon ecoregions for furbearing species to the productivity for wolverine. Productivity for wolverine is the independent variable.

SPECIES	EQUATION	r ²
MARTEN	$\text{SQRT}(\hat{Y}) = 2.09 \text{ SQRT}(x)$	0.93
MINK	$\hat{Y} = 1.18x$	0.98
ERMINE	$\hat{Y} = 2.39x$	0.96
WOLF	$\hat{Y} = 1.38x$	0.95
RED SQUIRREL	$\text{SQRT}(\hat{Y}) = 4.74 \text{ SQRT}(x)$	0.86

^ap < 0.0001.

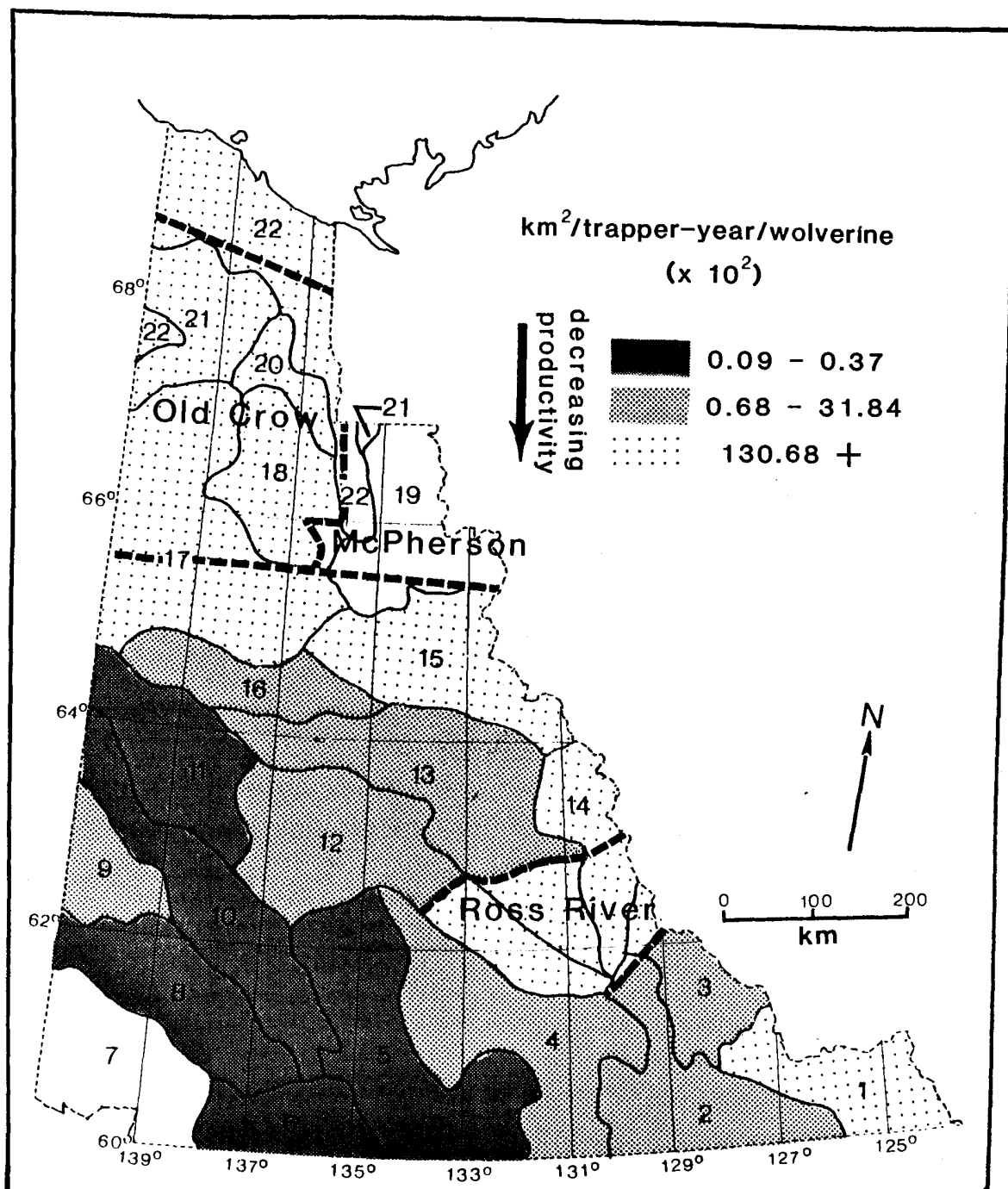


Fig. 6.4. Productivity among ecoregions of Yukon for wolverine harvested 1951/52 to 1981/82. Numbers represent ecoregions and dashed lines are boundaries of trapping areas.

Table 6.4. Estimated densities and numbers of resident wolverine within Yukon ecoregions.

ECOREGION	km ² /FEMALE	FEMALES	km ² /MALE	MALES	TOTAL
1	984	16	1968	8	24
2	640	34	1279	17	51
3	614	20	1229	10	30
4	341	93	681	47	140
5	55	625	109	312	937
6	140	95	280	47	142
8	265	82	530	41	123
9	407	23	814	12	35
10	147	180	293	90	270
11	161	127	322	64	191
12	232	157	463	78	235
13	482	83	963	42	125
14	837	16	1674	8	24
15	1167	22	2334	11	33
16	674	18	1349	9	27
17	963	17	1926	9	26
OLD CROW	1039	60	2079	30	90
TOTAL		1668		835	2503

Discussion

The close relationship and similarity of slopes indicates that the ratio of the number of trappers to number of seasons is constant among ecoregions and species. Thus, use of trapper-years as a measure of effort for comparisons among ecoregions is valid. For wolverine, harvest increases linearly with both number of trappers and number of seasons. The size of a harvest is a function of density, and since the ratio of harvest to effort does not differ among ecoregions, these results suggest that low densities are common to all ecoregions. As traplines that reported no harvest of wolverine were excluded from analyses, the proportion and effect of trappers that attempted to harvest wolverine but failed are unknown. However, the large percentage of these traplines in all ecoregions indicates most trappers did not actively trap wolverine, at least up to 1981/82. Whether this is attributable to trappers concentrating on other species or to a dearth of wolverine on traplines is unknown. The lack of a relationship for harvest with total area implies size of harvest is not a function of size of the area trapped and that ecoregions differ in habitat quality for wolverine.

The habitat requirements for wolverine, American marten, mink, ermine, wolf and red squirrel are diverse, from the mature coniferous forests required by American marten (Archibald and Jessup 1984) to similar use of habitats as wolverine by wolves. This diversity coupled with the correspondence of productivity of ecoregions for wolverine with that of the other species suggests that the ecoregion is a suitable unit of area for comparisons of habitat quality. The strength of this finding is increased when one considers the myriad of factors affecting harvest of the various species. Differences in size of harvests for each species are apparent and may be attributed to differences in furbearer densities.

Ecoregions 5 (Lake Laberge) and 8 (Ruby Range) were identified as being the most productive. More than half of the human population of Yukon live within the Lake Laberge ecoregion (Oswald and Brown 1986) and of all ecoregions, the greatest effort was expended here. However, Ecoregion 8 was the most productive, with more wolverine harvested per unit of effort. The Ruby Range ecoregion is

adjacent to Kluane Game Sanctuary and Kluane National Park. These large untrapped areas may provide sources of dispersing wolverine and transients for adjacent traplines. I commented on the diversity and abundance of prey within the Kluane Game Sanctuary and suggested that the capability of the area for wolverine was high (Chap. IV). This conclusion is supported by the harvest data.

Ecoregions in the next highest category of productivity (Ecoregions 6,10,11,12) occur in southern and western Yukon. These areas contain diverse habitats including significant portions of alpine and subalpine. Less productive ecoregions, particularly those in southeast Yukon, Beaver River (1), Liard River (2), and Wellesley Lake (9) in the west, are more uniform in topography and generally have low relief. I suggested that a diverse prey base, particularly of ungulates, is best for wolverine populations (Chap. IV). Ecoregions 1, 2 and 9 may be less productive because they have a low diversity of ungulates. Diversity in habitat promotes diversity in prey species, and may be important in determining the productivity of ecoregions for wolverine.

The least productive ecoregion is Wernecke Mountains (Ecoregion 15). This ecoregion contains steep, rugged topography. Large areas are likely not trapped because of inaccessibility and productivity for this ecoregion may be greater than estimated. Diversity and abundance of potential prey in northern Yukon (Old Crow) is lower than in the south, however, productivity is not accurately represented as the size of the area that was trapped is unknown. Because low densities are the rule for wolverine, a relative comparison cannot be made without additional information.

The resident sex ratio used for Ecoregion 8 from my estimate of a resident population (Chap. IV) was 2 females : 1 male, which is not necessarily representative of all resident populations. For example, Magoun (1985) suggested that a male monitored 4–6 females in arctic Alaska. The variance in resident sex ratios is unknown and estimated densities are best guesses using available information. A fall population of 4171 wolverine was estimated for trapped ecoregions of Yukon. Assuming non-trapped areas contain 5% of this estimate,

population size for Yukon after reproduction and before trapping is 4380 wolverine. Although this estimate was derived using broad assumptions, it is reasonable considering wolverine home range size, habitat productivity and reproduction.

PART E
SUMMARY AND MANAGEMENT RECOMMENDATIONS

INTRODUCTION

This study was initiated in 1983 to investigate the ecology of wolverine in Yukon. A carcass submission program, initiated by the Yukon Department of Renewable Resources, netted 461 wolverine over 3 trapping seasons, 1982/83 to 1984/85. Behavioural data was collected using radio-collared wolverine. Objectives of the thesis were to determine and describe reproduction, morphology and condition in winter, seasonal food habits, home range and habitat use, vulnerability patterns of sex/age classes in harvests, and productivity and densities of wolverine within ecoregions of Yukon. Results and major conclusions are presented.

CHAPTER 1.

The trapping season for wolverine in Yukon extends from 1 November to 31 March. Description of reproduction is limited to this period. Pro-estrus could not be defined using ovarian structures. Females did not breed as young of year and only a small proportion of subadults (7%) were pregnant. This proportion is the lowest reported for wolverine. Of the first adult age class (2+ years), 50% were pregnant. Percent of older females pregnant or post-partum ranged from 62 to 93%. The mean *in utero* litter size was $3.2 \pm \text{S.D. } 0.8$ ($n=22$). Natality was estimated using the relationship between number of corpora lutea and fetuses for females having macroscopic embryos. Natality increased with age, ranging from a mean of 2.8 to 3.4 fetuses per female. A pregnancy rate determined from carcasses does not account for *in utero* and pre-weaning losses and overestimates productivity. Pregnant females were caught in all months of the trapping season, indicating implantation occurred at least as early as November. The variability in the timing of implantation and parturition is likely to be a function of local conditions, primarily food availability. This study is the first to comment on the incidence of non-reproducing females within adult age classes. Adequate food during pregnancy is suggested as the most critical factor determining reproductive success. Males were sexually mature at 2+ years. Bacula weights and measurements should not be used as criteria of age without other evidence.

CHAPTER II.

Adult males had greater body weights than young of year males, but age classes did not differ in body measurements. Adult females weighed more than subadults but not young of year. Subadult females may lose weight during their initial period of independence. Sexes were highly dimorphic with respect to body weight and all measurements. The kidney fat index and a subjective index based on a visual estimate of total body fat were too variable to be of use in predicting winter body condition. As wolverine contend with unpredictable food supplies, fasting endurance may be the best indicator of physiological condition. The allometry of body fat and body weight needs to be established.

CHAPTER III.

Seasonal food habits were determined from winter stomachs, scats and observations of wolverine. There were no differences for proportions of empty stomachs and typical bait items between wolverine caught using quick-killing or restraining trap types. These results indicated that consumption of trap bait was rare and not likely to bias results. Of prey species, ungulates (primarily moose and caribou) had the highest frequency of occurrence. Snowshoe hare had the highest contribution of individual prey species. Porcupine may be important to the diet but its contribution could not be estimated due to retention of quills in stomachs. Sciurids that hibernate (arctic ground squirrel, least chipmunk, and hoary marmot) were found in the winter diet. These prey were likely obtained from caches. The most common sciurid in the diet was red squirrel. Red squirrels are available all winter and their distribution in Yukon is widespread. The importance of soft body parts and bone in the diet is rarely noted but may be significant for scavengers. Contribution of these food items in winter diet of wolverine was relatively large. The source of scavenged prey appeared to be ungulate.

No differences among sexes or age classes were apparent in the types and frequencies of prey consumed. Over time, the greatest differences in food habits were attributed to November, a month more fall-like in weather than other months of the trapping season. There were trends for greater consumption of small prey

during November, possibly indicating greater availability of small mammals and birds. Ungulates were consumed all winter. The diversity of prey within stomachs of wolverine indicated supplemental prey were important. The prevalence of empty stomachs suggested that food was generally difficult to obtain. In order of importance, prey in the diet consisted of ungulate, snowshoe hare, sciurids, birds and small mammals. Wolverine may select prey on the basis of size and nutritional value. Small mammals were associated with low incidence of ungulate, indicating consumption of small prey occurs when large prey are unavailable. Summer food habits are not well known but appear to be more varied than in winter.

CHAPTER IV.

Home range and habitat use were investigated for wolverine in a study area located in the Kluane Game Sanctuary of southwest Yukon. Ten wolverine were outfitted with radio-collars; 3 adult females, 2 young of year females, 3 adult males, 1 subadult male and 1 young of year male. In-detail analysis was possible for 3 adult females, 1 adult male and 1 subadult male. Sample sizes were small and the following results should be regarded as preliminary until habitat relationships can be examined further. All adult females made 1 or 2 long distance movements in summer. The inclusion of these excursions in calculations may inflate estimates of home range size. When excursions were omitted, summer home ranges of adult females were smaller or the same size as their winter home ranges. The female with kits had a yearly home range size one-half the size of the home ranges of the 2 females without kits. Use of small, isolated areas in winter by females for extended periods was attributed to the presence of ungulate kills. Home range size of the adult male is the smallest reported for adult male wolverine. This male did not expand his home range in spring and summer. This was attributed to adequate access to both food and females. The increased activity observed in other studies by adult males at this time of the year has been attributed to breeding behaviour but may also be a function of seasonal changes in the distribution and availability of prey. Female movements do not appear to be influenced by breeding activity.

Juvenile males, either as young of year or subadults, made extensive movements, likely dispersal. Interactions between the adult and subadult male may have contributed to the movements made out of the study area by the younger male. Field studies indicate variation in spatial patterns of wolverine exist. An apparent abundant and diverse prey base is hypothesized as the reason behind the small home ranges observed for wolverine in the Kluane Game Sanctuary. Results support Macdonald's (1983) resource dispersion hypothesis; for a given patch richness, the minimum sized territory is smaller where food patches are not dispersed. The sex/age compositions of wolverine harvested in traplines containing salmon frozen in river ice were examined. A food source of high quality that is persistent and predictable, but not easily defended, may allow extensive overlap of home ranges within sexes.

Only 1 of 3 adult females was reproductive. The demands of providing for young appear to be extreme and influence a female's probability of reproducing successfully the following year. Interactions between wolverine and wolves were documented in this study, and appear to have been food related. Two young of year females are believed to have died from starvation. Starvation and wolf attacks are consistent with King's (1983) hypothesis that mortality factors are mediated almost solely by food in opportunistic mustelids. Within the 1590 km² area that was monitored, 3 adult males and 6 adult females were present during 3 summers and 2 winters of the study. This corresponds to a density of 1 resident/177 km². Wolverine did not use all areas within the study area. For a region having a diverse and apparently abundant prey base, wolverine densities are low, relative to carnivores of similar size.

Generally, habitat use for females was proportional to availability. Males used subalpine coniferous habitats more than other habitat types in winter. This increased use was attributed to the presence of ungulate kills. Individual variation in use of forest cover types, aspects, slopes and elevations was apparent. Habitat use appears to be determined by prey distribution and availability. Patterns of habitat use are expected to vary seasonally and regionally.

CHAPTER V.

A consistent bias towards males was apparent in Yukon harvests. This increased vulnerability is attributed to the larger home ranges and greater movements of males. More young of year males were caught during November to January. No other age class demonstrated this tendency to be captured early in the trapping season. This vulnerability is a function of the extensive post-natal dispersal of males. Young of year females did not show this tendency, consistent with Magoun's (1985) findings that females establish home ranges near their natal area. Vulnerability patterns of young of year females and adult males were similar. Age classes not subject to strong behavioural influences are expected to demonstrate similar vulnerability patterns. Adult females had a peak in catch in February. Pregnant females also exhibited this peak. The increased nutritional requirements of pregnancy are likely responsible for an increase in movements and subsequent increase in vulnerability. Snow affects the mobility of trappers and effort expended. Yearly differences in trapper effort may be attributed to weather and likely alter harvest patterns. Prey distribution and availability affect all age classes and their effects are not predictable. The relationship between harvest patterns and trapper effort needs to be quantified.

CHAPTER VI.

A productivity index of wolverine for ecoregions of Yukon was derived using harvest statistics. Trapper-years (number of trappers x number of seasons) was used as a measure of effort. A large percentage of traplines within ecoregions reported no harvest of wolverine. Harvest was not related to the total area trapped. Differences existed among ecoregions in habitat quality. The productivity of ecoregions for wolverine corresponded with that for American marten, mink, ermine, wolf and red squirrel. Ecoregions 5 and 8 were identified as being the most productive. The least productive ecoregions are generally uniform in topography and low in relief. Diversity in habitat promotes diversity in prey and is important in determining productivity of ecoregions for wolverine. A resident population of 2503 wolverine was estimated for trapped ecoregions. A fall

population including juveniles and transients was estimated as 4171. If wolverine in non-trapped areas contain 5% of this value, a population size for Yukon after reproduction and before trapping is 4380 wolverine.

MANAGEMENT RECOMMENDATIONS

Home range and habitat use are functions of the distribution and availability of prey and are likely to be variable across Yukon. No one habitat type may be identified as important to wolverine. A diverse prey base, particularly in ungulates, is critical. The need for large tracts of wilderness implies that the effects of small habitat losses would be difficult to detect but may prove important over a long period. Although the relationship between human activity and habitat use of wolverine is not well understood, the severe curtailment of original distribution of wolverine in North America suggests the species does not tolerate development well. An index capable of assessing the status of wolverine populations was not readily apparent from this study. Furthermore, the predicted variability in reproduction and in population size suggests that the usefulness of such an index would be limited. Investigations of reproduction and population dynamics indicated that the proportion of females that reproduce successfully is an important limiting factor. However, to use this information, a means of monitoring reproductive rate is necessary as well as an estimate of what proportion of the population is harvested. The latter necessitates having an estimate of population size. It does not appear likely that an easily applied index to population size of wolverine can be derived.

Use of large home ranges by wolverine requires that large areas be monitored and suggests management on a trapline basis is not possible. Ecoregions are suggested as a suitable management unit. Capability of ecoregions for wolverine, in terms of habitat quality, corresponded to capability for mink, American marten, ermine, wolf and red squirrel. The use of an easily monitored furbearer as an indicator of habitat quality for wolverine is a possibility. The utility of ranking productivity of ecoregions with respect to density of wolverine is twofold. Ecoregions which cannot support intensive harvesting are identified and appropriate

limits may be set if necessary. Changes in the harvest per effort expended may be detected by monitoring current conditions and comparing to past productivities.

The vulnerability of wolverine to trapping is a function of the size of their home ranges and the extent of their movements. This vulnerability differs among age/sex classes and over time and is apparent in the harvest data. However, observed harvest patterns are not necessarily consistent and are modified by the allocation of trapper effort. Understanding the relationship between harvest and effort would assist in interpreting and predicting patterns, and would allow greater control of the sex/age composition of the harvest. A difficulty is that female harvest tends not to show any distinct patterns, except possibly an increase in vulnerability for pregnant females in February. Minimization of harvest for females through selective manipulation of the trapping season implies that truncation by at least 2 months is necessary for an effect to be apparent.

This study did not uncover evidence that indicated wolverine populations in Yukon were declining. Presently, management of this species is best achieved through trapper education. The link between reproduction and food must be emphasized. Higher than average survival of ungulates in winter will result in fewer carcasses for scavenging by wolverine. These times of low food availability also will be times of curtailment of reproduction. During these seasons, trappers should be encouraged to forego harvesting wolverine present on their traplines. If harvests are consistently high, and there is a concern of overharvest, two strategies are recommended: a) entire closure of the trapping season for selected ecoregions or b) truncating the trapping season to the end of January.

Wolverine in Yukon are classified both as a furbearer and a big game animal. The latter permits harvest by hunters, from 1 August to 31 October. I recommend that wolverine be re-classified and the big game status deleted. My reasons are:

1. Summer and fall appear to be the worst times for wolverine in terms of food availability. At this time, females are subject to the increased demands of raising young. The magnitude of natural mortality factors on wolverine in summer is unknown but cannot be assumed to be small. Mortality by hunting

- and by natural means are not necessarily compensatory but may be additive.
2. Age/sex classes which are killed by hunting do not necessarily reflect behaviour of wolverine, but are more likely attributable to incidental encounters between hunter and wolverine. The composition of the harvest cannot be readily estimated, or controlled by manipulating hunter effort.
 3. Harvest by hunters has recently been about 10% of the total harvest. The impact of this proportion on the population is unknown, however, it cannot be assumed to be negligible. This study has emphasized the tenuous relationship between wolverine and their environment. A second mortality factor exerted by humans but not easily controlled and having an unknown impact not only complicates management but could be detrimental.
 4. Pelt quality of furbearers in summer is vastly inferior to that in winter. Hunters take wolverine incidental to other big game. There does not appear to be an economic necessity to maintain this harvest.

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APPENDIX I. WOLVERINE TOOTH SECTIONING AND AGING PROCEDURE

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A. DECALCIFICATION:

1. Mix a solution of 200 g sodium citrate with 1000 ml distilled water.
2. Mix a solution of formic acid and distilled water.
3. Mix a decalcification solution of 50:50 formic acid solution and sodium citrate solution.
4. Place teeth in the decalcification solution at a ratio of 1:20 by volume. When decalcification is complete (60–72 hours for premolars, longer for larger teeth), the teeth should be soft and flexible.
5. Rinse under running water for approximately 12 hours.

B. SECTIONING:

Section teeth in the cryostat at -15°C and set for 10 micron thick slices. The cut should be longitudinal and parallel to the root canal, cutting from the crown to the root. Take 4 sets of a dozen sections, obtained adjacent to or surrounding the root canal. Float these sets separately in a sectioned glass dish containing slightly alkaline water (1 drop of 45% potassium hydroxide to 100 ml of distilled water, should be < 8.5 pH).

C. MOUNTING:

To mount, make a large bead of distilled water on the albumated slide. Handle the tooth sections with a thin wire attached to a pencil, floating the sections into position. Place all sections facing one direction. Label 2 slides for each tooth (one is a duplicate). Mount 2 sections from each set on a slide (8 sections per slide). Blot slides well after mounting and air dry.

D. STAINING:

Stain with Tolulene Blue (80 mg Tol. Blue in 250 ml of slightly alkaline water. Stir on electric stirrer for 15 minutes and filter). Stain is only fresh for a few days as it oxides. Rinse in 25% ethanol for 3 minutes and a final fresh bath of 25% ethanol for 1/2 - 1 minute. This draws eccess stain off the slide and from the sections, leaving more distinct annuli. Let slides dry fully. Mount a rectangular cover slip with a drop of slightly alkaline water. Slides are easiest to read while damp.

APPENDIX II. A POPULATION MODEL FOR YUKON WOLVERINE

The concept that counts of births, deaths, dispersals and animals are sufficient to define a population is valid but deceptively simple. A population's birth rate is a function of age at first reproduction, litter size, breeding interval and age-specific differences in natality. Similarly, mortality rates are functions of harvest mortality, natural mortality, and age- and sex-specific differences. Reproductive parameters may be determined from a sample of randomly collected carcasses. Mortality rates are more difficult to estimate. Frequencies of age classes in a harvest are functions of trapper effort and differential trapping vulnerability, as well as abundance of animals, and do not indicate survivorship in the living population. If the proportion of the population that the harvest represents is known and the age distribution of the harvest or a representative sample is available, mortality from trapping can be estimated. However, estimates of natural mortality are difficult to obtain and available for few wild populations. Dispersal is also difficult to measure and emigration is generally assumed to be equal to immigration.

Assuming it is possible to obtain reasonable estimates of natality, mortality and density, population size at any future time can be projected. However, this logic assumes constant birth and death rates, i.e. a stable age distribution. Wild populations are rarely so predictable. The time and funds necessary to estimate the variability of population parameters over time for one species are not luxuries a wildlife manager can afford. Alternatively, insufficient data is not an acceptable excuse for an inability to make decisions regarding harvested and economically important furbearer populations. A solution to this quandry is to enlist the aid of models.

Wolverine (*Gulo gulo*) are important in the fur harvest of Yukon. However, use of isolated wilderness habitat, large home ranges, low densities and a solitary lifestyle have made the study of this species logistically difficult. Research on the biology of wolverine in North America is scant and recent (Hornocker and Hash 1981, Gardner 1985, Magoun 1985). As part of a population study on Yukon wolverine, I determined reproductive parameters (Chap. I), harvest rates (Chap. V),

and I estimated a population size (Chap. VI). However, I was unable to quantify population mortality rates and my estimates of density were self proclaimed best guesses. Lack of information has hampered attempts at predicting the dynamics of wolverine populations and identifying limiting factors. My objective is to develop a population model for Yukon wolverine which integrates known and estimated parameters and has the capability to be enhanced or altered as new information is acquired. This model is preliminary and an initial attempt in modelling populations of wolverine.

Input

Because wolverine are born in late winter and spring and trapped the following winter, ages at capture are 0.5, 1.5, 2.5 years and so on (Chap. I). For purposes of clarity, I present ages as 1 year (0–1 years), 2 years (1–2), 3 years (2–3), etc. Females are sexually mature at 3 years, although a small proportion of 2 year olds reproduce. Age-specific natality, the mean number of fetuses per female, has been estimated using the relationship between number of corpora lutea and fetuses for females having macroscopic embryos (Chap. I). Natality increases with age, ranging from a mean of 2.8 to 3.4 (Fig. I). The proportion of females pregnant within a harvested sample of Yukon wolverine was 73% (Chap. I). However, although females breed yearly they do not necessarily reproduce each year (Magoun 1985). Observations on live wolverine indicated only 33% (Yukon, Chap. IV) to 50% (Montana, Hornocker and Hash 1981) of adult females produce kits yearly. In arctic Alaska, an adult female produced no young in the 3 years she was observed (Magoun 1985). The discrepancy between the low reproductive success observed in the wild and pregnancy rates determined from ovarian structures is attributed to *in utero* losses which are not detectable and constitute resorption of entire litters (Chap. I). Pregnancy rate used in the model is defined as the fraction of females which give birth, and accounts for non-detectable losses. Not all fetuses within litters survive *in utero*. Resorption of 2 of 19 fetuses (10%) was observed for female wolverine with macroscopic litters (Chap. I). The population model incorporates a fraction for an *in utero* loss within litters. Pulliainen (1968) recorded a loss of 1 kit each from 2 litters of 4 (25%) after parturition, in Finland. Magoun

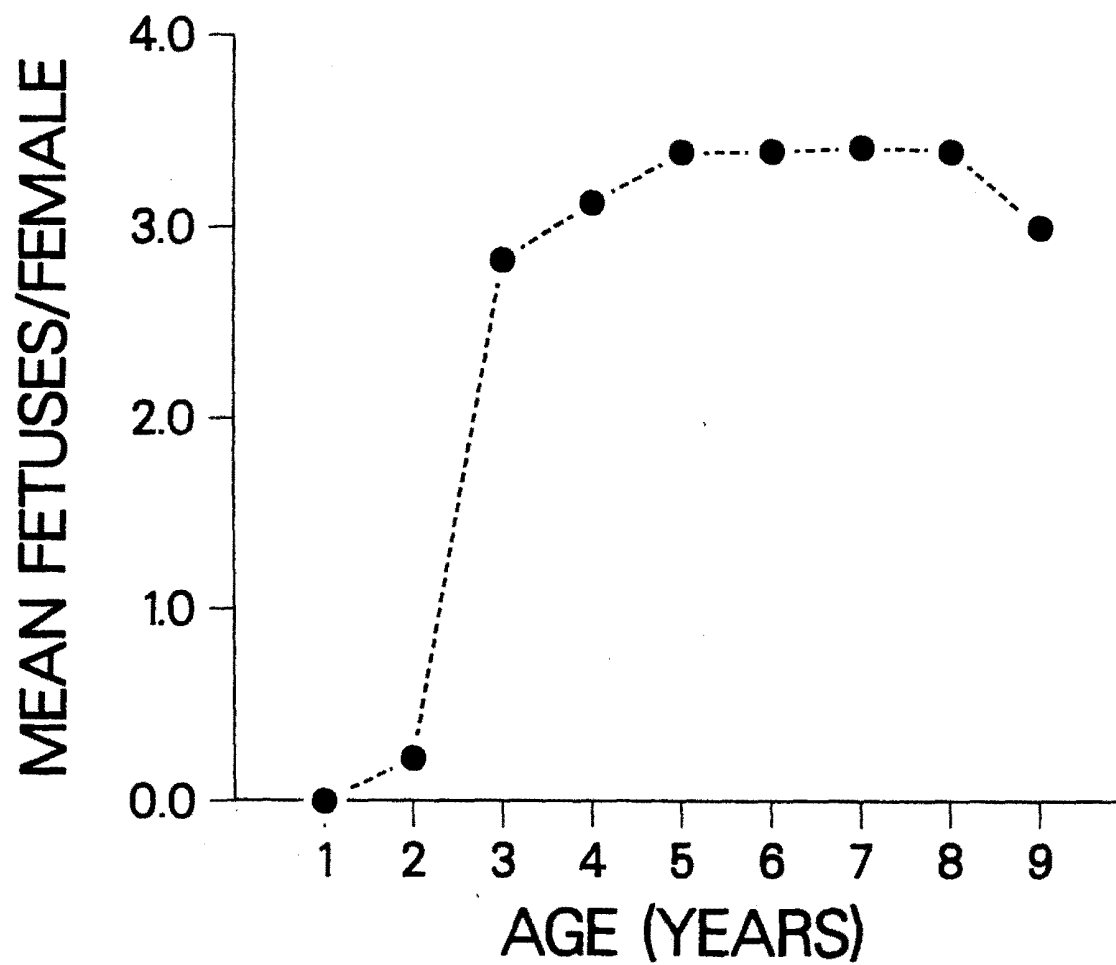


Fig. 1. Estimated age-specific natality for wolverine females in Yukon, 1982-1985 (Chap. 1).

(1985) observed a maximum of 2 kits after den abandonment in arctic Alaska. A fraction for survival of young to weaning is also included in the model.

Trapping rates were determined from a sample of carcasses submitted by Yukon trappers over 3 seasons, 1982/83 to 1984/85 (Chap. V). Sample sizes by sex and age were insufficient for 1984/85 and trapping rates were computed as averages of the first 2 seasons only. The frequency of 3 year old females in the harvest was greater than 2 year old females for both 1982/83 and 1983/84 (Fig. IIa). However, it was unknown if this result was attributable to small sample sizes or represented an increase in vulnerability for 3-year-olds. Thus, an average frequency was computed for these 2 age classes combined (Fig. III). Trapping rates for ages 8-10 were assumed equal. The frequencies were averaged for males up to 6 years in age (Fig. IIb) and assumed constant for older age classes (Fig. III). Sex differences in trapping rates of wolverine occur because of differential vulnerabilities of sex/age classes (Chap. V). However, allocation of trapper effort, a function of weather and economics, influences vulnerabilities. Thus, trapping rates used in the model reflect those conditions in effect during winters of 1982/83 and 1983/84.

Hornocker and Hash (1981) and Chap. IV documented starvation and attacks by wolves as agents of natural mortality in wolverine; the youngest and oldest age classes were the most vulnerable. The magnitude of these mortality factors is unknown. The model can invoke age-specific natural mortality using rates supplied by the user. Harvests of wolverine are typically biased towards males (Chap. V). Sex ratios (male:female) observed in harvests from 1982/83 to 1984/85 ranged from 1.2 to 1.4 (Chap. V). The effect of sex ratio in the harvest on population sex ratio is examined by simulation. I estimated a fall population of 4380 wolverine for Yukon (Chap. IV). Harvests during 1982/83 to 1984/85 represent 6-10% of this estimate. Assumptions and initial values in the model are based on these estimates.

The mathematics of the model are simple. There are ten age classes for each sex. Age-specific natality is applied to the number of females in each age class

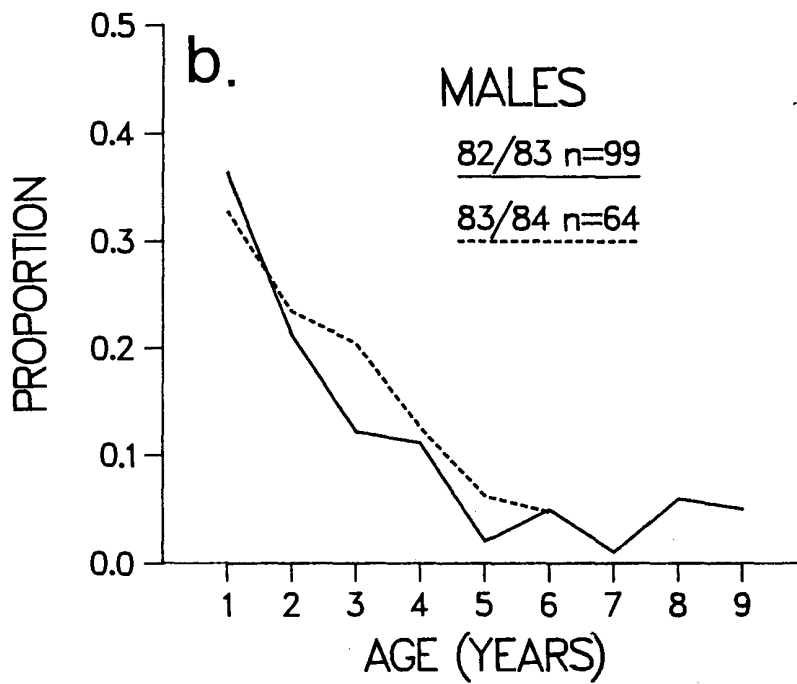
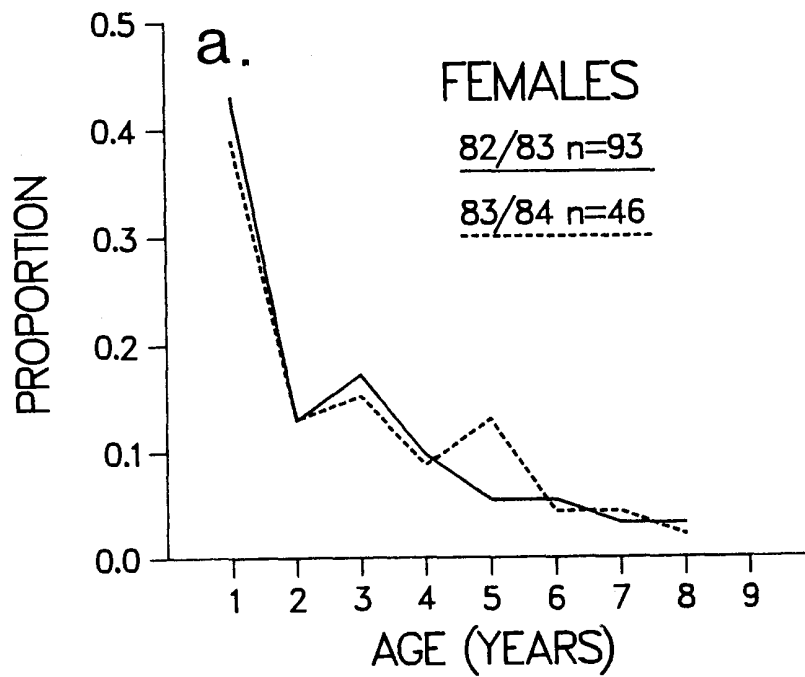


Fig. II. Observed age distributions of Yukon wolverine in harvests during 1982/83 and 1983/84.

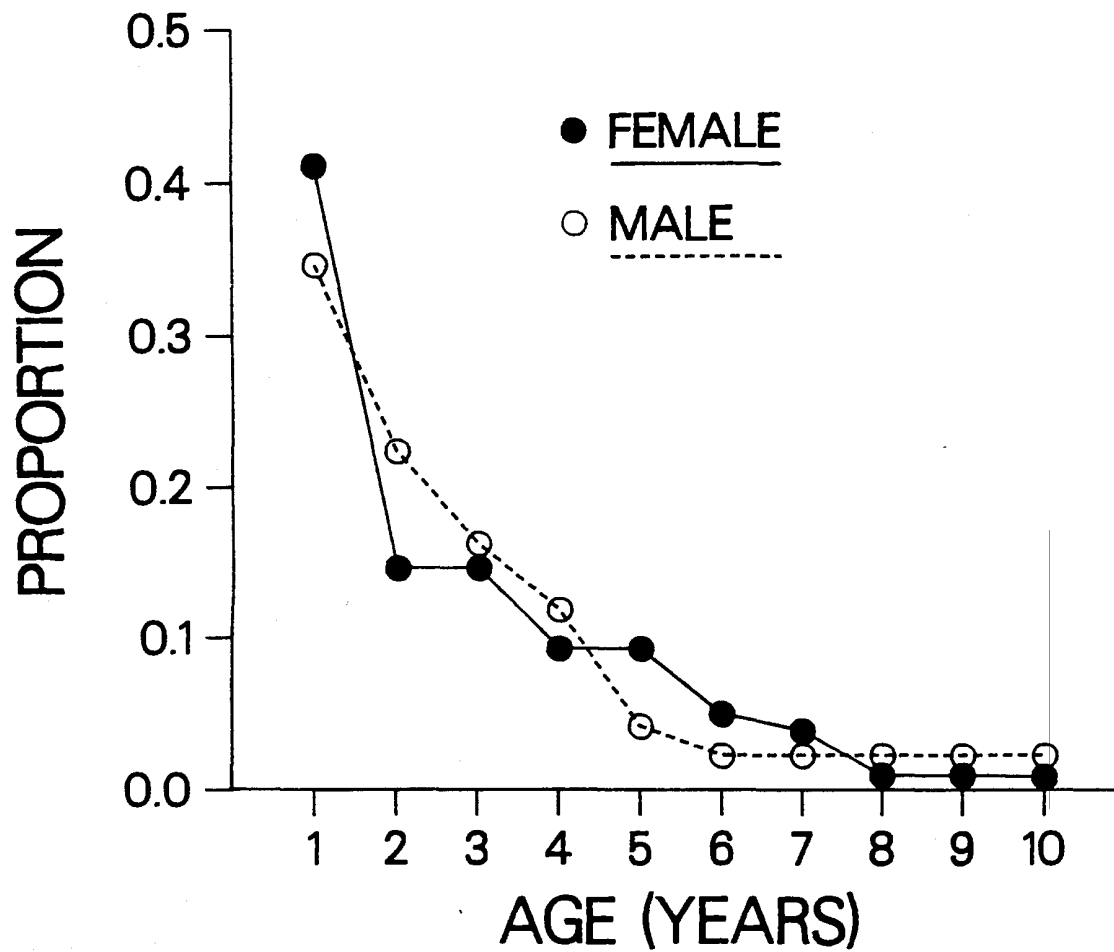


Fig. III. Age and sex composition of Yukon wolverine in harvest used as input to a simulation model.

to generate births. Each age class is aged one year older; newborn wolverine become the first age class and all wolverine in the last age class are assumed to die. A proportion of the population is harvested and a sex ratio is applied. Sex- and age-specific trapping rates are then applied to generate the number of deaths by trapping. Deaths are divided by the number of wolverine in each age class to calculate population harvest rates. Reproductive losses and natural mortality are added at appropriate steps (Fig. IV).

Materials and Methods

Assumptions inherent in the model and not explicitly stated above are:

1.
 - a. Pregnancy rate, if unspecified, is 0.50.
 - b. *In utero* survivorship is 0.90.
 - c. Pre-weaning survivorship is 0.75.
 - d. Sex ratio in the harvest is 1.3 males:females.
2. There is a 1:1 sex ratio at birth.
3. Pregnancy rate is constant for all age classes of females. Reproductive data suggests there are age-specific differences (Chap. I), however these have not been quantified.
4. Natural mortality affects females and males equally. There is no field evidence supporting or refuting this assumption.

The population model is written in FORTRAN (Appendix II) and runs on the simulation package SIMCON. Three birth rates were calculated and are defined:

1. At conception: births per reproductive female after applying age-specific natality. The number of reproductive females is obtained by multiplying all females by the fraction that are pregnant and thus also includes 1 and 2 year olds.
2. At weaning: the birth rate after subtracting *in utero* and preweaning losses from births.
3. Population birth rate: net births divided by the sum of all females in the population.

1. START
2. PUT INITIAL POPULATION SIZE INTO A STORE VARIABLE (OLD).
3. CALCULATE FRACTION OF ADULT FEMALES THAT ARE REPRODUCTIVE
4. MULTIPLY FEMALES IN EACH AGE CLASS BY FRACTION PREGNANT. THIS IS THE AGE-SPECIFIC DISTRIBUTION OF REPRODUCTIVE FEMALES.
5. MULTIPLY REPRODUCTIVE FEMALES BY AGE-SPECIFIC NATALITY. SUM UP THE NUMBER OF OFFSPRING PRODUCED BY EACH AGE CLASS (BIRTHS).
6. CALCULATE BIRTH RATE AT CONCEPTION: SUM OF BIRTHS/SUM OF REPRODUCTIVE FEMALES.
7. CALCULATE FRACTION SURVIVING IN-UTERO.
8. CALCULATE FRACTION SURVIVING TO WEANING.
9. MULTIPLY BIRTHS BY IN UTERO AND PRE-WEANING SURVIVAL.
10. CALCULATE BIRTH RATE AT WEANING: BIRTHS/SUM OF REPRODUCTIVE FEMALES.
11. SUM UP ALL FEMALES.
12. CALCULATE POPULATION BIRTH RATE: BIRTHS/SUM OF ALL FEMALES.
13. ASSUME 1:1 SEX RATIO (MALE:FEMALE) AT BIRTH. AGE WOLVERINE ONE YEAR OLDER. BIRTHS BECOME THE FIRST AGE CLASS, ALL OF THE LAST AGE CLASS DIES.
14. SUM UP: A.) FEMALES. B.) MALES. C.) POPULATION AFTER BIRTHS AND BEFORE MORTALITY (POP).
15. CALCULATE WHAT PROPORTION OF THE POPULATION WILL BE HARVESTED.
16. MULTIPLY THE POPULATION BY THIS PROPORTION TO DETERMINE NUMBER OF WOLVERINE IN HARVEST.
17. CALCULATE THE SEX RATIO WITHIN THE HARVEST.
18. APPLY SEX RATIO AND CALCULATE NUMBERS OF FEMALES AND MALES WITHIN HARVEST.
19. CALCULATE AGE-SPECIFIC MORTALITY RATE DUE TO TRAPPING FOR EACH SEX:
 - a. MULTIPLY EACH SEX IN HARVEST BY RESPECTIVE TRAPPING RATE (TRAPPING RATES SUM TO 1.0) TO PRODUCE AGE-SPECIFIC DISTRIBUTION OF NUMBERS HARVESTED.
 - b. MORTALITY DUE TO TRAPPING IS EQUAL TO AGE SPECIFIC HARVEST DIVIDED BY NUMBERS IN EACH AGE CLASS.
20. CALCULATE NET RATE OF POPULATION MORTALITY: (TRAPPING) + (NATURAL) - (TRAPPING X NATURAL).
21. APPLY POPULATION MORTALITY RATES TO AGE DISTRIBUTIONS OF EACH SEX. SUM UP NUMBER OF DEAD WOLVERINE BY SEX.
22. SUM UP: A.) FEMALES. B.) MALES. C.) TOTAL.
23. IF NO FEMALES ARE PRESENT IN THE POPULATION, THEN NO MALES AND VICE-VERSA.
24. AGGREGATE AGE CLASSES 3 YEARS AND OLDER. THIS REPRESENTS THE ADULT SEGMENT OF THE POPULATION. THE FIRST AGE CLASS ARE YOUNG OF YEAR AND THE SECOND, SUBADULT.
25. CALCULATE POPULATION DESCRIPTORS:
 - a. SEX RATIO IN POPULATION (MALE:FEMALE).
 - b. CHANGE IN POPULATION PER INDIVIDUAL (OLD/TOT).
 - c. % MORTALITY PER YEAR: (TOTAL DEAD/POPULATION AFTER BIRTHS) X 100.
 - d. PROPORTIONAL AGE DISTRIBUTIONS FOR EACH SEX.
 - e. PROPORTIONS OF AGE CLASSES BY SEX: YOUNG OF YEAR, SUBADULT, ADULT.
26. INCREMENT BY ONE YEAR.
27. RETURN TO START.

Fig. IV. Flow chart of a model designed to simulate the yearly growth of Yukon wolverine populations.

APPENDIX III. WOLVERINE AGE STRUCTURE MODEL

This is the FORTRAN source listing (GULO.S) of a population model designed for a simulation package (SIMCON). Variables are initialized in the data file (GULO.D). All variables are declared in the common file (GULO.C).

```

      SUBROUTINE UMODEL(ITIME)
C
C      WOLVERINE AGE STRUCTURE MODEL
C
C      OLD      = STORE VARIABLE FOR POPULATION SIZE (OLD=TOT)
C      TOT      = TOTAL POP SIZE
C      FEM(I)   = NUMBER OF FEMALES PER AGE CLASS
C      ZMAL(I)  = NUMBER OF MALES PER AGE CLASS
C
C      REPO(I)  = PREGNANT FEMALES PER AGE CLASS
C      OFF(I)   = YOUNG PRODUCED BY FEMALES WITHIN AN AGE CLASS
C      PREG     = PROP. OF REPRODUCTIVE FEMALES PREGNANT PER YEAR
C      BRATE(I) = BIRTH RATE PER FEMALE
C      BRTHS    = TOTAL NUMBER OF OFFSPRING BORN
C      PWSURV   = PRE-WEANING SURVIVAL
C      USURV    = IN UTERO SURVIVAL
C      BRCONC   = BIRTH RATE OF REPRODUCTIVE FEMALES AT
C                CONCEPTION
C      BRWEAN   = BIRTH RATE OF REPRODUCTIVE FEMALES AT
C                WEANING
C      BR       = POPULATION BIRTH RATE (FOR ALL FEMALES)
C                CALCULATED AFTER LOSSES
C
C      POP      = POPULATION SIZE AFTER BIRTHS & BEFORE MORTALITY
C      SUMF     = TOTAL FEMALES IN POP
C      SUMM     = TOTAL MALES IN POP
C
C      XP       = PROPORTION OF POPULATION HARVESTED
C      HARV     = NUMBER OF WOLVERINE HARVESTED
C      TFEM     = FEMALES IN HARVEST
C      TMAL     = MALES IN HARVEST
C      SR       = SEX RATIO IN HARVEST(M:F)
C      DTRPF(I) = HARVEST RATE PER FEMALE PER AGE CLASS
C      DTRPM(I) = HARVEST RATE PER MALE PER AGE CLASS
C      DEADF(I) = FEMALES IN HARVEST PER AGE CLASS
C      DEADM(I) = MALES IN HARVEST PER AGE CLASS
C      DF(I)    = POPULATION TRAPPING MORTALITY RATE (FEMALES)
C      DM(I)    = POPULATION TRAPPING MORTALITY RATE (MALES)
C      DNATF(I) = NATURAL MORTALITY RATE (FEMALES)
C      DNATM(I) = NATURAL MORTALITY RATE (MALES)
C      DPOPF(I) = POPULATION MORTALITY RATE (FEMALES)
C      DPOPM(I) = POPULATION MORTALITY RATE (MALES)
C
C      TOTSR    = SEX RATIO IN POPULATION (M:F)
C      DPOP     = RATE OF POP INCREASE (ORIG POP/NEW POP)
C      CLASSF(I)= PROPORTIONS OF FEMALE AGE CLASSES
C      CLASSM(I)= PROPORTIONS OF MALE AGE CLASSES
C      PROPF(I) = AGE DISTRIBUTION (FEMALES)
C      PROPM(I) = AGE DISTRIBUTION (MALES)
C
C      OLD=TOT
C      CALCULATE FRACTION OF ADULT FEMALES THAT ARE REPRODUCTIVE
C
C      DO 10 I=1,10
C          OLDF(I)=FEM(I)
C          REPO(I)=PREG*FEM(I)
C          IF(REPO(I).LT.1.0)REPO(I)=0.0
10      CONTINUE
C
C      CALCULATE OFFSPRING
C          BRTHS=0.0
C          TREPO=0.0

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      DO 15 I=1,10
        OFF(I)=BRATE(I)*REPO(I)
        BRTHS=BRTHS+OFF(I)
        TREPO=TREPO+REPO(I)
15    CONTINUE
C
C    BIRTH RATE OF REPRODUCTIVE FEMALES AT CONCEPTION:
      IF(TREPO.LE.1.0)TREPO=1.0
      BRCONC=BRTHS/TREPO
C
C    APPLY IN-UTERO AND PRE-WEANING SURVIVAL
      BRTHS=BRTHS*USURV*PWSURV
C
C    BIRTH RATE OF REPRODUCTIVE FEMALES AT WEANING:
      BRWEAN=BRTHS/TREPO
C
C    POPULATION BIRTH RATE: FOR ALL FEMALES
      I=1
      SUMF=0.0
2    SUMF=SUMF+FEM(I)
      I=I+1
      IF(I.LE.10)GOTO 2
      IF(SUMF.LE.1.0)SUMF=1.0
      BR=BRTHS/SUMF
      IF(SUMF.LE.1.0)BR=0.0
C
C    AGE WOLVERINE ONE YEAR OLDER ASSUMING 1:1 SEX RATIO AT BIRTH
C    FEMALES:
      DO 20 I=1,9
        J=11-I
        FEM(J)=FEM(J-1)
20    CONTINUE
      FEM(1)=BRTHS/2
C
C    MALES:
      DO 25 I=1,9
        J=11-I
        ZMAL(J)=ZMAL(J-1)
25    CONTINUE
      ZMAL(1)=BRTHS/2
C
C    SUM UP
C    POP=POPULATION SIZE AFTER BIRTHS AND BEFORE MORTALITY
      I=1
      SUMF=0.0
      SUMM=0.0
      POP=0.0
30    SUMF=SUMF+FEM(I)
      SUMM=SUMM+ZMAL(I)
      I=I+1
      IF(I.LE.10)GOTO 30
      IF(SUMF.LE.1.0)SUMF=0.0
      IF(SUMM.LE.1.0)SUMM=0.0
      POP=SUMM+SUMF
C
C    CALCULATE HARVEST:
C
      IF(POP.LE.1.0)POP=0.0
      HARV=XP*POP
C
C    APPLY HARVEST SEX RATIO (MALE:FEMALE)
C
      TFEM=HARV/(SR+1)

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      TMAL=HARV-TFEM
      IF(TFEM.LE.1.0)TFEM=0.0
      IF(TMAL.LE.1.0)TMAL=0.0
C
C   DTRPF(I) AND DTRPM(I) ARE AGE DISTRIBUTIONS OBSERVED
C   IN THE HARVEST, FOR FEMALES AND MALES RESPECTIVELY.
C   EACH HARVEST DISTRIBUTION SUMS TO 1.0.
C   CALCULATE MORTALITY RATE DUE TO TRAPPING:
C   FEMALES:DF(I)  MALES:DM(I)
C
      DO 35 I=1,10
        HARVF(I)=(TFEM*DTRPF(I))
        IF(FEM(I).LE.0.0)FEM(I)=1.0
        IF(HARVF(I).GT.FEM(I))HARVF(I)=FEM(I)
        DF(I)=HARVF(I)/FEM(I)
        HARVM(I)=(TMAL*DTRPM(I))
        IF(ZMAL(I).LE.0.0)ZMAL(I)=1.0
        IF(HARVM(I).GT.ZMAL(I))HARVM(I)=ZMAL(I)
        DM(I)=HARVM(I)/ZMAL(I)
35    CONTINUE
C
C   CALCULATE NET RATE OF TRAPPING AND NATURAL MORTALITY
C   (POPULATION MORTALITY RATES)
C   FEMALES:DPOPF(I)  MALES:DPOPM(I)
      DO 40 I=1,10
        DPOPF(I)=DF(I)+DNATF(I)-(DF(I)*DNATF(I))
        DPOPM(I)=DM(I)+DNATM(I)-(DM(I)*DNATM(I))
40    CONTINUE
C
C   APPLY POPULATION MORTALITY RATES
      DEDF=0.0
      DEDM=0.0
      DEAD=0.0
      DO 45 I=1,10
        DEADF(I)=FEM(I)*DPOPF(I)
        FEM(I)=FEM(I)-DEADF(I)
        IF(FEM(I).LE.1.0)FEM(I)=0.0
        DEDF=DEDF+DEADF(I)
        DEADM(I)=ZMAL(I)*DPOPM(I)
        ZMAL(I)=ZMAL(I)-DEADM(I)
        IF(ZMAL(I).LE.1.0)ZMAL(I)=0.0
        DEDM=DEDM+DEADM(I)
45    CONTINUE
      DEAD=DEDF+DEDM
C
C   SUM UP
      SUMF=0.0
      SUMM=0.0
      TOT=0.0
      I=1
50    IF(FEM(I).LE.1.0)FEM(I)=0.0
      IF(ZMAL(I).LE.1.0)ZMAL(I)=0.0
      SUMF=SUMF+FEM(I)
      SUMM=SUMM+ZMAL(I)
      I=I+1
      IF(I.LE.10)GOTO 50
C
C   IF NO FEMALES - NO MALES & VICE VERSA:
C
      I=1
51    IF(SUMM.LE.1.0)FEM(I)=0.0
      IF(SUMF.LE.1.0)ZMAL(I)=0.0
      I=I+1

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        IF(I.LE.10)GOTO 51
        IF(SUMM.LE.1.0)SUMF=0.0
        IF(SUMF.LE.1.0)SUMM=0.0
        IF(SUMF.LE.1.0)SUMF=0.0
        IF(SUMM.LE.1.0)SUMM=0.0
        TOT=SUMM+SUMF
C
C  AGGREGATE AGE CLASSES INTO 3 GROUPS:
C  YOUNG OF YEAR, SUBADULT, ADULT
        I=1
55    AGFEM(I)=FEM(I)
        AGMAL(I)=ZMAL(I)
        I=I+1
        IF(I.LE.2)GOTO 55
        AGF=0.0
        AGM=0.0
        I=3
56    AGF=AGF+FEM(I)
        AGM=AGM+ZMAL(I)
        I=I+1
        IF(I.LE.10)GOTO 56
        IF(AGF.LE.1.0)AGF=0.0
        IF(AGM.LE.1.0)AGM=0.0
        AGFEM(3)=AGF
        AGMAL(3)=AGM
C
C  CALCULATE OVERALL DESCRIPTORS:
C  A.  POPULATION SEX RATIO (MALE:FEMALE)
        IF(SUMF.LE.1.0)SUMF=1.0
        IF(SUMM.LE.1.0)SUMM=0.0
        TOTSR=SUMM/SUMF
C
C  B.  CHANGE IN POPULATION PER INDIVIDUAL
        IF(TOT.LT.1.0)TOT=1.0
        DPOP=OLD/TOT
C
C  C.  PERCENT MORTALITY PER YEAR
        IF(POP.LT.1.0)POP=1.0
        PMORT=(DEAD/POP)*100
C
C  D.  PROPORTIONAL AGE DISTRIBUTION
        IF(SUMM.LE.0.0)SUMM=1.0
        DO 60 I=1,10
            PROPF(I)=FEM(I)/SUMF
            PROPM(I)=ZMAL(I)/SUMM
60    CONTINUE
C
C  E.  PROPORTIONS FOR 3 AGE CLASSES
        DO 65 I=1,3
            CLASSF(I)=AGFEM(I)/SUMF
            CLASSM(I)=AGMAL(I)/SUMM
65    CONTINUE
C
        IF(SUMM.LE.1.0)SUMM=0.0
        IF(SUMF.LE.1.0)SUMF=0.0
        IF(TOT.LE.1.0)TOT=0.0
        RETURN
        END

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