

BIOLOGY OF THE WOLVERINE IN CENTRAL IDAHO

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Wildlife Resources

in the

College of Graduate Studies

University of Idaho

by

Jeffrey P. Copeland

May 1996

Major Professor: James M. Peek, Ph.D.

THE UNIVERSITY OF CHICAGO PRESS

1997

THE UNIVERSITY OF CHICAGO PRESS

THE UNIVERSITY OF CHICAGO PRESS

1997

THE UNIVERSITY OF CHICAGO PRESS

1997

THE UNIVERSITY OF CHICAGO PRESS

THE UNIVERSITY OF CHICAGO PRESS

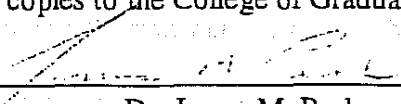
THE UNIVERSITY OF CHICAGO PRESS

1997

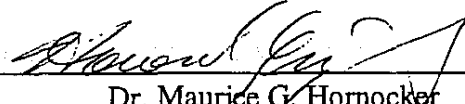
THE UNIVERSITY OF CHICAGO PRESS

AUTHORIZATION TO SUBMIT THESIS

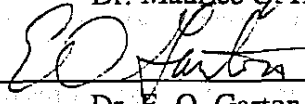
This thesis of Jeffrey P. Copeland, submitted for the degree of Master of Science with a major in Wildlife Resources and titled "Biology of the wolverine in central Idaho", has been reviewed in final form, as indicated by the signatures and dates given below. Permission is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor  Date 10 May '96

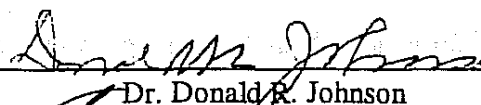
Dr. James M. Peek

Committee Members  Date 10 May '96

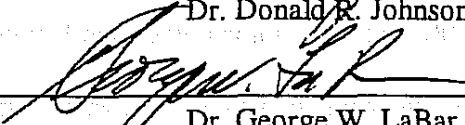
Dr. Maurice G. Hornocker

 Date 10 May 1996

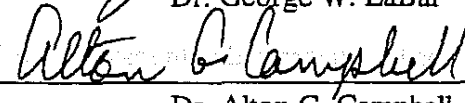
Dr. E. O. Garton

 Date 10 May '96

Dr. Donald R. Johnson

Department Administrator  Date 5/16/96

Dr. George W. LaBar

Discipline's College Dean  Date 5/16/96

Dr. Alton G. Campbell

Final Approval and Acceptance by the College of Graduate Studies

Date _____

Jean'ne M. Schreeve

ABSTRACT

I determined wolverine (*Gulo gulo*) presence, ecology, spatial characteristics, movement, demographics, social structure, and habitat use in central Idaho from 1992-1995. My study area encompassed approximately 8,000 km² of primarily roadless and statutory wilderness habitats. The study area was characterized by montane coniferous forests at lower elevations, to high elevation subalpine habitats associated with talus scree and non-forested mountain tops. Nineteen wolverines were captured and instrumented with intraperitoneal implant transmitters. I monitored wolverines weekly, by ground and aerial telemetry, collecting 1,050 relocations. Annual home ranges of resident adults averaged 384 km² for females and 1,582 km² for males. Adult home ranges were segregated by sex, with female home ranges overlapping < 10% and male home ranges overlapping < 15%. Offspring of both sexes remained associated with the natal area for up to 2 years corresponding with sexual maturation. Juveniles and subadults interacted with resident kin, including their mother, the resident male, and siblings. Evidence of resident adult wolverine associating with subadult wolverine was previously undescribed. Periods of association lasted as long as 7 days with individuals traveling together or localizing at foraging sites. The extended association of subadults and adults may be related to the highly dispersed nature of food resources and may account for large home range sizes of resident females. Adult male home ranges encompassed up to 3 female home ranges. Snow-tracking sessions were conducted to document scent-marking and foraging behavior. Food resources were widely dispersed but consistent in timing and presence which may produce traditional foraging routes. Such sites were revisited within a season of use and between years and were shared within kinship groups. Urination

was the primary method of scent-marking observed during this study. The reproductive rate for 4 adult females was less than 1 kit/female/year. Females used secluded high elevation cirque basins for natal den sites. Human disturbance at maternal dens resulted in den abandonment but not kit abandonment. Kits remained with the adult female for approximately 3 months subsequent to weaning at 9 to 10 weeks of age. Females commonly left dependent kits at rendezvous sites comprised of large boulder talus or riparian areas associated with mature overstory and dense timber deadfall. Boulder talus associated with subalpine habitats was also used for resting and foraging sites. Four male wolverines dispersed at sexual maturity, with 2 emigrating distances greater than 185 km. Two of these individuals appeared to establish at the new location while the other 2 returned to the study area. Seven wolverines died during the study, with predation accounting for 43% of the mortality. Distinct seasonal shifts in elevational use were recorded, with higher elevational talus/rock cover types preferred during summer months, and montane coniferous forest cover types preferred during winter. Wolverines avoided lowland grass/shrub and ponderosa pine (*Pinus ponderosa*) cover types. Movement to lower elevations during winter months may be correlated with increased presence of carrion attributable to the fall big game hunting seasons. Ungulate species including mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), and domestic cow (*Bos bos*) and horse (*Equus* sp.) were present at similar proportions in both summer and winter scat and foraging site collections. Other prey items included 5 species of carnivores; 12 rodent species, including 5 sciurids; and 1 lagomorph species. Avian species constituted 4.9% of species occurrences while insects, primarily ants, occurred at 5.9%.

ACKNOWLEDGEMENTS

Funding was provided by the Sawtooth and Challis National Forests, the Idaho Department of Fish and Game (IDFG), and the U.S. Fish and Wildlife Service; grants from the Devlieg Foundation, and the National Fish and Wildlife Foundation; and private funding from Water and Wastewater Equipment Company, United Water Corporation, Michelle and Troy Baker, Clint and Judy Long, and Phillip Moore. I am grateful for the support of the Idaho Conservation League and thank the Hornocker Wildlife Research Institute for their support and guidance. The efforts of many were critical in the initiation of this research including the folks that wrote letters of concern for the wolverine's status in Idaho, and former Congressman Richard Stallings who secured appropriation of the first year's funding. Most important were the tireless efforts of Craig Groves and Wayne Melquist, without which the project would never have reached reality. I am also grateful to my supervisor, Chuck Harris, for allowing me the freedom to stretch the limits and take some chances. I am most grateful to Tom Reinecker, Chief of Wildlife, IDFG, and my major professor Dr. James Peek. They were most responsible for giving me this opportunity and I will be forever grateful. I wish to extend my deepest respect and gratitude to my graduate committee: Dr. Oz Garton, Dr. Maurice Hornocker, and Dr. Donald Johnson for their helpful discussions, inspiration, and friendship over the past 20 years. Many U.S. Forest Service folks provided critical support, equipment, and field assistance. Special thanks to Mike Rath, Bill Ruediger, Howard Hudak, Robin Garwood, Dave Reeder, and Todd Williams. Above all I want to thank my wife Cheryl and daughters Jodi and Maggie for their love and support, and willingness to turn their lives

upside down so I could fulfill a dream; mom and Bob for always being there to help us hold it together; and all of our friends who helped us along the way.

Many folks participated in the field work with tremendous dedication, effort, and sacrifice. I am most grateful to the heart of the field crew, Wildlife Technicians Sparky Easom and Beth Bratlie for caring enough about *Gulo* to put up with me, and always giving one-hundred percent, along with Rusty Anderson who single-handedly ran the Boise River traps, Alice Whitelaw for spending the summer swinging a hammer, and Mary Terra-Berns for keeping me in line and volunteering so much effort in field work and hair analysis. The project would have been so much less without the participation of Clint and Judy Long. Their totally selfless appreciation and love of *Gulo* profoundly affected us all. Our success in capturing wolverines was largely due to Ed Cesar's trap design and his continuing support and advise on trapping technique. The Idaho Department of Fish and Game Wildlife Health Lab was crucial in the success of the project. Special thanks to Wildlife Veterinarian David Hunter for always being there when we needed him, Sharon Landin for the hair analysis, and Jules, Mary Ann, and Terry for always jumping to our needs. Help was always there when we needed it from the local IDFG Conservation Officers and Regional Biologists. Special thanks to Gary Gadwa for all those miles on snowmachine and to Laurii Gadwa for making me feel at home. Thanks to all the Region 7 and Region 4 folks for their willingness to help on a minute's notice, providing snowmachines, and keeping the freezer full of meat; to the Sawtooth Hatchery for opening the facility to all our needs, and for providing field help, housing, and especially Jim Nixon to repair our accidents; and the Hayspur Hatchery for pickup loads of fish morts. Much of the data collection was dependent on the skill of airplane drivers. Thanks to all my friends at Western Air Research. You will be missed by many.

Thanks to Stanley Air Taxi, Bob's Aircraft, and all the folks at Idaho Helicopter. A special thanks to the community of Stanley for your support and interest in the study.

I also wish to thank Stewart Lincoln and the staff at Cain Veterinarian School for processing tissue samples, and a special thanks to Dr. Rodney Mead for his patient guidance through reproductive physiology and gland histology, and the many hours he volunteered in analysis of reproductive tracts, tissue samples, and blood serum. Thanks to Glenn Haas and J. Ralph Lichtenfels for identifying parasites. I am especially grateful to Roly Redmond, Melissa Hart, and Troy Tady at the Montana Spatial Analysis Lab for their extra effort in processing my habitat data. Special thanks to Fred Leban and his programming skills. The special *kinship support* of my fellow graduate students at the U of I will never be forgotten.

I also wish to thank Howard Quigley, Ted Chu, Chuck Harris, Mary Terra Berns, and Clint Long for their review and edit of the final draft.

DEDICATION

Lord, let me die but not die out.

*James Dickey
For The Last Wolverine
Poems 1957-1967*

In dedication to the memory of Fred Reed, President and co-founder of Western Air Research, who died 23 October 1995 in an airplane crash near his home in Alta Wyoming.
The wildlife profession lost a colleague; I lost a friend.

TABLE OF CONTENTS

AUTHORIZATION TO SUBMIT THESIS	ii
ABSTRACT	iii
ACKNOWLEDGEMENTS	v
DEDICATION	viii
TABLE OF CONTENTS	ix
LIST OF TABLES	xi
LIST OF FIGURES	xiii
INTRODUCTION	1
STUDY AREA	7
METHODS	9
Wolverine Capture and Instrumentation	9
Morphology	11
Monitoring	11
Home Range and Movement	12
Denning Activity	13
Food Habits and Scent-marking	13
Habitat Analysis	14
RESULTS AND DISCUSSION	16
I. CHARACTERISTICS OF THE STUDY POPULATION	16
Capture and Study Animals	16
Age and Sex Ratios	18
Morphology	19
Chemical Communication	22
Parasites	26
Spatial and Temporal Structure of the Study Population	27
Residency	31
Density	31
Reproduction	33
Mortality	44

II. HOME RANGE	49
RESULTS	49
Female Home Range Size	49
Male Home Range Size	52
Home Range Overlap	55
DISCUSSION	68
Home Range Size	68
Seasonal Shifts in Distribution	73
Home Range Overlap and Spatial Strategy	74
III. MOVEMENTS AND DISPERSAL	77
RESULTS	77
Movements	77
Dispersal	80
DISCUSSION	80
Movements	80
Dispersal	87
IV. BEHAVIOR AND SOCIAL ORGANIZATION	92
Denning	92
Natal Dens	94
Maternal Dens	95
Rendezvous sites	97
Resting sites	99
Related activities	99
Food Habits	100
Foraging behavior	105
Social Organization	107
Scentmarking	115
Behavior	118
V. HABITAT USE	120
RESULTS	120
DISCUSSION	124
VI. SUMMARY AND MANAGEMENT RECOMMENDATIONS	128
VII. LITERATURE CITED	131

LIST OF TABLES

Table 1.1. Capture dates, trap location, and age at capture of wolverines in central Idaho 1992-1995.	17
Table 1.2. Physical characteristics of wolverines captured in central Idaho, 1992-1995. ...	20
Table 1.3. Reproductive history for female wolverines in central Idaho, 1992-1995.	36
Table 2.1. Total and annual home range by kernel, minimum convex polygon (MCP), and harmonic mean (HM) core estimates for wolverines in central Idaho, 1992-1995. ...	50
Table 2.2. Home range estimates of female wolverines with kits, and solitary female wolverines for the period - March through August, in central Idaho, 1992-1995.	51
Table 2.3. Seasonal home ranges of female wolverines by kernel, minimum convex polygon (MCP), and harmonic mean (HM) core estimates in central Idaho, 1992-1995.	53
Table 2.4. Seasonal home ranges of male wolverines by kernel, minimum convex polygon (MCP), and harmonic mean (HM) core estimates in central Idaho, 1992-1995.	54
Table 2.5. Home range overlap of wolverine pairs in central Idaho, 1992-1995.	57
Table 2.6. Seasonal home range overlap and elevational use of wolverines in central Idaho, 1992-1995.	69
Table 3.1. Seasonal daily movements (meters) of wolverines in central Idaho, 1992-1995.	79
Table 3.2. Monthly mean daily movements of adult wolverines in central Idaho, 1992-1995.	84
Table 3.3. Movements that occurred outside of home ranges for wolverines in central Idaho 1992-1995. Distances are approximate measures from point of relocation to nearest boundary of 90% kernel home range.	88
Table 4.1. Species and item incidence within scat and foraging site collections for wolverine in central Idaho, 1992-1995	101
Table 4.2. Age and sex stratification of association for wolverines in central Idaho, 1993-1995.	109
Table 4.3. Association data for wolverines in central Idaho, 1993-1995.	110

Table 5.1. Cover type classification and pooling for habitats in central Idaho wolverine project study area, 1995.	121
Table 5.2. Percentage cover type composition pooled for 13 wolverines within 3 scales of use and availability in central Idaho.	122
Table 5.3. Cover type ranking matrices for wolverines in central Idaho based on comparing proportional habitat use from all relocations to habitat available within merged 99% kernel home range polygon for all wolverines (Level 1); proportional habitat use from all relocations to availability within individual 99% home ranges (Level 2); and proportional habitat use from relocations within core home ranges to availability within individual core home ranges.	123
Table 5.4. Aspect ranking matrices for wolverines in central Idaho based on comparing proportional use of aspect from all relocations to availability of aspects within individual 99% home ranges.	125

LIST OF FIGURES

Fig. 1. Central Idaho wolverine project study area and trap locations, 1992-1995.	8
Fig. 1.1. Temporal distribution of wolverine study population in central Idaho, 1992-1995.	28
Fig. 1.2. Spatial distribution of wolverine study population in 1992 (a), 1993 (b), 1994 (c), and 1995 (d), in relation to the Idaho study area.	29
Fig. 1.3. Reproductive history and status of marked female wolverines in central Idaho, 1992-1995.	37
Fig. 1.4. Relocations and den sites of adult female wolverine F502 from parturition to kit weaning in central Idaho, 1993.	38
Fig. 1.5. Relocations and den sites of adult female wolverine F703 from parturition to kit weaning in central Idaho, 1994-1995.	40
Fig. 2.1. Annual home range fidelity and overlap of adult male wolverine M123 and adult female F703 in central Idaho.	56
Fig. 2.2. Home range distribution and overlap of resident adult male and resident adult female wolverines in the northern portion of the central Idaho study area, 1993.	58
Fig. 2.3. Core home range distribution and overlap of resident adult male and resident adult female wolverines in the northern portion of the central Idaho study area, 1993.	59
Fig. 2.4. Home range distribution and overlap of adult male wolverines in central Idaho, 1992-1995.	60
Fig. 2.5. Home ranges of adult wolverine male M123 and female F703, and subadult wolverine male F803 and female M913 in central Idaho, 1993-1994.	62
Fig. 2.6. Home ranges of adult wolverine male M123 and female F502, and subadult wolverine female F203 in central Idaho 1993-1994.	63
Fig. 2.7. Home ranges of adult wolverine male M123 and female F703, and subadult wolverine female F204 and male M104 in central Idaho, 1994-1994.	64
Fig. 2.8. Combined annual home ranges of adult male wolverine M123, and subadult and adult home ranges of male wolverine M913 in central Idaho.	65

Fig. 2.9. Home ranges of adult male wolverine M403 and subadult male M423 in central Idaho, 1993-1994.	66
Fig. 2.10. Home ranges of adult male wolverines M403 and M333, and subadult male M814 in central Idaho 1993-1995.	67
Fig. 2.11. Monthly mean elevational use with confidence intervals of wolverines in central Idaho, 1992-1995.	70
Fig. 3.1. Histograms of daily movement distances of wolverines in central Idaho, 1992-1995.	78
Fig. 3.2. Dispersal of male wolverines M423 and M003 in central Idaho, 1993-1994.	81
Fig. 3.3. Long distance movements of wolverine M913 in central Idaho, 1994-1995.	82
Fig. 3.4. Long distance movements of wolverine M814 in central Idaho, 1994-1995.	83
Fig. 3.5. Daily movement sequences for 8 wolverines in central Idaho, 1992-1995.	86
Fig. 4.1. Seasonal frequency of occurrence of 4 major prey groups in wolverine scats collected in central Idaho, 1992-1995.	103
Fig. 4.2. Maximum spanning tree of closest associates (Morgon et al. 1974) for wolverines in central Idaho, 1993-1995.	111

INTRODUCTION

Historical records of wolverine presence in Idaho consist of sightings and occasional trap captures. Davis (1939) believed the wolverine was extinct in Idaho by the 1930's. Pengelly (1951) reported 7 records of wolverine from northern Idaho for the period 1930 to 1949. The next verified records were 2 kills, one in northern Idaho in 1953 and one in southern Idaho in 1954 (Groves 1988). Koehler and Hornocker (1979) compiled a list of 25 reported wolverine observations from northern Idaho occurring between 1976 and 1979. Groves (1987) documented 10 confirmed reports and 89 probable reports of Idaho wolverines for the period 1960 to 1987 from a state-wide mail questionnaire survey of natural resource managers and trappers.

The state of Idaho lists the wolverine as a Species of Special Concern (Conservation Data Center 1994). The Forest Service and the Bureau of Land Management (BLM) list the wolverine as a Sensitive Species (Conservation Data Center 1994). In the late 1980s, appellants of the Sawtooth National Forest Management and Travel Plans raised the status of the wolverine as an issue in reference to wilderness designation and forest management of motorized and non-motorized travel. In 1989 and 1990 the Idaho Department of Fish and Game conducted field surveys to determine the distribution, and population status, of wolverines on the Sawtooth National Forest (Groves and Gadwa 1989, Bachman et al. 1990). A federal supplemental appropriation to the Sawtooth National Forest in 1991 provided funding to initiate this study. My primary objectives were to live-trap, radio instrument, and monitor wolverines to determine:

- 1) Population characteristics including morphology, age and sex structure, reproductive rate, survival rate, density, and causes of mortality.
- 2) Population spatial structure including movements and dispersal, and home range size overlap and fidelity.
- 3) Behavior and social organization including denning, foraging and scent-marking, and conspecific social interaction.
- 4) Availability and use of habitat.

The wolverine is an uncommon inhabitant of boreal coniferous forests and arctic tundra.

It's distribution is world-wide within northern latitudes. Canada harvests about 800 wolverines each year yet still considers it one of it's rarest mammals (Hatler 1989). Wolverine presence in the western United States is well-documented however only Montana manages for a limited harvest.

A large home range, low population density, and solitary lifestyle, combined with a wilderness habitation, has made study of the wolverine difficult and infrequent. The majority of literary references to the wolverine are either anecdotal or document incidental

observations. Banci (1982) lists 607 titles, while Hatler (1989) considered only 10 of 180 references in his annotated bibliography provided important management insights.

Early attempts to research wolverines commonly used snowtracking surveys to assess movements, denning habits, and prey selection (Haglund 1966, Pulliainen and Ovaskainen 1975). Pulliainen (1968) and Myrberget (1968) collected data on wolverine breeding biology by snowtracking and through hunter reports. Van Zyll de Jong (1975) determined population trends and distribution through Canadian fur harvest records. Wright and Rausch (1955) described reproductive biology through carcass study.

Biotelemetry enabled researchers to study wolverine ecology on a more comprehensive level. Hornocker and Hash (1981) described a wolverine population in northwest Montana as demographically stable although socially dynamic due to periodic population turnover caused by trapping mortality. Their study was the only prior investigation of wolverines in the contiguous U.S. Gardner (1985) found wolverines in southcentral Alaska more spatially stable than the Montana population, reporting exclusive home range use with only limited trapping exploitation. Magoun (1985) included behavior in her assessment of factors important to management of an arctic Alaska wolverine population dependent on migrating ungulates. Whitman et al. (1986) used logarithmic extrapolations to estimate wolverine home range size in southcentral Alaska, and found variation in seasonal habitat use probably linked to prey abundance. Banci (1987) conducted an extensive analysis of reproductive morphology and food habits from wolverine carcasses and studied wolverine ecology and habitat use in Yukon. To date, the wolverine has only been studied in areas where regulated trapping occurs. Others have focused on wolverine spatial requirements (Hornocker et al. 1983), reproduction (Mead et al. 1991, Mead et al. 1993), and census technique (Becker 1991).

The most common attributes derived from previous field studies of wolverine are large spatial requirements, low population density, and nonspecific habitat requirements; at least in terms of vegetative structure. It is believed that historical reductions in the wolverine's North American distribution are correlated with the westward advancement of human civilization (Banci 1994), but the specific cause of extirpation is not clear. The fossil record suggests the wolverine may have been even more ecologically diverse than today (White et al. 1984). Human presence within historical wolverine range may have regulated population growth and

stability, or simply displaced wolverines through habitat alteration and destruction. Our primary tasks should be to determine the life history requirements of the wolverine and identify what factors regulate populations.

Wolverine densities in 3 of the primary radio-telemetry studies varied from 1 wolverine/48 km² in arctic Alaska (Magoun 1985) to 1/177 km² in Yukon (Banci 1987). Hornocker and Hash (1981) reported a density of 1/65 km² in northwest Montana. Density estimates from the 3 studies relied on trap capture and spatial relationships of study animals. Reliable estimates from such data require an accurate and long-term accounting of residency status, age and sex structure, and familial relationships of study animals (Hornocker and Hash 1981, Magoun 1985).

The wolverine may have larger spatial requirements than energetics alone would predict. Home ranges appear more stable in populations subjected to the least intensive harvest, displaying some level of intrasexually exclusive home ranges (either seasonally or within a sex class) (Gardner 1985, Magoun 1985, Banci 1987) as generally predicted for wolverine (Powell 1979, Sandell 1989). Such a spatial structure likely requires established tenure of individuals. Home ranges of Montana wolverines overlapped between and within sexes possibly due to a consistent harvest removal of individuals (Hornocker and Hash 1981). The relationship between home range size and animal movements predicts resource (either food or mates) availability as a causal effect (Macdonald 1983, Swingland and Greenwood 1984, Sandell 1989). The factors that control spacing and movements in the wolverine are unclear and some inconsistencies with this hypothesis are evident. Magoun (1985) described an arctic Alaska environment of scarce and unpredictable food resources associated with female wolverine home ranges that were less than half the size of Yukon female home ranges that

were supported by a relatively stable and abundant food resource (Banci 1987). This may reflect distributional variation in food availability (arctic wolverines are dependent on migrating ungulates such that home range expansion during times of low availability may only result in energetic loss in pursuit of an unavailable resource), or variation in data collection and analysis. Hornocker et al. (1983) believed that spatial strategies are dependent upon both external (trapping mortality, habitat alteration) and internal (behavior and social organization) influences within a particular population. An analysis of spatial characteristics within a population relatively free of human exploitation may provide a more accurate depiction of a naturally regulated spatial organization (Hornocker et al. 1983).

Patterns of social behavior are diverse and develop in response to adaptive pressures associated with mating (Rubenstein and Wrangham 1986) and foraging (Moehlman 1983). Social behavior is often most evident, and relatively easy to measure, as resource partitioning and spatial structuring that include patterns of behavior associated with mating and the rearing of young. Social organization in the wolverine has received little attention beyond description of spatial structuring. Limited data suggest an early onset of maturity in juvenile wolverines associated with social pressures to disperse and function independent of conspecifics although the factors regulating wolverine social structure have not been addressed beyond speculation. Hornocker and Hash (1981) and Koehler et al. (1980) recognized that strict maintenance of such a large territory would be extremely difficult, and suggested that scent-marking may play a role in the temporal spacing of individuals. To understand the ecological basis of social organization, it is imperative to understand separately the ecological and social pressures operating on each sex (Rubenstein and Wrangham 1986). This requires focusing not just on

mating systems but on understanding social relationships other than those between mated pairs (Rubenstein and Wrangham 1986).

There is a growing body of research on the social relationships of non-mated individuals in primate groups. This research has shown that non-mated individuals can have complex social relationships with other individuals in the group, including forming alliances, engaging in grooming, and participating in social play. These relationships can be important for understanding the social structure and dynamics of primate groups. For example, in some species, non-mated individuals may form alliances that help them to compete for mates or resources. In other species, non-mated individuals may engage in grooming or social play that helps to strengthen social bonds and reduce tension within the group. Understanding these social relationships is important for understanding the overall social structure and dynamics of primate groups.

References

STUDY AREA

The study area involves approximately 8,000 km² of the Sawtooth (SNF), Challis (CNF), and Boise National Forests (BNF) in central Idaho (latitude 44°N, longitude 115°E) (Fig. 1). The climate is generally temperate but extreme low winter temperatures do occur (-41C, December 1990). Mean temperatures range from -8C in January to 15C in July. Mean annual precipitation is 58 cm with 48 cm of snow (R. Garwood, Sawtooth Nat. For., pers. commun.). Elevations range from 1,400-3,279 m.

Vegetative communities in the study area are diverse, with sagebrush-grass associations dominant at lower elevations interspersed with willow-meadow communities on more mesic sites. Dense lodgepole pine (*Pinus contorta*) interspersed with Douglas-fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*) occur at lower elevations. Mid-slope elevations support spruce (*Picea engelmannii*)-fir forests interspersed with savanna grassland mosaics. Subalpine forests associated with talus and cirque basins dominated by whitebark pine (*Pinus albicaulis*) and subalpine fir characterize upper-slopes. Alpine/rock scree habitats associated with talus and open mountain tops above timberline generally occur above 2,700 meters.

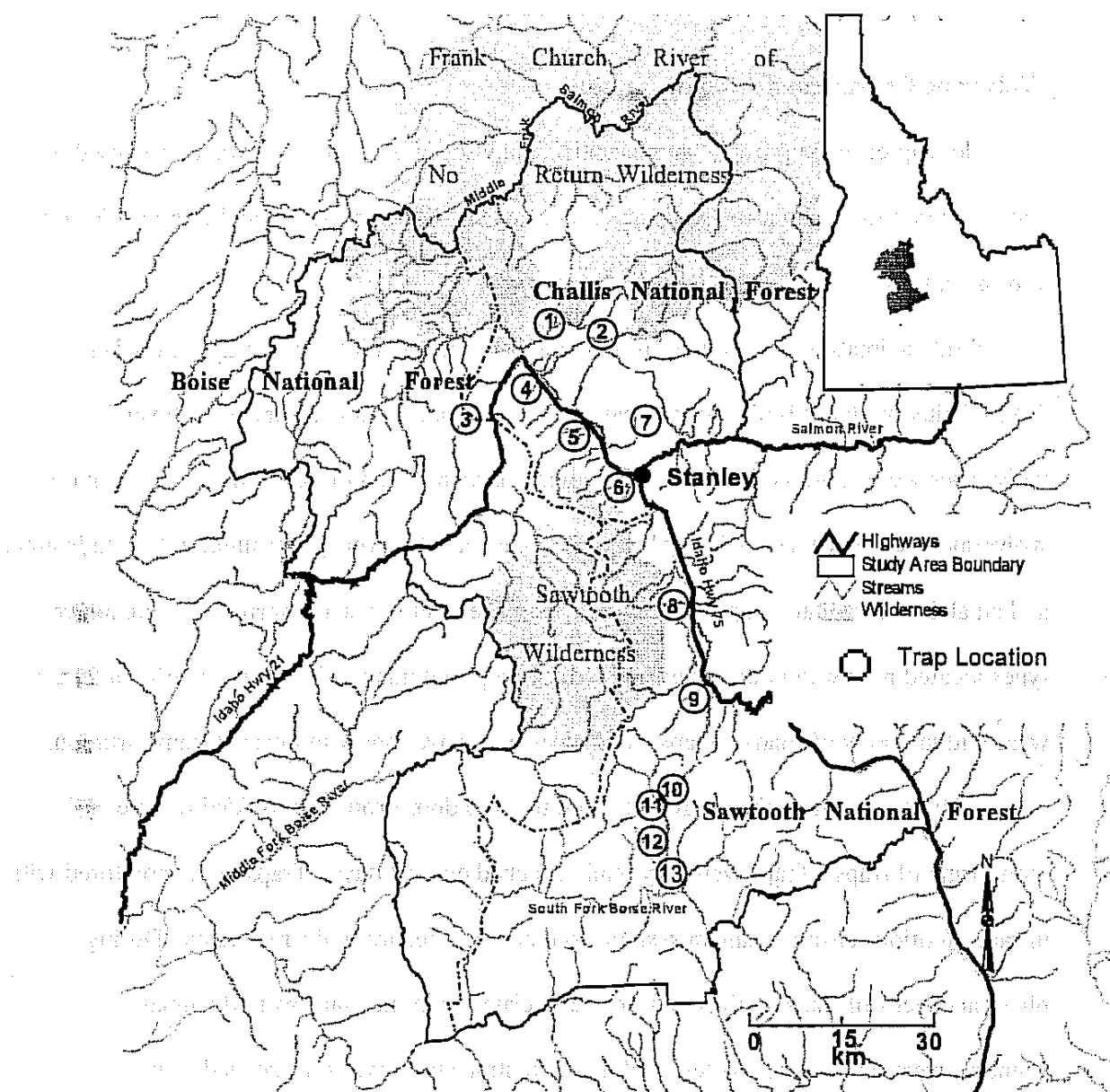


Fig. 1. Central Idaho wolverine project study area and trap locations, 1992-1995. Trap locations: 1 = Shake Creek, 2 = Big Kahuna (Beaver Creek-CNF), 3 = Cape Horn Creek, 4 = Swamp Creek, 5 = Elk Creek, 6 = Iron Creek, 7 = Yankee Fork, 8 = Mays Creek, 9 = Beaver Creek, 10 = Emma Creek, 11 = Bear Creek, 12 = Skunk Creek, 13 = Fleck Creek.

METHODS

Wolverine Capture and Instrumentation

Helicopter, pickup truck, snowmachine, snowshoes, skis, and foot travel was used for transportation throughout the study area. A Maule M-5, Piper PA-14, and Cessna 180 fixed-wing aircraft were used for aerial radio-telemetry.

Study animals were captured using metal barrel traps and log box-traps (Copeland et al. 1995), baited with road-killed deer, beaver carcasses, and dead hatchery fish. Juvenile wolverines were captured by hand. Trap locations were based on previous documentation of wolverine occurrence, accessibility by trapping personnel, coverage throughout the study area, and an ability to monitor trap transmitters. Trap sites were typically spruce/fir community types located near waterways or upland lodgepole pine communities (Fig. 1). All but 2 traps were within 100 m of roads. Traps were accessed by over-snow motorized transportation.

Radio-transmitters that activated when the trap door dropped provided remote monitoring of traps. Traps were physically checked every 4 days. Traps were monitored with infrared-motion sensitive camera systems to detect and record wolverine visits. During physical checks of traps, wolverine tracks associated with trap sites were documented.

Cameras were checked for battery and film condition and serviced as needed. I used

Ektachrome 36 exposure EPR 64 color slide film and 36 exposure TX 400 black and white print film.

Captured animals were immobilized using a ketamine/xylazine combination at 100 mg Ketamine with 20 mg Xylazine per 10 pounds (4.54 kg) administered by a syringe attached to a fiberglass pole 2-m in length and 5-mm in diameter (jab stick). Ophthalmic ointment was

placed into the eyes and the animal's head was covered. Study animals were instrumented with transmitter collars and/or intraperitoneal implant transmitters (150-154 mhz. Telonics, Mesa, AZ). Implant transmitters were gas-autoclaved using ethylene oxide at a sterilization temperature of 94°C.

Implant surgery was conducted at capture sites by a licensed veterinarian. The surgical site was prepped using standard aseptic surgical procedures and heat packs were placed under the length of the animal. A 7-cm incision was made in the ventral-medial area near the umbilicus. Omentum and small intestine was reflected to the right quadrant and the implant transmitter inserted into the left lower quadrant of the abdomen. The transmitter signal was checked and a 4-layer closure used to close the incision. Linea alba, subcutaneous layers, and subcuticular sutures were closed with absorbable suture. The skin was then closed with a surgical glue (Vetbond). The procedure required an average of 20 minutes to perform.

The reproductive status of adult females was determined at the time of capture by palpation and a blood test measuring plasma progesterone levels (Mead et al. 1993). Once pregnancy was determined, movements and activities of the female were closely monitored from February through May. When the kits were weaned and able to travel with the female, a helicopter and a fixed-wing aircraft were used to locate and access the female and the kits. Kits were then captured by hand.

Study animal identification notation, e.g., F203 refers to animal sex (M = male, F = female), ear tag number (20), and year of capture (3 = 1993). Capture and handling protocol was approved by the University of Idaho Institutional Animal Care and Use Committee.

Morphology

Animals were sexed, aged, weighed, measured, photographed, ear tagged, and blood and tissue samples collected. Wolverine age was subjectively classified as adult (morphologically/reproductively mature), subadult (morphologically mature/reproductively immature), or juvenile (morphologically/reproductively immature) by tooth wear, body size and morphology, and teat/testis measurement (Magoun 1985). A premolar was extracted in some individuals for aging by tooth cementum analysis. Age at capture of juvenile wolverines was based on tooth eruption data of captive-reared wolverines (Clint Long pers. commun). Animals were held in the log traps until full recovery from anesthesia and then released. Captured non-target species were released without handling. To test for differences in weights between central Idaho and northern populations, values were ranked and compared by t-test (Conover and Iman 1981). Differences in mean weights between age classes of Idaho wolverines were tested with a Wilcoxon Rank Sum test.

Monitoring

Aerial radio telemetry was attempted at 5-day intervals. Relocations were recorded at the point of collection on 1:24000 topography maps or stored in an on-board global positioning system (GPS). Aerial relocation accuracy was tested against known location transmitters. Daily sequential relocations were collected by aerial and ground tracking.

Minimal habitat data were collected for relocation sites during aerial telemetry flights. Detailed habitat information was recorded for ground telemetry locations. Locations were plotted on USGS 7.5 minute topographic maps and entered, along with habitat information, into a computer data base for later entry into a Geographic Information System (GIS).

Home Range and Movement

A kernel home range estimation program developed by E. O. Garton (Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho) provided total, and 90% annual and seasonal home range estimates. Harmonic mean core areas (Samuel et al. 1985) were estimated using Program Home Range (Ackerman et al. 1990). Minimum convex polygon (Hayne 1949, Ackerman et al. 1990) estimates were provided for comparison with other studies. Wolverines are capable of traveling over 30 km/day (Haglund 1966, Magoun 1985), therefore relocations occurring >1 day apart were considered independent (White and Garrott 1990). To gauge sample size adequacy for home range estimation, I measured home range area from randomly selected samples of 5 to 75 relocations from study animal data sets. Resulting area curves were asymptotic at 25 to 35 relocations. Home range estimates based on less than 25 relocations may underestimate home range area.

Annual home ranges were calculated for either June-May or December-November. Seasonal home ranges were measured for summer (June-November) and winter (December-May) based on the presence or absence of snow, and for mating (January through August) and non-mating (September through December) periods.

Home range overlap was calculated by utilization distribution volume based on 100% kernel home range estimates (E. O. Garton and F. Leban, Dept. Fish and Wildl. Res., University of Idaho, Moscow). To measure volume overlap, grid parameters for the kernel estimator were identically proportioned and positioned in space for the 2 home ranges under comparison, and each run through the kernel estimator. The 2 resulting utilization distributions were then overlaid and the volume proportion for each corresponding grid cell compared. The smaller of the 2 proportions was selected (either of the 2 was selected if

proportions were equal) and summed over the entire grid providing a utilization volume estimate of overlap.

Mean differences in home range size were analyzed with a Kruskal-Wallis test.

Differences in seasonal elevational use by wolverines were tested by Wilcoxon Signed Rank test. I used ANOVA for pairwise comparisons of seasonal elevation use within individuals.

Daily movement rates were normalized through logarithmic transformation (Zar 1984). I added 100 to each movement value prior to transformation to eliminate zero values. Mean differences in movement by season, sex, and age was tested by ANOVA. Statistical tests were considered significant at $P < 0.05$.

Denning Activity

Sites related to female reproductive and kit rearing activities were classified as natal dens, Maternal dens, and rendezvous sites. The attributes of investigative dens, resting sites, and snow excavations associated with non-reproductive activities were also investigated. Dens were excavated and mapped in cases where I felt disturbance would have no adverse effect on study animals.

Food Habits and Scent-marking

Scat processing and terminology followed Kelly (1991). Scats suspected but not confirmed of wolverine, were collected and analyzed but included in the data only if they contained wolverine hair. Prey items were reported as the number and percent of occurrences within total and seasonal collections. Scent marks were recorded as to type (urine, scat, musk, unknown), object marked, and frequency.

Habitat Analysis

A raster-based analysis of landsat TM images by the Montana Spatial Analysis Lab, Missoula, Montana identified 22 cover types within the study area. Locations for 13 wolverines were analyzed. Cover type polygons classified as cloud or cloud shadow, and water, and wolverine locations associated with these types (wolverines were occasionally relocated during winter on frozen lakes) were dropped from the analysis. Urban and agriculture cover types that constituted only 0.04% of available and 0% of used habitats were also eliminated. The remaining cover types were pooled to 10 types for investigative analysis and condensed to 6 for the final analysis (Table 5.1). This included pooling 2 shrub types and a foothill grassland type to *shrub/grassland*; a mixed xeric forest type and broadleaf forest type with *ponderosa pine* (*Pinus ponderosa*); 6 coniferous forest types comprised of lodgepole pine, Douglas-fir, and subalpine fir were pooled to *montane coniferous forest*; and mixed barren, exposed rock, and snow grouped as *rock*. Landsat images used in cover type classification were primarily June photographs with snow still persistent at higher elevations. Of 60 wolverine relocations that fell within the snow cover type, field data confirmed 50 as occurring within talus-rock habitats.

Habitat availability and use by study animals was measured on 3 scales: (Level 1) habitat use by total relocations for each study animal compared with habitat availability within a composite polygon of all identified 99% kernel home ranges within the study area boundary (common availability for all animals), (Level 2) habitat use by total relocations for each study animal compared with habitat availability within that animal's 99% kernel home range (distinct availability for each animal), and (Level 3) habitat use measured for relocations occurring within each animal's core home range compared with habitat availability within each

individual's core home range. I tested the hypothesis that use of cover types was random at $P < 0.05$, following Aebischer et al. (1993), using only cover types from the second pooling (6 types) to avoid Type II error (Allredge and Ratti 1986).

RESULTS AND DISCUSSION

I. CHARACTERISTICS OF THE STUDY POPULATION

Capture and Study Animals

Nineteen wolverines were captured in winter from February 1992 to May 1995. Fifteen individual wolverines were captured 43 times in 2,727 trap, for a capture rate of 47.0 trap nights/capture. Log traps required 35.9 trap nights/wolverine capture while barrel traps required 174.6 trap nights/capture. Four kits were captured by hand. Remote cameras recorded a visitation by 1 wolverine that was not captured.

Responses of wolverines to capture and immobilization varied from defensive (charging the trap entrance) to submissive (presentation of the ventral surface) posturing. Three wolverines escaped by chewing out of log traps. Females were generally more defensive than males with the highest level of antagonism observed in a lactating female. Other responses included vocalization, anal musking, and elevated salivation. Only 1 injury of a trapped wolverine was noted; a minor scalp laceration was caused by an exposed spike.

Twelve of the 19 animals were recaptured more than once (Table 1.1). Only 2 individuals (F602-1993, M814-1995) were not recaptured in years subsequent to their first capture. The annual rate of recapture varied among individuals although it did not differ significantly between the adult and subadult age classes ($P = 0.461$). Excluding the multiple recaptures of subadults M104 and F203, the annual number of recaptures/individual was 1.5 (SD = 0.9).

Two kits were captured by hand in May 1993. They and their mother (F502) were forced under the snow by helicopter. The kits were excavated and immobilized by jab stick,

Table 1.1. Capture dates, trap location, and age at capture of wolverines in central Idaho 1992-1995. Listing of study animals reflects chronological order of capture. See Fig. 1 for trap locations 1-13: 0 = non-trap capture, 14 = barrel trap capture (see footnote for trap or capture location).

ID	1992			1993			1994			1995		
	Age	Date	Trap	Age	Date	Trap	Age	Date	Trap	Age	Date	Trap
F502	A	4 Feb	14 ^a	A	7 Feb	2						
F822	A	12 Mar	14 ^b	A	14 Jan	9						
	A	16 Mar	14 ^b									
	A	22 Mar	14 ^b									
F602	A	28 Mar	14 ^c									
F703				A	7 Feb	1	A	17 Jan	1	A	3 Feb	1
				A	2 Apr	1	A	16 Mar	1	A	11 Apr	2
										A	21 Apr	1
M003				A	7 Feb	10						
M913				SA	12 Feb	2	A	21 Jan	2	A	11 Apr	6
				SA	7 Mar	2						
F803				SA	14 Feb	1						
				SA	6 Mar	1						
				SA	30 Apr	1						
M333				A	14 Feb	2	A	14 Mar	6	A	31 Jan	6
							A	24 Mar	6	A	14 Mar	8
							A	22 Apr	6	A	18 Apr	9
M423				SA	4 Mar	10	A	9 Apr	4			
M123				A	8 Apr	2	A	21 Mar	4	A	3 Apr	2
							A	9 Apr	2	A	15 Apr	3
M403				A	15 Apr	6	A	25 Mar	9			
							A	5 Apr	9			
F103	J	20 May	0 ^d				SA	16 Jan	2			
F203	J	20 May	0 ^d				SA	23 Jan	1			
							SA	26 Jan	1			
							SA	28 Jan	2			
							SA	22 Feb	1			
							SA	24 Feb	2			
							SA	6 Mar	2			
							SA	10 Mar	1			
							SA	3 Apr	2			
							SA	4 Apr	2			
							SA	14 Apr	2			
M814							SA	11 Apr	9			
F204				J	25 May	0 ^e	J	25 May	0 ^e	SA	28 Mar	3
M104										SA	9 Apr	2
										SA	18 Apr	4
										SA	19 Apr	4
										SA	20 Apr	4
										SA	21 Apr	4
										SA	28 Apr	4
										SA	1 May	1
M685										SA	5 Feb	11
M975										SA	10 Feb	11
F885										A	8 Apr	8

^a Barrel trap capture at Bernard Lake, Fekham Creek (CNF).

^b Barrel trap capture in Beaver Creek (SNF).

^c Barrel trap capture on Fir Creek Summit (BNF).

^d Hand capture at Kidney Lake, Frank Church River of No Return Wilderness (CNF).

^e Hand capture in Fall Creek, Frank Church River of No Return Wilderness (CNF).

while their mother escaped. The 2 kits of female F703 were chased down by foot and immobilized by hand syringe in May of. Kits were estimated to be 13 weeks of age.

In 1992, 3 adult females were captured and instrumented with transmitter collars. One collar was shed within 2 weeks of capture and a second shed within 2 months. The third was carried 10 months until recapture and re-instrumentation with an implant transmitter.

Although guard hair was substantially worn beneath the collar, no tissue abrasion or injury was apparent. During the 1993 trapping season, 1 adult male was fitted with a collar transmitter. The slipped collar was found the following day 2 km from the trap.

All study animals except female F885, including radio-collared individuals, received intraperitoneal implant transmitters, with 6 individuals implanted twice. Of 23 implant surgeries, post-surgery complications occurred in 2 individuals, the 1993 kits of F502. Kit F103 died within 6 days of capture due to a torsion of the small intestine; a result of chewing through the surgical site. The second kit (F203) survived an intestinal hernia at the incision site. The hernia was discovered at her first recapture 11 months post-surgery. She was transferred out of the study area for surgery, held for 3 days, then transported and released back at the trap site.

Age and Sex Ratios.--Ten males and 9 females were captured (Table 1.1). During the 1992 trapping season, using only metal barrel traps, I captured 3 adult females. During the 1992-1993 trapping season, using only log traps, 3 adult females, 1 subadult female, 4 adult males, and 2 subadult males were captured. In the 1993-1994 trapping season my sample was 1 adult and 1 subadult female, 5 adult males and 1 subadult male. The 1994-1995 trapping season sample was comprised of 3 adult males, 3 subadult males, 2 adult females, and 1 subadult female. These samples include between-season but not within-season recaptures of

individual wolverines and most likely reflect age variation in vulnerability to trapping. Two adult females produced 4 female and 2 male kits, and 2 kits of unknown sex, during the study.

Morphology.--Adult male wolverines averaged 12.4 ± 1.2 kg while the mean for adult females was 7.8 ± 0.96 kg (Table 1.2). Weights for subadult males averaged 12.2 ± 1.2 kg and did not differ from adult males ($P = 0.674$). Weights for subadult females averaged 7.8 kg but too few were captured for statistical comparisons. Mean weights for Idaho wolverines were significantly smaller than those for wolverine in Canada and Alaska (male: $\bar{x} = 14.9$ kg., $T = 3.183$, 26 df, $P = 0.004$; female: $\bar{x} = 9.7$ kg., $T = 4.062$, 17 df, $P = 0.001$) (Gardner 1985, Magoun 1985, Banci 1987).

Four kits were captured and weighed at age 13 weeks. Two female kits captured in 1993 (F103, F203) weighed 2.0 kg each. A female and a male kit (F204, M104) captured in 1994 weighed 3.8, and 4.2 kg, respectively. Fourteen week old kits captured in arctic Alaska averaged 3.8 kg (Magoun 1985). F203 was recaptured in 1994 at 11 months of age weighing 6.5 kg.

Wolverine reach adult body size within their first year (Iversen 1972), while sexual maturation is delayed until the second year (Rausch and Pearson 1972, Banci 1987).

Consequently, potentially large genotypic variation may make separation of the subadult and adult age classes difficult when based solely on morphology. Although tooth wear may not provide a reliable method for separating all age classes (Vivian Banci, pers. commun.), in conjunction with body conformation, pelage quality, and teat and testes characteristics (Magoun 1985), it may accurately indicate a subadult. Little to no wear on incisal surfaces of incisor teeth and a lack of blunting of the buccal tips of carnassial and canine teeth,

Table 1.2. Physical characteristics of wolverines captured in central Idaho, 1992-1995.

Animal ID	Capture Dates	Status ¹	Sex	Age ²	Wt. (kg)	Measurements (cm)							
						Tot.	Tail	Head	Neck	Chest	Foot	Testes ³	Teats ⁴
F502	4 Feb 1992	R	F	A (3-5)	8.6	90.0	19.0		29.0	41.0			0.5
F502	8 Feb 1993	R	F	A	9.0	89.0	17.0		28.0	37.5	15.5		0.5 (0.4-0.7)
F822	12 Mar 1992	R	F	A	7.3	84.0	20.0	30.0	24.0	41.5			0.2 (0.1-0.3)
F822	15 Jan 1993	R	F	A	8.2								<0.2
F602	28 Mar 1992	R	F	A (5-6)	7.0	88.0	17.0	30.0	28.0	38.0	15.5		0.6 (0.3-0.9)
F703	8 Feb 1993	R	F	A (2-3)	8.6	88.0			30.0	40.5	16.0		0.5 (0.3-0.7)
F703	17 Jan 1994	R	F	A	8.2	88.5	17.0	30.0	32.0	44.0	16.0		0.6 (0.4-0.7)
F703	3 Feb 1995	R	F	A	8.6	87.5	18.0	34.5	32.0	43.5	16.0		0.6 (0.3-0.8)
F803	14 Feb 1993	R	F	S (1)	8.2	89.5	18.5	32.0	29.0	44.0	16		<0.2
F103	20 May 1993	R	F	J	2.0	54.0	11.0		17.5	23.5	12.0		
F203	20 May 1993	R	F	J	2.0	58.0	12.0		19.0	27.0	12.0		
F203	16 Jan 1994	R	F	S	6.5	86.2	17.9	27.0	25.8	39.0	15.2		<0.2
F204	25 May 1994	R	F	J	3.8	67.0	17.5		21.0	29.0	13.5		
F204	28 Mar 1995	R	F	S	8.8	87.0	19.2	31.5	28.5	41.5	16.0		<0.2
M003	8 Feb 1993	R	M	A		99.0	19.5		36.0	49.0	14.5	23.5	
M913	12 Feb 1993	R	M	S	11.5	96.5	19.0	36.0	35.0	46.0	16.1	17.0	
M913	21 Jan 1994	U	M	A	11.2	95.0	17.0	35.5	34.5	48.0	17.5	24.5	
M913	11 Apr 1995	U	M	A (1-2)	11.3	97.0	18.5	36.5	34.0	54.5	17.0	27.0	
M333	14 Feb 1993	T	M	A	13.6	98.5	17.0	39.0	35.0	51.0	18.3	27.5	
M333	14 Mar 1994	R	M	A	13.7	97.5	18.4	36.0	34.2	48.0	18.0	33.5	
M333	31 Jan 1995	R	M	A (3-4)	14.0	97.5	19.0	38.0	39.0	49.0	18.0	27.0	

Table 1.2. Continued.

Animal ID	Capture Dates	Status ¹	Sex	Age ²	Wt. (kg)	Measurements (cm)							
						Tot.	Tail	Head	Neck	Chest	Foot	Testes ³	Teats ⁴
M423	3 Mar 1993	R	M	S	12.0	96.0	21.0	38.0	36.0	46.5	15.5	22.0	
M423	9 Apr 1994	T	M	A	12.3	96.0	19.5	36.4	36.2	48.1	16.5	25.5	
M123	8 Apr 1993	R	M	A	12.2	101.5	18.5		32.8	44.2	18.0	30.0	
M123	21 Mar 1995	R	M	A	13.3	100.5	20.0	37.5	36.5	48.0	17.0	32.0	
M123	3 Apr 1995	R	M	A (7-8)	13.2	99.0	18.0	36.0	34.5	48.0	17.0	29.8	
M123	15 Apr 1995	R	M	A	12.4							30.0	
M403	15 Apr 1993	R	M	A	13.8	100.0	19.5	38.5	37.0	49.5	17.5	30.0	
M403	25 Mar 1994	R	M	A (3-5)	14.2	98.0	20.0	38.0	37.0	53.0	17.5	28.5	
M814	11 Apr 1994	R	M	S	14.7	98.5	20.0	38.0	35.5	52.0	17.5	26.5	
M104	25 May 1994	R	M	J	4.2	66.0	17.0	27.0	22.0	28.0	14.0		
M104	9 Apr 1995	R	M	S	11.6	96.5	19.0	36.0	35.0	52.0	17.5	24.5	
M685	5 Feb 1995	U	M	S (1)	13.1	96.5	17.0	40.0	35.5	48.0	17.0	20.5	
M975	10 Feb 1995	R	M	S (1)	11.1	92.0	20.0	38.5	37.0	51.0	15.5		

¹ R=resident, T=transient, U=unknown

² A=adult, S=subadult, J=juvenile. Numbers in parenthesis represent age based on tooth cementum analysis.

³ Testes measurement is the mean length of right and left testes.

⁴ Teat measurements are mean lengths of all 6 teats followed by the range of teat lengths. Teats too small for accurate measurement were given the notation <0.2.

appears suggestive of a subadult. While little variation between subadult and adult weights was noted, adults were more robust in appearance. The fuller pelage that develops with physical maturity, possibly correlated with stabilizing of the basal metabolic rate occurring in the individual's second year (Iversen 1972), may contribute to this perception. Teats and testes of study animals subjectively classified as subadults were strongly regressed and difficult to measure. Of 6 study animals subjectively classified as subadults, 3 were subsequently confirmed by tooth cementum analysis.

Pelage color varied extensively among captured wolverines. Dorsal guard hair coloration varied from near black to dark brown. A light facial mask was prominent in some individuals and nearly absent in others. Lateral stripes varied from near white to medium brown. White feet and/or digits were common on front feet. White feet and digits were prominent on adult male M123, with a complete white coverage extending up to the tarsus on his front right foot and across the digits of his front left foot. All subadult and kit wolverines associated with adult females within M123's home range displayed white feet or digits. No wolverines captured in the southern portion of the study area displayed this characteristic. Considerable variation in chest and throat markings was also present. White pelage on the chest and throat occurred to some degree on all individuals. Markings varied from nearly absent to extensive with white hair present across the throat and chest, and in some instances radiating down the front legs and ventral surface.

Chemical Communication--Chemical communication in carnivores has received substantial attention (Pocock 1914, Stoddard 1980a, Stoddard 1980b, Macdonald 1985, Gorman and Trowbridge 1989). Odor plays an important role in carnivore social organization by providing a spatial and historical record of an individual's movement and behavior (Gorman

and Trowbridge 1989). Methods of dispersing scent are highly varied and well documented however behavior and responses tied to social odors are not well understood. The role of odors in the social behavior of the Canidae has received more attention than any other family of the Carnivora (Macdonald 1985). Data on scent production and behavioral responses in Mustelidae are less comprehensive. Sites of potential chemical transmission most commonly associated with communication in the mustelids are the ventral surface, and ano-genital region (Ewer 1973, Stoddard 1980a) however urine was the most common method of scent-marking in free-ranging wolverines in Idaho and Montana (Koehler et al. 1980) and in captive studies on wolverine (Long 1987). Hall (1926) first described the morphology of an abdominal gland in the marten (*Martes americana*) and wolverine as an elongated depression of the skin located on the posterior ventral surface. Hall's description was based on gross morphology and provided no histological evidence for the presence of glandular tissue specific to scent production. His description of the "abdominal gland" is commonly referenced as a morphological and behavioral foundation for abdominal rubbing in marten and wolverine although data to support ventral rubbing as communicative in these species is limited. Research on captive wolverines (Long 1987) concluded that urination followed by abdominal rubbing were the primary methods of scent-marking. Magoun (1985) observed wolverines straddle and "mark" tussocks with a side-to-side or forward-and-backward motion. She also described urination as the most common form of marking. de Monte and Roeder (1990b) observed abdominal rubbing as the primary marking method in marten and found no evidence of anal marking. A number of authors have described anal musking as a scent-marking method in the wolverine (Haglund 1966, Pulliainen and Oyaskainen 1975, Koehler et al. 1980, Magoun 1985) while others suggest anal glands function primarily as a fear-defense

mechanism (Ewer 1973, Long 1987). The wide genotypic variation that exists in the anatomy of scent producing organs in the Mustelidae should suggest caution in assigning behavior or conspecific response to scents. Such as with urine and feces, it may be difficult to distinguish between excretion and communication (Gorman and Trowbridge 1989).

Skin glands are primarily concerned with thermoregulation and pelage dressing, although in certain areas the skin glands are believed to secrete substances that act as a means of communication (Ewer 1973). de Monte and Roeder (1990a) conducted a histological study of abdominal gland tissue in the marten and found it composed exclusively of sebaceous glands. Similar efforts have not been attempted on the wolverine.

Buskirk et al. (1986) suggest that the hind feet of the wolverine may function in passive communication, based on gross morphology of what they described as "wart-like inflorescences", termed plantar glands, on the tarsus pads. Their histological examination of plantar tissue revealed no specialized glands and suggested the need for further investigation. Foot glands have been described in canids with gland sites generally occurring either interdigital (Ewer 1973) or in spaces between pads, as in arctic fox (*Alopex lagopus*) (Pocock 1914).

To supplement histological data on abdominal and plantar gland structure in the wolverine, I examined tissues from carcasses of 1 adult male and 2 adult female wolverines. My objective was to identify glands associated with the abdominal and plantar regions noting any indication of gland specialization by structure, type, or density. The "abdominal gland" is an elongated, oval patch of hair located caudal-abdominal, anterior to the preputial region on the male wolverine. The site appears as a contrasting patch of light brown hair that is shorter and coarser than the surrounding pelage. The location is less distinct in females. I collected

skin samples 5 cm long and 1 cm wide, centered on the "abdominal gland", and control sections of similar size from the thoracic-lumbar region. From the feet, I collected tissue that encompassed the "wart-like inflorescences" on the tarsal pads, and from the pads of the 2nd and 3rd digit of 1 hind foot. Corresponding samples were taken from a front foot as control. Tissue sections were fixed in 10% buffered formalin and processed for sectioning using routine histopathologic tissue processing (Luna 1992). Tissues were imbedded in paraffin and sections cut at 4 microns, mounted on slides, and stained with hematoxylin and eosin. Selected tissues were stained by Gomori's trichrome.

Freezing of carcasses prior to sample collections resulted in tissue degradation and poor histological preservation in some samples. Abdominal tissue contained sebaceous and apocrine sweat glands associated with hair follicles. Sebaceous glands in the suspected region of "abdominal glands" were large and more abundant than in the control tissue. The histology of the gland cells was consistent with a holocrine mode of secretion. It was also noted that secretory ducts of some sebaceous glands projected towards the surface of the integument. However, the distal end of the duct was never observed in the sections. Control tissues contained both eccrine sweat glands and sebaceous glands at lower concentrations. de Monte and Roeder (1990a) found a decrease in sebaceous gland density moving from cheek to flank in marten.

Sebaceous glands produce an oily secretion functioning primarily in hair and skin lubrication but may become modified to form scent glands (Banks 1981). Apocrine glands are commonly associated with scent production and are typically located in the axillary, areolar mammary region, penis, and circumanal region of many mammals including humans (Hickman

et al. 1974). In conjunction with behavioral data, the described properties of abdominal sebaceous glands in the wolverine is consistent with the presence of abdominal scent glands.

No atypical or specialized glands were observed in histological analysis of foot pad sections. Eccrine sweat glands were present in all sections, with some sebaceous glands associated with hair follicles. Densities of eccrine glands appeared higher in hind foot tarsal pad sections than hind foot digit pads or front foot control pads. Eccrine glands of the plantar region have been shown to produce odors of biological significance without specialization in gland morphology (Adams 1980). The "wart-like inflorescences" on the tarsal pads of live study animals varied in size and appearance among individuals. Tissue was glabrous and appeared columnar and somewhat diffuse but no orifice was evident. The analysis provided no support for specialization of these structures in chemical communication.

Parasites.--Wolverine are susceptible to parasites most commonly contracted through prey species acting as intermediate hosts. Addison and Boles (1978) found 3 species of cestodes, 2 nematodes, and 1 trematode in the digestive tracts of 38 of 39 wolverines. The wolverine was considered the primary host of the cestode *Taenia twitchelli* (Rausch 1959). A single ascarid (*Toxascaris* sp.) was collected from an Idaho wolverine scat in 1994. The collected individual was a female which precludes identification to species level (J. R. Lichtenfels pers. commun.). In Alaska, *Toxascaris* sp. has been found in black bear (*Ursus americanus*), lynx (*Felis lynx*), arctic fox and wolves (*Canis lupus*) (Dieterich 1981). Infection occurs either through contact with contaminated feces of infected individuals, or by ingesting rodents harboring the larvae (Dieterich 1981). Rausch (1959) reported helminth infestations in 69 of 80 wolverines examined in Alaska, although the genus *Toxascaris* was not mentioned. Holland (1949) identified the wolverine as "recorded host" for 2 species of fleas in British Columbia, including

the species *Chaetopsylla setosa*. A single specimen of this species was collected from M423 at his 1994 capture.

Spatial and Temporal Structure of the Study Population

My analysis of population structure was based on temporal and spatial distribution of marked animals (Figs. 1.1, 1.2). A description of spatial requirements of an individual is more meaningful when compared to a neighbor and more so if it accompanies a knowledge of kinship, site tenure, and reproductive history (Hornocker et al. 1983). Variations in trap site accessibility and trapping intensity combined with natural drainage divisions, and possibly site selection of study animals, dictated the study area be divided into northern and southern regions. The northern study area (NSA) provided more information on population characteristics than the southern study area (SSA). The study sample and population structure varied from year to year (Fig. 1.2) dependent on trapping success, reproduction, mortality, and dispersal.

Three wolverines were captured in 1992 (Fig. 1.2a). Female F502 shed her collar within a week of capture. Female F602 and female F822 were spatially separated by 50 km throughout 1992. Another wolverine (later identified as male M123) in the NSA was detected by remote camera photography.

Female F502 was recaptured in 1993 and was pregnant with 2 kits. Female F602 was not recaptured in 1993, but remained resident in the NSA. The capture of adults M123 and F703, and subadults M913 and F803 appeared to constitute the resident population of the NSA (Fig. 1.2b). An additional adult male, M333, was captured in the NSA but shed his

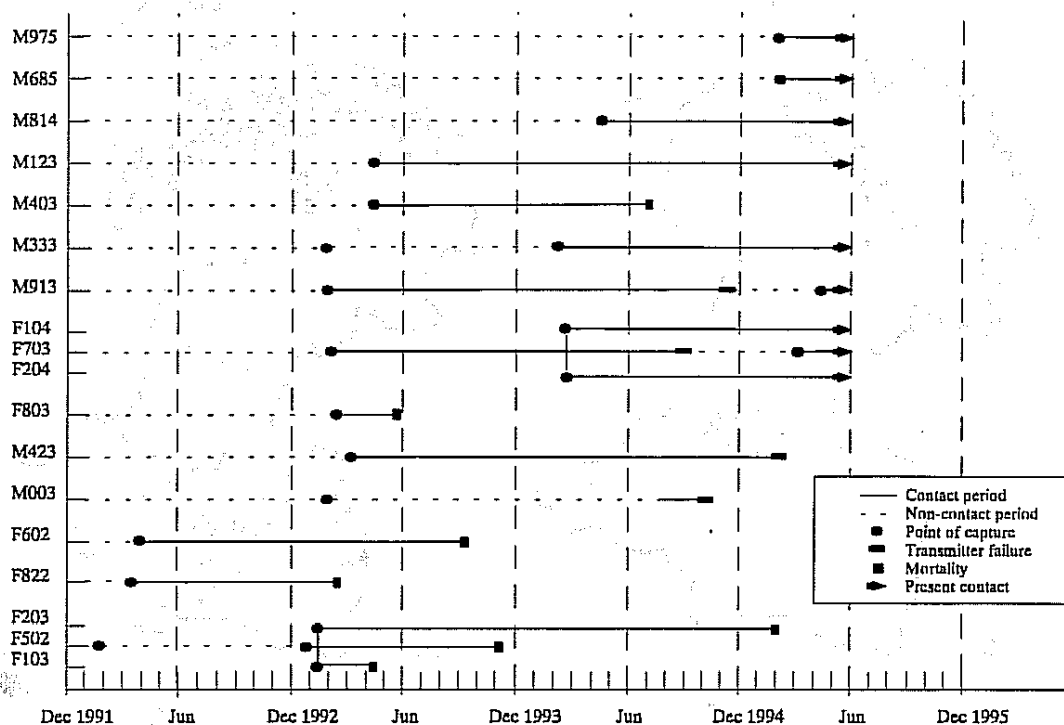


Fig. 1.1. Temporal distribution of wolverine study population in central Idaho, 1992-1995. Vertical dashed lines separate seasonal (summer-winter) analysis periods. Annual home range analysis periods were measured for December through November, or June through May. Winter analysis period was December through May, and summer analysis period was June through November.

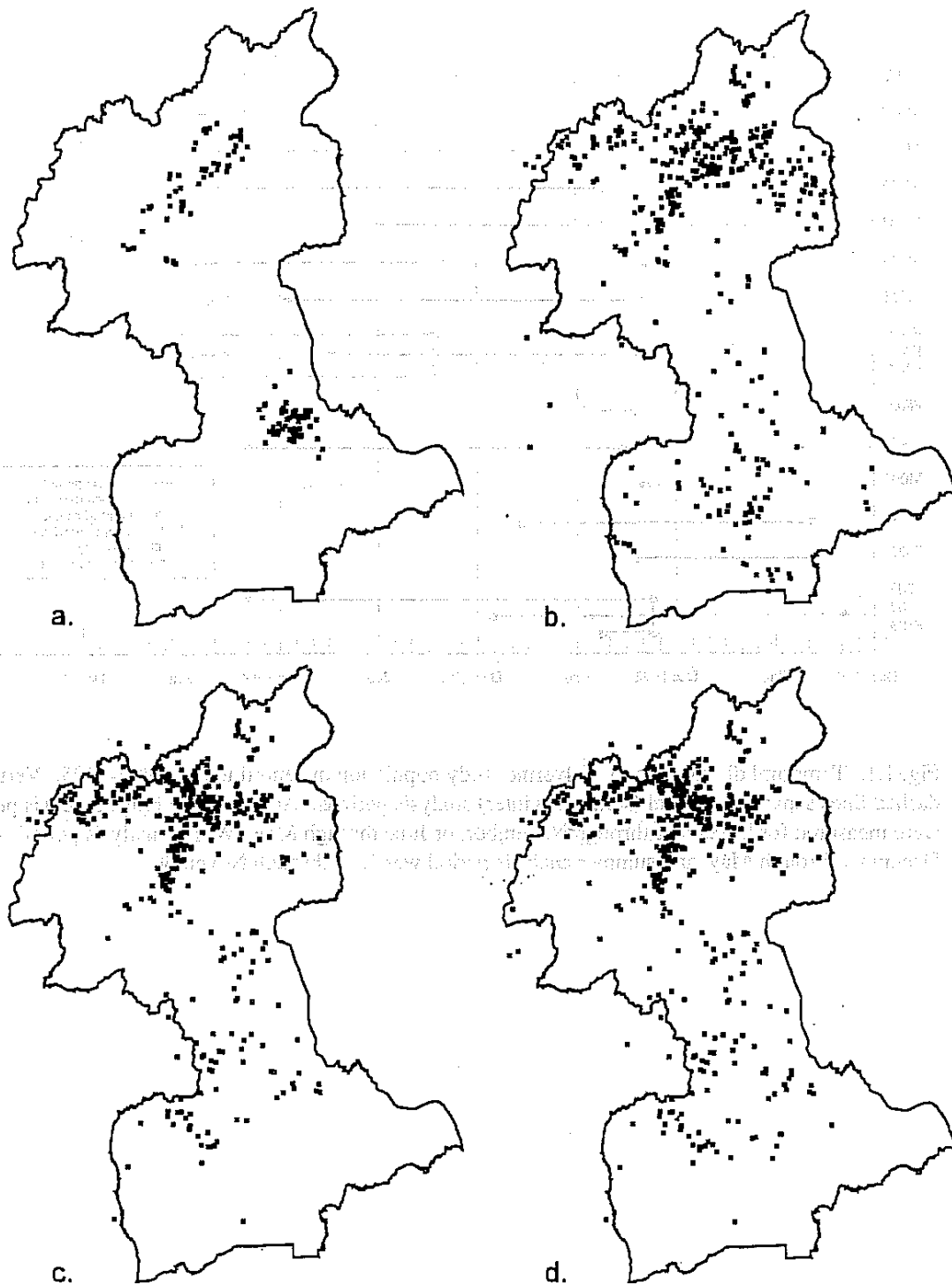


Fig. 1.2. Spatial distribution of the wolverine study population in 1992 (a), 1993 (b), 1994 (c), and 1995 (d) in relation to the central Idaho study area. Relocation points are not cumulative through years.

radio collar shortly after capture. He was 2-years-old at capture and likely not resident to the NSA. He was recaptured in the SSA in 1994. The 1993 SSA sample included adult males M403 and M003, and subadult male M423. The 3 adult females captured in 1992 died during the 1993 season as did subadult female F803.

The likelihood that all resident individuals in the NSA had been captured was reinforced during the 1994 and 1995 trapping seasons when no new individuals were captured, photographed, or observed (Fig. 1.2c). Female F203, the one remaining kit of F502, established her home range squarely over her mother's area, bordering that of F703, and remained within adult male M123's home range boundaries. F703 produced an additional 2 kits in the NSA in 1994 (M104, F204), that survived to subadults, and the end of the study. F203 died in early 1995 leaving the NSA with only 1 known adult resident female. Four males (M333, M814 in 1994; M975, M685 in 1995) were captured in the SSA during 1994 and 1995 trapping seasons (Fig. 1.2d). The capture of a lactating female (F885) in the SSA in 1995 provided evidence of adult female presence.

Wolverines are most susceptible to trapping during winter months when carrion constitutes most of their diet (Hornocker and Hash 1981, Magoun 1985, Banci 1987). By mid-February parturient females begin to restrict their range to the vicinity of natal den sites, making them less available for capture from late February through May. The accessibility of the NSA allowed for earlier trapping with greater intensity during the periods of high female activity. This resulted in greater trap coverage and female captures than in the SSA where the lack of roads and severe terrain restricted access. Along with trapping, a disproportionate amount of time was spent in other activities such as snowtracking and radio telemetry on the

NSA. Consequently, most of the measures of population demographics are based on the the NSA wolverines.

Residency

Hornocker et al. (1983) considered a knowledge of site attachment and tenure requisite to understanding the internal characteristics of a population. Hawley and Newby (1957) defined 3 categories of resident status: resident territory holders, temporary residents that remain for short periods living a peripheral existence, and transients that merely pass through.

I defined resident wolverines as reproductively mature individuals that appear to have

established site tenure. Residency status was also given to reproductively immature

individuals still residing in their natal area. Nonresidents are sexually mature transient

individuals without site attachment. Wolverines determined to be >2 years old and remained

within the study area for >1 year, were considered resident. M333 was considered transient in

1993 although he later established residency in the SSA. He was first detected in the NSA

within the home range of M123. He was trapped once, photographed by remote camera on 3

occasions, and I observed in the field on 1 occasion. In 1994, he was recaptured in the SSA

where he remained. He was first captured as a 2-year-old and was likely in a transitory

dispersal phase when first contacted.

Density

Home ranges of Idaho wolverines remained stable in size among years while the

observed density of resident individuals varied. The resident population of the NSA varied

from 8 wolverines in early 1993 to as few as 4 wolverines in mid-1994. The home range of

resident male M123 supported 3 resident females in 1993 while only 1 adult female was

present by mid-1995. Two subadults and 1 juvenile occupied this area in early 1993 while 1

subadult and 2 juveniles were present through 1994. A single transient male (M333) was detected in this area in 1993 and 2 transient males were present in 1994 (M423, M913).

My estimate of density is based on the assumption that I contacted all wolverines resident to the NSA. The observed reproductive output of resident females suggests that females may be accompanied by 2-3 juveniles and the area may support 2-3 subadults in addition to the resident male. The 1993 home ranges of 3 resident adult females occupied 904 km². Dividing the home range area of the resident adult females by the potential number of residents provides a density estimate of 1 wolverine/90-113 km². A more conservative estimate may be based on the 1,980 km² total home range area of the resident male. This produces a density range of 1 wolverine/198-248 km².

Estimating density based on reproductive potential and home range size was also used by Magoun (1985) in her estimate of 1 wolverine/48-139 km² in arctic Alaska. Home range estimators may inject bias into a density estimate due to variability in sample size and home range estimation technique, which may preclude comparison to other regions. However, these may be the best estimates available until long-term capture-recapture studies can provide precise, empirical estimates.

Hornocker and Hash (1981) and Quick (1953) reported population density estimates of 1 wolverine/65 km² in northwest Montana and 1 wolverine/207 km² in British Columbia, respectively, based on capture and snowtracking data. Banci (1987) estimated Yukon wolverine densities at 1/177 km² based on capture data. Becker (1991) proposed a density estimator based on aerial track surveys that may prove effective in open country.

Reproduction

Wolverine reproductive biology has been described from *in utero* examination (Wright and Rausch 1955, Rausch and Pearson 1972, Liskop et al. 1981, Banci 1987, Banci and Harestad 1988), captive wolverines (Mead et al. 1991, Mead et al. 1993), and free-ranging wolverines (Hornocker and Hash 1981, Gardner 1985, Magoun 1985, Banci 1987). The wolverine's breeding season may extend from April through August (Rausch and Pearson 1972, Mead et al. 1991). Implantation is delayed (Wright and Rausch 1955) with nidation generally occurring from December through March, primarily in January and February (Rausch and Pearson 1972). Litter size is normally 2 to 4 kits born in late winter or early spring (Wright and Rausch 1955, Rausch and Pearson 1972, Magoun 1985). Data on reproductive potential from *in utero* studies is substantial while data on reproductive success from free-ranging populations is scarce.

Wolverine reproductive success in central Idaho was measured by direct field evidence of reproduction and survival of kits, *in utero* examination of study animal mortalities, and measures of serum progesterone (Mead et al. 1991). The incidence of pregnancy, presence of lactating females, and the presence of post-weaned kits all provide a measure of reproductive success, although trap sampling provides little control of the timing of capture and type of reproductive data collected. As a result, reproductive success in central Idaho wolverines was based on the number of litters produced, the number of kits produced, and the number of pregnancies documented. The frequency of litters produced included only reproductively mature females that survived a reproductive period. Frequency of kits/female was based on documented litter sizes (the capture of a lactating female without subsequent confirmation of kit numbers was excluded from this measure). Frequency of pregnancy was based on

reproductively mature females in which pregnancy was indicated or confirmed either by presence or absence of kits, *in utero* evidence of pregnancy in pre-parturient mortalities, and/or elevated serum progesterone levels. Adult females captured in traps were palpated for fetal presence and blood collected for measurement of serum progesterone levels (Mead et al. 1991), or inspected for presence of lactation and suckling. Adult females were closely monitored in the field for evidence of parturient behavior, followed by visual confirmation of kits. Presence or absence of juveniles and subadults in the trap capture also provided insight into local reproduction. Young wolverines may remain close to their natal area for at least 2 years (Magoun 1985) and appear to be more vulnerable to trapping than older age individuals (Rausch and Pearson 1972, Banci 1987). This proximity of young wolverines to their mother's home range through their first winter would likely expose them to my trap sites.

Even without capture, remote camera systems provided a relatively high rate of detection of visitation (78 of 138 documented wolverine visits were recorded by remote camera, Copeland unpubl. data). It was therefore assumed that juvenile and/or subadult wolverines associated with marked females would be detected in the trap or camera capture.

Field confirmation of successful parturition required close monitoring of movements of female from mid-February through mid-March. Magoun (1985) reported decreased movements by post-partum females, centering around the natal den site from mid-March through den abandonment in late April or early May. Magoun (1985) rarely found females away from the natal den, with no excursions exceeding 2 km. Fidelity to the natal den was maintained through weaning. In contrast, Pulliainen (1968) reported daily forays of 30-40 km from natal dens in Finland.

Six reproductively mature female wolverines provided data on reproduction in central Idaho (Table 1.3, Fig. 1.3). Three females (F822, F602, F203) produced no documented litters during 3 reproductive seasons, while 3 females (F502, F703, F885) produced 5 documented litters in 7 reproductive seasons for an overall reproductive rate of 0.50 litters/female/year. Number of individual kits/female was calculated from 4 females that produced 8 kits in 9 reproductive seasons for a rate of 0.89 kits/female/year. Evidence of pregnancy was measured for 6 females and confirmed 6 times in 13 reproductive seasons for an annual pregnancy rate of 0.46.

At her initial capture in February 1992, pregnancy was not detected in F502. She was instrumented with a radio collar but dropped it after only 2 weeks of monitoring. At her recapture 7 February 1993, she was pregnant. F502 remained associated with the natal den for 3 weeks, moving to a new den about every 2 weeks thereafter (Fig. 1.4) until the kits were weaned at about 10 weeks. The lack of fidelity to the natal den differed from Magoun's (1985) findings of strong natal den site association until weaning. Presence of F502's kits was not confirmed until tracks were found at a nursery den on 1 May. On 20 May, F502's 2 kits were captured. Tooth eruption suggested kits were 13 weeks old putting their date of birth at 20 February at which time F502 was associated with the Horseshoe Lake den site. F502 died in November 1993 carrying 2 unimplanted blastocysts.

Female F703 produced 2 kits in 1992, 1994, 1995, and none in 1993. Her 1992 kits were captured as subadults in February 1993. Their classification as siblings and kits of F703 was based on their association with each other prior and subsequent to capture, as noted by remote camera photographs and snowtracking, and their post-capture association with F703. This type of association is consistent with sibling and parent/offspring association

Table 1.3. Reproductive history for female wolverines in central Idaho, 1992-1995.

ID	1992		1993		1994		1995	
	Status	Kits	Status	Kits	Status	Kits	Status	Kits
F502	N ^{a,P,v2}		P ^{a,P,v1}	♀ ♀	P ^{a,pm}	0		
F703	P ^{a,v1}	♂ ♀	N ^{a,P,v2}		P ^{a,P,pr,v1}	♂ ♀	P ^{a,P,pr,v1}	2*
F885							P ^{a,s,v2}	
F822	N ^{a,P}		N ^{a,P}					
F602	N ^{a,s,v2}		N ^{a,v2}					
F203							N ^{a,pm}	

^a N = No parturition in this year, P = Parous.

^P Test for evidence of pregnancy by palpation.

^{v1} Visual confirmation of kits.

^{v2} No visual confirmation of kits.

^{pm} Post-mortum evidence

^{pr} Pregnancy test by measurement of serum progesterone levels (Mead et al. 1993)

^s Presence of lactation or suckling.

* Sex unknown

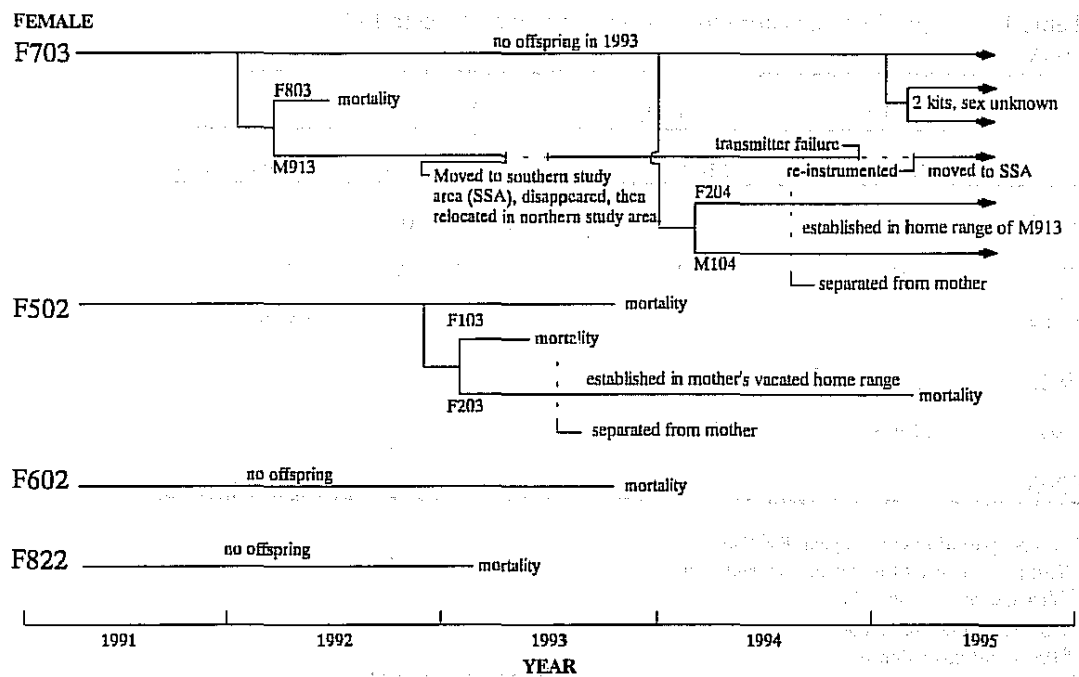


Fig. 1.3. Reproductive history and status of marked female wolverines in central Idaho, 1992-1995. Females F703, F502, and F602 were resident to the home range of M123 in the northern portion of the study area. Female F822 resided in the southern portion of the study area (SSA) within the home range of resident male M403.

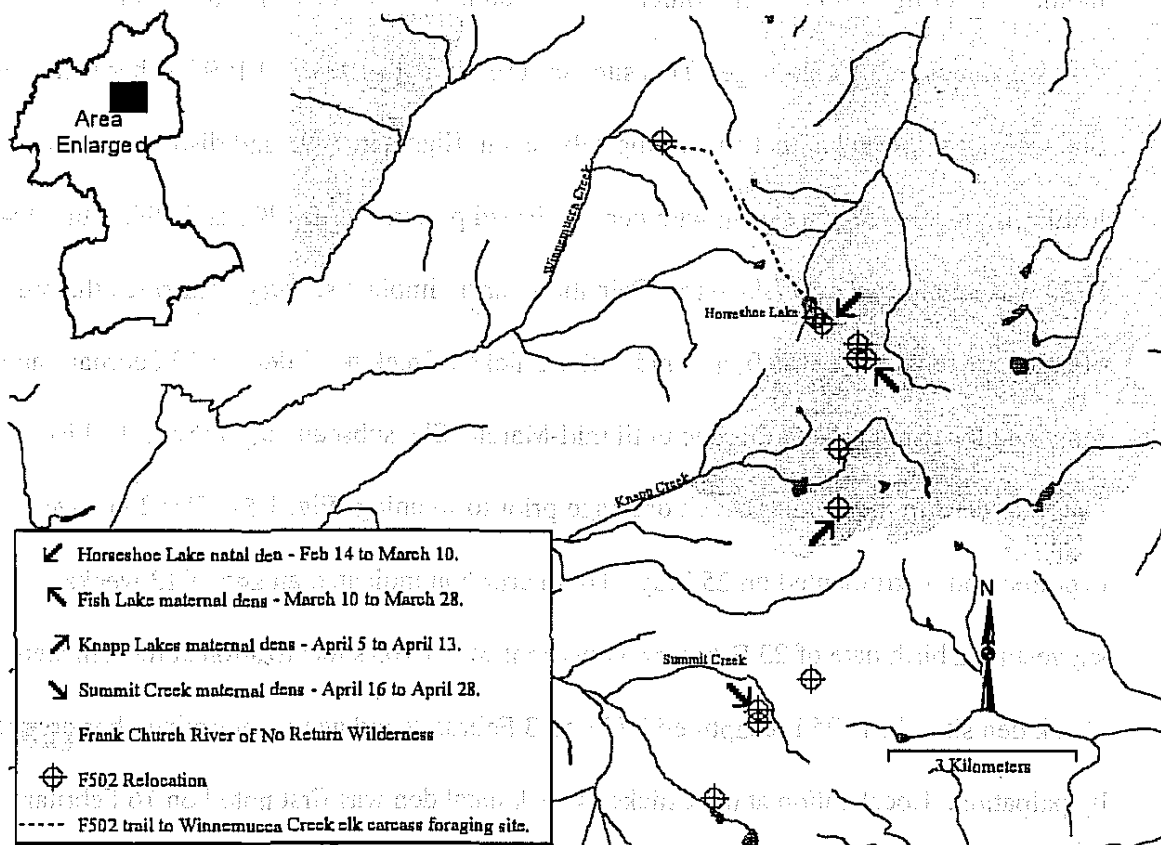


Fig. 1.4. Relocations and den sites of adult female wolverine F502 from parturition to kit weaning in central Idaho, 1993. Graphic includes snow trail from natal den to elk carcass foraging site.

described by Magoun (1985). F703 was first captured on 7 February 1993. Uterine palpation during implant surgery provided no evidence of fetal presence. Her activities were closely monitored during February and March. On 4 March she was located at a den site in the Chicken Creek (CNF) drainage. This site was used in both 1994 and 1995 as her natal den. She was not relocated at that site during subsequent flights in 1993 and displayed none of the localized movements consistent with her confirmed parturition in 1994 and 1995. In 1994, F703 was recaptured on 17 January. Palpation during implant surgery confirmed the presence of at least 1 fetus. She was first found at the Chicken Creek natal den on 20 February and remained localized around this site until mid-March. She subsequently moved the kits to 2 maternal dens in the Soldier Creek drainage prior to weaning (Fig. 1.5). Her 2 kits were captured and instrumented on 25 May. Tooth eruption indicated an age of 13 weeks suggesting a birth date of 23 February, consistent with F703's localization at the Chicken Creek den site. In 1995 I recaptured F703 on 3 February and again determined her pregnant by palpation. Localization at the Chicken Creek natal den was first noted on 16 February with movement to the Soldier Creek maternal den occurring in early April (Fig. 1.5). On 8 May, F703 was observed traveling with 2 kits.

Incidence of pregnancy within age classes and individual female wolverines was variable.

The age at reproductive maturation was described as 15+ months (subadult) for female wolverines by Rausch and Pearson (1972). This would be the first summer following the animal's first birthday. Pregnancy in subadult wolverines was reported at 7.4% in Yukon females (Banci 1987), and as high as 50% for Alaska wolverines (Rausch and Pearson 1972). Both these studies used fetus and corpora lutea counts to measure pregnancy rates. Banci (1987) noted that the variation between studies may be due in part to variation in age class

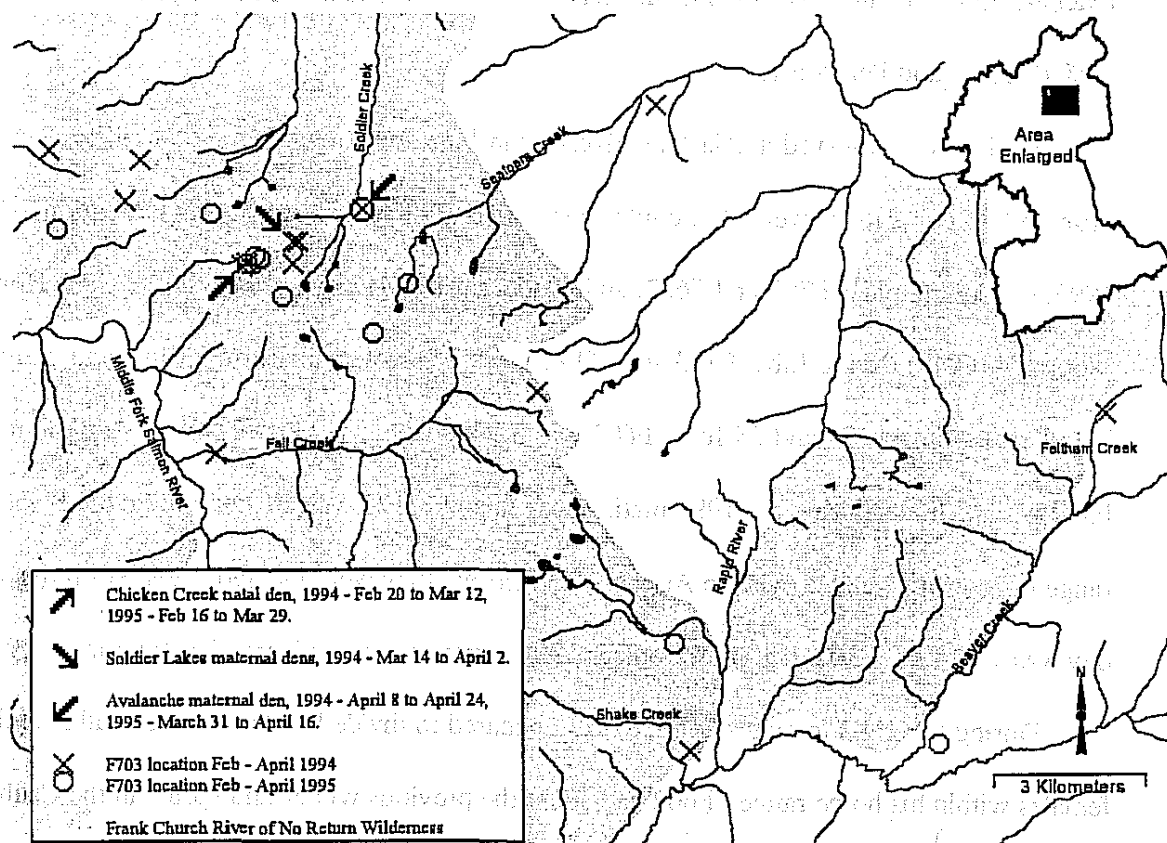


Fig. 1.5. Relocations and den sites of adult female wolverine F703 from parturition to kit weaning in central Idaho, 1994-1995.

partitioning between investigators. Age-specific natality rates measured in Yukon increased significantly between the second and third year age classes with overall pregnancy rates reaching 73.4% (Banci 1987) while the Alaska study described an adult pregnancy rate of 92% (Rausch and Pearson 1972).

Mating was observed in Alaska wolverines in June and August (Magoun 1985). I observed no copulatory events but could speculate on timing of mating from relocations. In 1993, resident females F703 and F602, and resident male M123 were located on Cape Horn Mountain (CNF) during July. F703 and M123 were 300 meters apart on 25 July and within 2 km of each other on 24 and 25 July. F602 was 3.9 km from M123 on 21 July. Adult female F502 was with kits during the 1993 mating season and M123 was located within her home range once in June and 2 twice in August. The closest they were located together on the same day was 12.7 km. F502 died in November 1993 carrying 2 unimplanted blastocysts.

During the 1993 mating season, M123 appeared to divide his time between all 3 adult females within his home range. F602 had spent the previous winter and spring in the Cache Creek area in the SW portion of her home range. In mid-July she moved 15.7 km to the Cape Horn area where she localized for 5 days in the vicinity of F703 and M123. Her reproductive tract was too decomposed for analysis when found subsequent to her death in early August, 1993. F703 made a similar movement of nearly 13 km to the SW from her wintering area proximate to the Soldier Creek drainage, localizing near F602 and M123 in mid to late July. Magoun (1985) noted a similar case of an apparent mating involving a female that moved 6 km out of her normal home range to pair with a male. Heinemeyer (1988) reported that home ranges of some female fishers (*Martes pennanti*) expanded during the mating season and suggested that females may seek out lone adult males.

During the 1994 mating season, F703 moved from Soldier Creek to Cape Horn Mountain 3 times; a 1-way distance of approximately 13 km. On 15 July 1994 she and M123 were located in the Cape Horn area 2 km apart. On 25 July they were within 300 meters of each other in Cape Horn Creek. On 21 August they were in Marsh Creek within 300 meters of each other.

Female F203 was 15+ months old during the 1994 mating season. She and M123 were not located closer than 18 km during the mating season. An examination of her reproductive organs subsequent to her death in February 1995, provided no evidence of reproductive activity.

In 1995 relocation sampling was reduced to 1 flight/month. On July 24, F703 was again located in Cape Horn Creek. M123 was not located on that flight.

One North American study (Magoun 1985) and several Fennoscandian studies (from Pulliainen 1968) of free-ranging wolverines reported mean post partum litter sizes of approximately 2.2 kits. Post mortem trapped animals (Wright and Rausch 1955, Rausch and Pearson 1972, Banci 1987) indicated a mean litter size of 2.7 kits. The reproductive potential of the wolverine from post-mortem studies appears to be higher than reproductive success reported in field studies. Magoun's (1985) reported reproductive rate was based on the reproduction of 3 adult females over a 4-year period with 1 of these females producing no kits. Capture/recapture data on Montana wolverines (Hornocker and Hash 1981) indicated that females did not produce young every year. Two of my study animals (F822, F602) produced no kits in the 2 years they were monitored while 1 study animal (F703) produced 3 litters of kits in 4 successive years. Another female (F502) contained 2 unimplanted blastocysts the fall following a successful reproduction.

Nutrition would appear to play an important role in the reproductive output of northern wolverine populations (Magoun 1985, 1987; Banci 1987). Fetal resorption of unimplanted embryos is common in mustelids (Mead et al. 1993) and may be nutritionally related (Mead pers. commun.), potentially resulting in reproductive senility in older nutritionally stressed wolverines. Female F822 did not reproduce during the only reproductive season she was monitored. She was subjectively classified an older age female as evidenced by substantial tooth loss and scarring from probable trap encounters. Magoun (1985) used teat length as an indication of age suggesting a correlation with sexual maturation. She concluded that teat lengths >10 mm suggested sexual maturity noting lengths of 12-17 mm for females with suckling kits. Teat measurements for F822 averaged 1.9 mm, falling well within Magoun's range of non-reproductive condition. Morphologically, F822 appeared to be of reproductive age suggesting reduced teat size may reflect reproductive senility rather than nullipary. A strong habituation to one of my bait sites just prior to her death may suggest a nutritional stress similar to that recorded in Montana wolverines (Hornocker and Hash 1981).

The lack of reproductive output by F602 may also be age and/or nutritionally related. At first capture on 28 March 1992, she weighed only 7 kg and was missing 7 toes and 3 canine teeth, with her remaining teeth suffering severe wear. Tooth cementum analysis placed her age at 3-5 years at this capture. Although her teat measurements averaged 6.1 mm, within the range of Magoun's (1985) non-reproductive class, I was able to obtain a drop of milk from one teat. No evidence of suckling was present. Extensive snowtracking and aerial monitoring subsequent to capture produced no evidence of kits. Apparent lactation in a female lacking kits was also noted by Magoun (1985). Female F602 was not recaptured in 1993 thereby providing no opportunity for uterine palpation or blood serum examination. Her activity and

movements were monitored closely during late winter with no evidence of denning activity.

F602 died in the fall of 1993 apparently of natural causes. Her reproductive tract was severely decomposed when recovered providing no information on her reproductive history.

No juveniles or subadults not connected with other females were captured within the home ranges of either F822 or F602 further reinforcing the concluded lack of reproduction for these females.

Mortality

Seven radio-marked wolverines (6 females, 1 male) died during the study period; 3 from predation, 3 of unknown cause, and 1 research related. F822 was first captured on 12 March 1992, fitted with a radio transmitter, then recaptured on 15 January 1993 and instrumented with an implant transmitter. On 14 February her implant transmitter was found buried under a few cm of snow. The wax coating on the transmitter was fractured and appeared to have been chewed. There was no evidence of F822's presence near the site suggesting that the transmitter was moved from another location. F822 had been subjectively classified as an old age wolverine. She was a common visitor to the Beaver Creek (SNF) trap sites during winter 1992. Her frequency of visitation increased dramatically during the second trapping season (1992-1993) as evidenced by 16 visitations recorded by remote camera from December 1992 to January 1993. The last relocation prior to her death was 10.5 km from the trap site and > 5 km outside her known home range. It is possible that the implant surgery played a role in her death, although no problems were encountered during surgery or recovery. Death in this case was classified as unknown.

Female F602 died in August 1993 of undetermined causes. She was found intact, in a talus area, but was too decomposed for a conclusive necropsy. There was no evidence of injury. She was aged at 5-6 years by tooth cementum analysis.

Predation appeared to play a role in the death of 3 study animals. Subadult F803 died in May 1993, found buried under 0.5 m of snow on a timbered ridgetop at 2,438 m elevation, near Sheep Mountain (CNF). Necropsy found several abrasions, a puncture wound over her left eye, and a hematoma on her right thorax associated with 2 fractured ribs resulting in a punctured and collapsed lung. Two nails were fractured on her right hind foot, and she had been scavenged from rectum to mid-abdomen. No infection was evident, but she was thin with little fat reserves. Snow-fall had covered any evidence of the predator.

F502 died in November 1993, also attributable to predation. Her remains were collected in Winnemucca Creek (CNF) within 24 hours of her death, but the species of predator could not be determined. The body was decapitated and the head was found lying next to the body. Most of the parietal plates, cervical vertebrae, and the ears were gone. The brain was intact. A large open wound was present on her left side with thoracic ribs 3 through 9 missing. The corresponding thoracic vertebrae were shattered but still in place. The internal organs were still present. Nearly all of her hair was missing on the right shoulder, flank, and back with some associated scratches and puncture wounds. Paired puncture wounds measured 2.7 cm from centers. There was virtually no blood present at the site of the carcass suggesting she had been moved from where she was killed.

In July 1994, adult male M403 was found dead in the Willow Creek drainage, South Fork Boise River (SNF). He was completely intact except for minor scavenging by birds and insects. He was lying on a southeast facing hillside with little overstory canopy, and appeared

to have died at that site. Necropsy revealed that his skull was punctured and separated from the first cervical vertebra. Hair collected from between his incisors and inside his mouth keyed to mountain lion (*Felis concolor*).

Female F103 was captured as a juvenile in association with the capture of F203 on 21 May 1993. Both kits were instrumented with implant transmitters. On a monitoring flight of 27 May I noted substantial spatial separation between adult female F502 and kit F203, and kit F103. Investigation of the site found F103 dead, attributable to complications associated with the implant surgery. The suture knots at the surgery site were intact but the sutures were chewed. Evisceration and torsion of a loop of small intestine was the apparent cause of death. The kit was found on a ridge-top lying on her side in a small natural depression in the forest floor. She had been partially covered with woody debris. The appearance of the site suggested the debris had been carried and placed on the body rather than scratched from the area surrounding the body.

In February 1995, F203 was found dead on a rocky hillside in Mayfield Creek (CNF). Cold temperatures and snow had protected her from decomposition and scavengers. Necropsy revealed severe trauma to her left abdomen resulting in perforation of the lower colon and diaphragm, but the cause of mortality was unknown.

Aside from human-caused mortality, starvation and predation appear to be primary causes of death in weaned wolverines. Starvation was the suspected cause of death in 2 juvenile wolverines in Yukon (Banci 1987) and 2 in Montana (Hornocker and Hash 1981), although food resources were relatively abundant in both areas. In contrast, NW Alaska wolverines appeared to survive using food items of low nutritive quality where food availability was highly variable (Magoun 1985). Starvation, however unlikely, may result

from factors other than food scarcity. Hornocker and Hash (1981) noted heavy dependence on bait sites by 2 study animals prior to death, consistent with our observations of F822. A foraging strategy that requires a knowledge of numerous widely dispersed food resource sites would be demanding on energy reserves. A reduction of foraging ability due to injury or inefficacy, or a lack of learned ability, might place an individual in energy deficit and lead to gradual starvation. Bait sites may only act to prolong life of animals predisposed to poor health by nutritive deficits.

Predation mortality may be exacerbated when wolverines scavenge kills in the presence of other carnivores. The role of more efficient carnivores as producers of carrion may be essential to survival in some areas, but the beneficiary may risk serious injury or death. Wolves may kill wolverines (Burkholder 1962, Boles 1977, Gill 1978, Banci 1987), but trees prove useful to escape wolves (Grinnell 1920, Boles 1977).

In Idaho, and other areas where mountain lions and wolverines coexist, the mountain lion may serve as provider and predator. A female wolverine in Montana was believed to have been injured by mountain lions on 2 occasions (Hornocker and Hash 1981). Periods of wolverine-mountain lion interaction probably vary due to seasonal niche separation. Mountain lions will occasionally pass through high, snow-filled passes as they move between big game winter ranges, but generally use lower elevation ungulate wintering areas below 1,800 m elevation (Seidensticker et al. 1973). The wolverine uses higher elevation habitats, likely taking advantage of ungulate mortality that occurred prior to winter migrations. Only 3 winter wolverine relocations occurred below 1,800 m, with a mean elevational use of 2,278 m. The likelihood of contact would increase as ungulate populations and mountain lions return to higher elevation summer habitats. Idaho wolverines summered between elevational

ranges of 1,400-2,900 m while mountain lions in Seidensticker's (1973) study area, 25 km north, used an elevational range of 1,500-2,400 m.

II. HOME RANGE

RESULTS

Seven female and 9 male wolverines provided 1,185 relocations from February 1992 through May 1995. Relocations separated by at least 1 day were considered independent; 874 relocations met this requirement for use in home range analysis. Telemetry flights occurred during daylight hours throughout the year averaging 5.9 (SD = 2.83) flights/month. Home range means that include multiple years for individuals are reported as animal-years (Magoun 1985).

Female Home Range Size

Home range size varied greatly among females (Table 2.1). Annual home ranges of resident adult females F203, F502, F602, F703, and F822 averaged 384 km² ($\bar{n}$ = 6 female-years, SD = 160). Core home range estimates averaged 254 km² ($\bar{n}$ = 5 female-years, SD = 117). The annual home range of female F703 increased 15% in 1994 from 1993 (1993 = 397 km², 1994 = 466 km²). Mean annual home ranges of subadult females, F203, F803, and F204, averaged 532 km² (SD = 105). Annual core areas for these subadults averaged 227 km² (SD = 157).

Movements of lactating females are restricted during the kit rearing period reducing home range size from mid-winter to early spring (Hornocker and Hash 1981, Magoun 1985). Home ranges of females with kits in central Idaho were 42% smaller than home ranges for unaccompanied females (Table 2.2).

Table 2.1. Total and annual home range by kernel, minimum convex polygon (MCP), and harmonic mean (HM) core estimates for wolverines in central Idaho, 1992-1995. Annual home ranges are annotated for either December through November^a or June through May^b. Sum of relocation samples for multiple annual home ranges may not equal total home range sample size due to inclusion of partial year relocations in total home range calculations.

Animal ID	Age ¹	Status ²	Analysis Period ³	Year(s) ⁴	# of Relocations	Area (km ²)		
						90% Kernel	95% MCP	HM Core ⁵
Females								
F203	SA/A	R	Total	1993-1995	91	473	524	262
F203	SA	R	Annual ^d	1993-1994	63	439	582	215
F203	A	R	Annual ^d	1994-1995	26	268	278	NC
F204	SA	R	Total/Annual ^d	1994-1995	29	646	370	390
F502	A	R	Total/Annual ^d	1992-1993	52	360	107	232
F602	A	R	Total	1992-1993	83	692	543	383
F602	A	R	Annual ^j	1992-1993	58	637	479	268
F703	A	R	Total	1993-1995	127	424	496	373
F703	A	R	Annual ^d	1993-1994	57	397	413	412
F703	A	R	Annual ^d	1994-1995	54	466	438	280
F803	SA	R	Total	1993	18	511	285	76
F822	A	R	Total/Annual ^d	1992-1993	50	175	108	85
Males								
M104	SA	R	Total/Annual ^d	1994-1995	35	845	776	438
M123	A	R	Total	1993-1995	92	1,980	1,864	1,181
M123	A	R	Annual ^j	1993-1994	53	1,783	1,479	1,177
M123	A	R	Annual ^j	1994-1995	31	2,127	1,380	NC
M333	A	R	Total	1994-1995	48	1,398	1,313	781
M333	A	R	Annual ^d	1993-1994	35	1,186	1,318	521
M403	A	R	Total	1993-1994	69	1,701	2,059	1,415
M403	A	R	Annual ^j	1993-1994	57	1,620	2,400	1,091
M423	SA	R	Total	1993-1994	49	1,611	3,692	956
M423	SA	R	Annual ^d	1992-1993	38	1,301	2,940	545
M814	SA	R	Total	1994-1995	31	919	3,012	479
M913	SA/A	R/U	Total	1993-1995	82	1,553	1,533	647
M913	SA	R	Annual ^d	1992-1993	46	1,353	994	619
M913	A	U	Annual ^d	1993-1994	35	893	953	463

¹A = Adult, SA = Subadult

²R = Resident, U = Status unknown.

³Total = Total of all relocations, Annual = December through November, Summer = June through December, Winter = December through May.

⁴Years marked with superscript^b denote data sets pooled among years. Years for Total data sets reflect actual periods of relocation collection. Years for Annual and Seasonal data reflect periods of data analysis (see superscript^b above) and do not necessarily define period of monitoring.

⁵NC = No core detected.

Table 2.2. Home range estimates of female wolverines with kits, and solitary female wolverines for the period - March through August, in central Idaho, 1992-1995.

ID	Year	Kit Dependency	Relocation (n)	95% MCP (km ²)	90% Kernel (km ²)
F602	1992	solitary	26	252	528
F822	1992	solitary	24	146	191
F602	1993	solitary	24	301	462
F502	1993	accompanied	36	335	265
F703	1993	solitary	34	414	462
F703	1994	accompanied	31	244	293
F703	1995	accompanied	14	115	152

Summer home ranges of adults averaged 359 km^2 ($n = 7$ animal-seasons, $SD = 169$) while winter home ranges averaged 256 km^2 ($n = 5$ animal-seasons, $SD = 152$) (Table 2.3).

Winter home ranges of 2 subadult females averaged 2.5 times larger than winter home ranges of adults. The 1993 summer home range of F602 was left out of the analysis because the bimodal distribution of relocation points provided an unrealistic area estimation for the 90% contour using the kernel estimator.

Male Home Range Size

Annual home ranges for resident adult males M123, M333, M403, and M913 averaged $1,522 \text{ km}^2$ ($n = 5$ animal-years, $SD = 488$) (Table 2.1). Home range size for M123 increased 19% in 1994 ($2,127 \text{ km}^2$) over 1993 ($1,783 \text{ km}^2$), but may be related to sampling. The annual home range of male M913 decreased in size from his subadult year ($1,353 \text{ km}^2$) to his first adult year (893 km^2). Annual home ranges for subadult males M104, M423, M814, and M913 averaged $1,104 \text{ km}^2$ ($n = 4$, $SD = 260$). Annual core home ranges for adults averaged 813 km^2 ($n = 4$, $SD = 373$) and 520 km^2 for subadults ($n = 4$, $SD = 79$). Seasonal home range data are presented in Table 2.4. Summer home ranges for adult males averaged $1,106 \text{ km}^2$ ($n = 5$ animal-seasons, $SD = 574$) while winter home ranges averaged $1,589 \text{ km}^2$ ($n = 9$ animal-seasons, $SD = 325$). Summer home ranges for subadult males averaged 728 km^2 ($n = 3$, $SD = 267$). Subadult males M913 and M104 used winter home ranges of 368 km^2 and $1,018 \text{ km}^2$, respectively.

Spatial patterns of solitary carnivores may change during the mating season depending on the availability of females and the influence of neighboring conspecific males (Sandell 1989, Erlinge and Sandell 1986). Presence of kits may reduce home range size for females, whereas males may increase their home range size during mating (Magoun 1985, Banci

Table 2.3. Seasonal home ranges of female wolverines by kernel, minimum convex polygon (MCP), and harmonic mean (HM) core estimates in central Idaho, 1992-1995.

Animal ID	Age ¹	Status ²	Analysis Period ³	Year(s) ⁴	Relocation (n)	Area (km ²)		
						90% Kernel	95% MCP	HM Core ⁵
F203	A	R	Summer	1994	21	259	150	NC
F502	A	R	Summer	1993	29	465	320	278
F602	A	R	Summer	1992	35	559	418	158
F602	A	R	Summer	1993	15	727	116	78
F602	A	R	Summer	1992-1993 ^P	50	721	461	246
F703	A	R	Summer	1993	34	487	371	278
F703	A	R	Summer	1994	20	263	134	78
F703	A	R	Summer	1993-1994 ^P	50	397	486	340
F822	A	R	Summer	1992	33	123	75	66
F203	SA	R	Winter	1993-1994	42	520	509	249
F502	A	R	Winter	1992-1993	23	80	50	40
F602	A	R	Winter	1992-1993	25	420	220	280
F602	A	R	Winter	1992-1993 ^P	35	785	568	331
F703	A	R	Winter	1992-1993	23	342	201	103
F703	A	R	Winter	1993-1994	38	331	438	252
F703	A	R	Winter	1994-1995	22	109	122	42
F703	A	R	Winter	1993-1995 ^P	81	388	499	306
F803	SA	R	Winter	1992-1993	18	511	285	76
F822	A	R	Winter	1992-1993 ^P	17	173	91	66

¹A = Adult, SA = Subadult

²R = Resident, U = Status unknown.

³Total = Total of all relocations, Annual = December through November, or June through May; Summer = June through December; Winter = December through May.

⁴Seasonal data reflect periods of data analysis and do not necessarily define period of monitoring. ^P Data set pooled among years.

⁵NC = No core detected.

Table 2.4. Seasonal home ranges of male wolverines by kernel, minimum convex polygon (MCP), and harmonic mean (HM) core estimates in central Idaho, 1992-1995.

Animal ID	Age ¹	Status ²	Analysis Period ³	Year(s) ⁴	Relocation (n)	Area (km ²)		
						90% Kernel	95% MCP	HM Core ⁵
M123	A	R	Summer	1993	28	1,726	1,209	994
M123	A	R	Summer	1994	17	1,018	688	234
M123	A	R	Summer	1993-1994 ^p	44	2,053	1,561	1,049
M403	A	R	Summer	1993	33	1,624	1,521	424
M403	A	R	Summer	1993-1994 ^p	40	1,515	1,545	749
M333	A	R	Summer	1994	20	806	471	234
M913	SA	R	Summer	1993	29	491	269	226
M913	A	R	Summer	1994	17	354	149	NC
M913	SA/A	R	Summer	1993-1994 ^p	46	468	304	267
M814	SA	R	Summer	1994	19	675	697	341
M104	SA	R	Winter	1994-1995	17	1,018	688	234
M123	A	R	Winter	1993-1994	26	1,705	1,305	886
M123	A	R	Winter	1994-1995	16	1,534	687	NC
M123	A	R	Winter	1993-1995 ^p	37	1,891	1,609	872
M403	A	R	Winter	1993-1994	24	958	1,393	1,071
M403	A	R	Winter	1993-1994 ^p	31	1,545	1,373	840
M333	A	R	Winter	1993-1994	15	1,484	1,161	147
M333	A	R	Winter	1994-1995	15	2,136	1,157	NC
M333	A	R	Winter	1993-1995 ^p	27	1,618	1,312	339
M913	SA	R	Winter	1992-1993	17	368	388	74
M913	A	R	Winter	1993-1994	17	1,430	794	263
M913	SA/A	R	Winter	1993-1994 ^p	34	1,848	1,623	485

¹A = Adult, SA = Subadult.

²R = Resident, U = Status unknown.

³Total = Total of all relocations, Annual = December through November, or June through May; Summer = June through December; Winter = December through May.

⁴Seasonal data reflect periods of data analysis and do not necessarily define period of monitoring. ^p Data set pooled among years.

⁵NC = No core detected.

1987) although this relationship has not been previously substantiated in wolverines. Home range size of adult males during the mating period (January through August, Mead et al. 1993) averaged 1,515 km² ($\bar{n}$ = 7 animal-seasons, SD = 365, range = 1,159-1,920). Data were inadequate to measure non-mating season home ranges.

Home Range Overlap

Annual home range fidelity was measured for 2 individuals (Fig. 2.1). Annual home ranges of female F703 overlapped 62.1% for the years 1993 and 1994. The annual home ranges of male M123 overlapped 60.8% for the same time period. Mating home range overlap of neighboring adult males averaged 12.7%

Average annual home range overlap of 4 adult females was 7.7% (Table 2.5).

Neighboring adult females F703, F602, and F502 occupied a combined space of 1,043 km² during 1993. Although not totally exclusive in total home range use, their distributions did appear spatially separated. Home ranges for females F703 and F602 overlapped 26.8% (Fig. 2.2). Overlap in this instance was more spatial than temporal with the majority of F602's activity restricted to the southern portion of her home range, out of the range of F703. Core areas for adult females were exclusive (Fig. 2.3). The death of both F602 and F502 in 1993 left only F703 and F203 (the 1 remaining kit of F502) occupying the former range of the 3 females. Female F203 overlapped 43.4% of her mother's former home range throughout her subadult and first adult year. Eighty-two percent of the area used by these 4 females fell within the home range of resident male M123 (Fig. 2.2).

Four adult male pairs averaged 16.0% overlap while 4 adult/subadult male pairs averaged 26.1% overlap (Table 2.5). Resident males M123, M403, and M333 overlapped on 119 km² in the northern end of the Sawtooth Wilderness (Fig. 2.4). This overlap may have

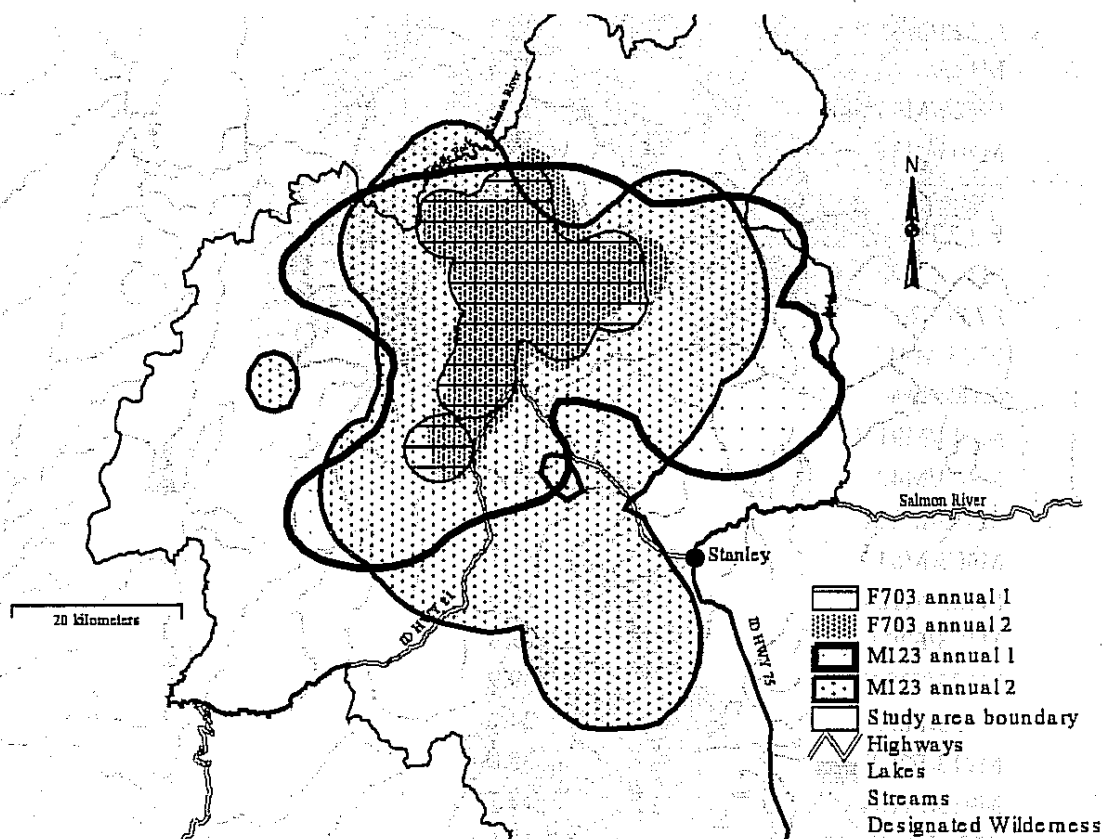


Fig. 2.1. Annual home range fidelity and overlap of adult male wolverine M123 and adult female F703 in central Idaho. Annual home ranges of F703 represent December-November 1993/1994 - 1994/1995. Annual home ranges for M123 represent June-May 1993 and 1994.

Table 2.5. Home range overlap of wolverine pairs in central Idaho, 1992-1995. Overlap represents the 99% kernel utilization volume estimate common in home range pairs. Home range pairs are stratified by age class.

Animal Pair	% Overlap
<u>Adult/Adult</u>	
M123/M913 ^a	26.2
M123/M403	02.0
M123/M333	08.1
M403/M333	26.9
F703/F602	19.7
F703/F502	05.4
F502/F602	01.7
F703/F203	04.1
F703/M913 ^a	13.7
<u>Adult/Subadult</u>	
M123/M913 ^a	25.3
M403/M423	37.1
M333/M814	09.3
M403/M814	32.7
M123/M104 ^a	59.0
M123/F203 ^a	29.8
M123/F204 ^a	39.9
M123/F803 ^a	24.2
M913/F204 ^c	35.0
M913/M104 ^c	17.7
F703/F203	10.5
F703/M913 ^a	11.0
F703/F803 ^a	38.7
F703/M104 ^a	40.1
F703/F204 ^a	38.0
F502/F803	05.6
F502/M913	04.0
F203/M104 ^d	16.1
F203/F204 ^d	02.3
<u>Subadult/Subadult</u>	
M913/F803 ^b	28.5
M104/F204 ^b	42.5

¹Superscript indicates category of known or assumed kinship. No annotation indicates unknown relationship. a = parent/offspring, b = sibling, c = half-siblings, d = cousin.

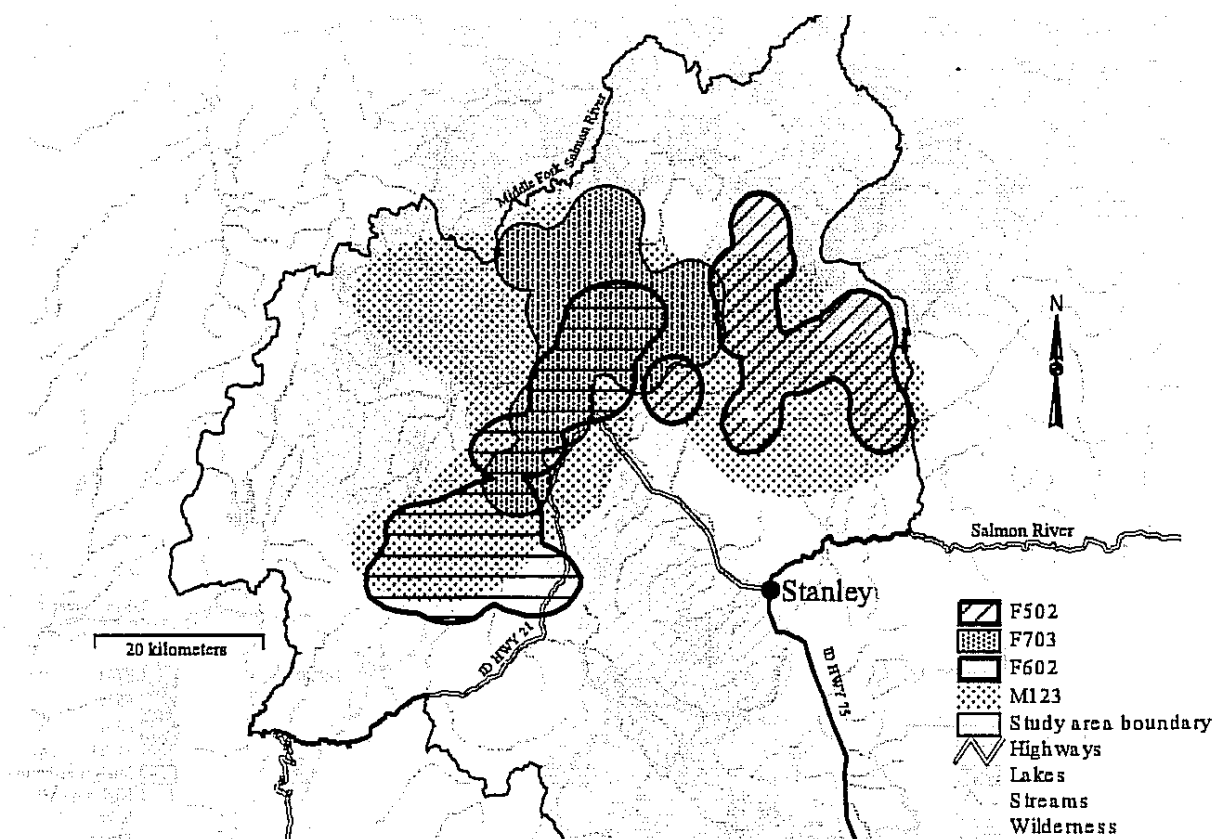


Fig. 2.2. Home range distribution and overlap of resident adult male and resident adult female wolverines in the northern portion of the central Idaho study area in 1993.

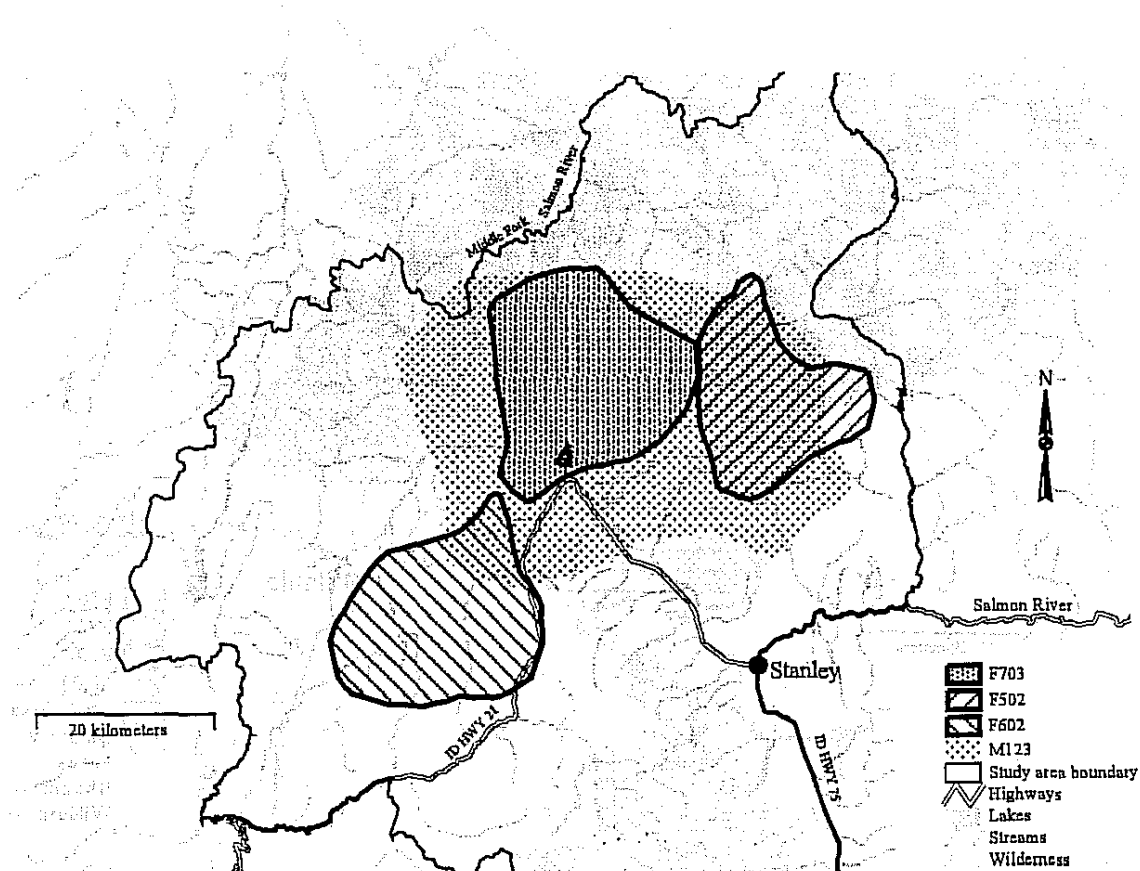


Fig. 2.3. Core home range distribution and overlap of resident adult male and resident adult female wolverines in the northern portion of the central Idaho study area, 1993.

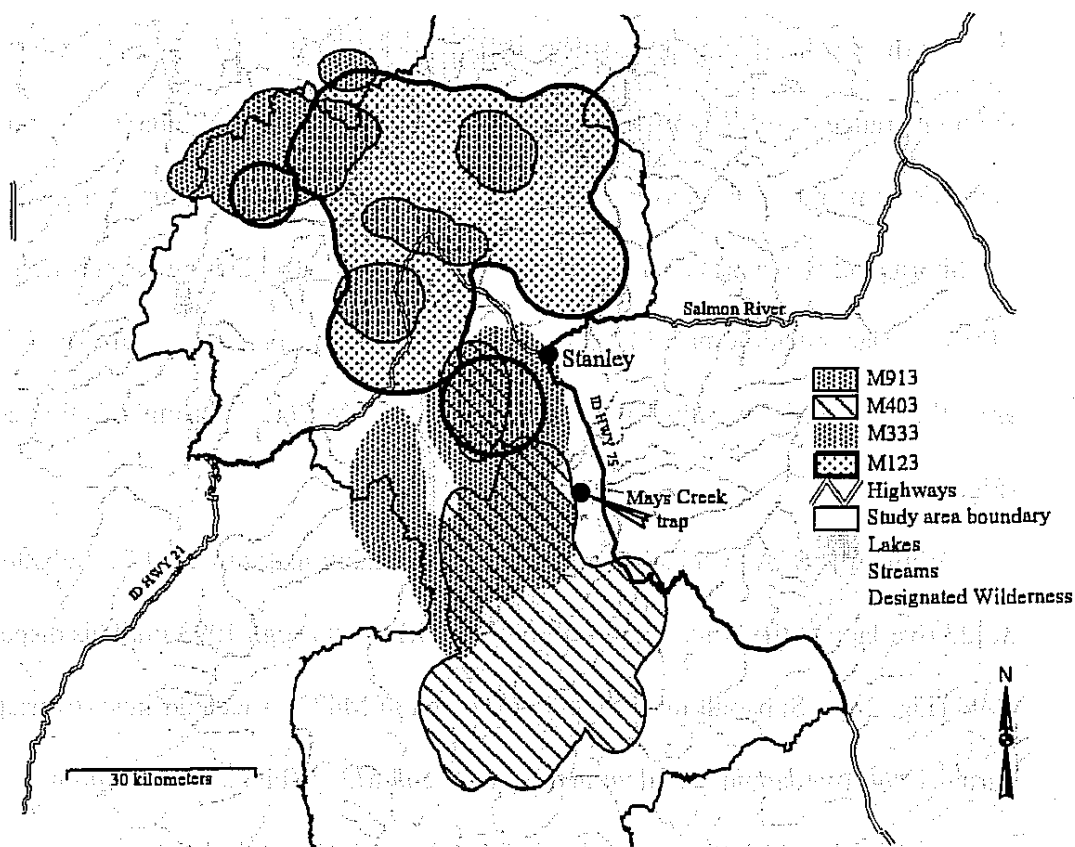


Fig. 2.4. Home range distribution and overlap of adult male wolverines in central Idaho. Home ranges for M123, M913, and M333 are 1994-1995 annual distributions while the polygon for M403 is his 1993-1994 home range. The May's Creek trap was the 1995 capture site for unmarked female F885.

been associated with the presence of unmarked female F885 captured in the May's Creek trap in 1995. Male M333's resident status likely developed from early 1993 to 1994 therefore his spatial position may have been in transition during the overlap period. Core areas for 2 of 3 adult males were exclusive. Males M403 and M333 overlapped core areas by 17.1%.

In the northern study area, subadults F203, F204, M104, M913, and F803 overlapped the home range of resident male M123 (Table 2.5, Figs. 2.5-2.7). Subadults overlapped their mother's home range by an average of 32.0% (SD = 14.0), and the home ranges of neighboring adult females by an average of 7.8% (SD = 4.0). During his subadult year, male M913 overlapped adult male M123 by 25.3%. Early in his first adult year, M913 left his natal area, then returned 2 months later, overlapping M123 by 26.2% through his first adult year (Fig. 2.8).

Within the SSA, 3 subadult males overlapped adult males by 26.4%. Subadult male M423 overlapped the home range of adult male M403 through 1993 until his dispersal in early 1994 (Fig. 2.9). Subadult male M814 used much of M423's vacated range (overlap = 30.5%) during 1994, overlapping resident males M403 and M333 (Fig. 2.10). Temporal overlap between M814 and M403 occurred only from April 1994 to July 1994.

Spatial changes in seasonal home range use were measured as lateral shifts calculated from home range overlap and vertical shifts measured as seasonal variation in elevational use.

Multiple summer and winter home ranges were measured for 5 wolverines. Seasonal home range use among years overlapped 46.1% ($n = 8$ animal-season pairs, SD = 11.6) within seasons and individuals. To measure overlap between seasons, relocations within seasons were pooled by individuals. Seasonal overlap varied from 13.3% to 65.5% and accompanied significantly higher elevational use ($P = 0.003$) during summer months for 6 of

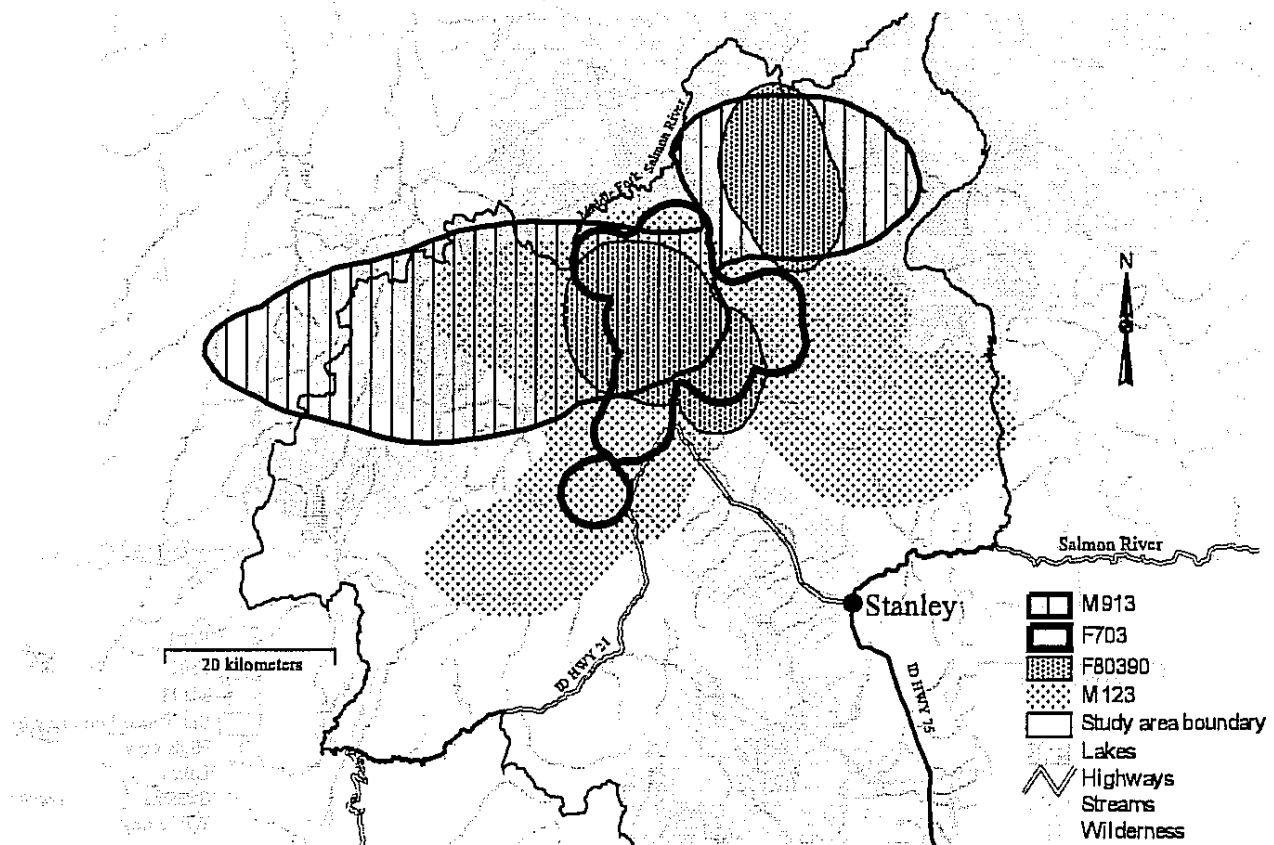


Fig. 2.5. Home ranges of adult wolverine male M123 and female F703, and subadult wolverine male F803 and female M913 in central Idaho, 1993-1994.

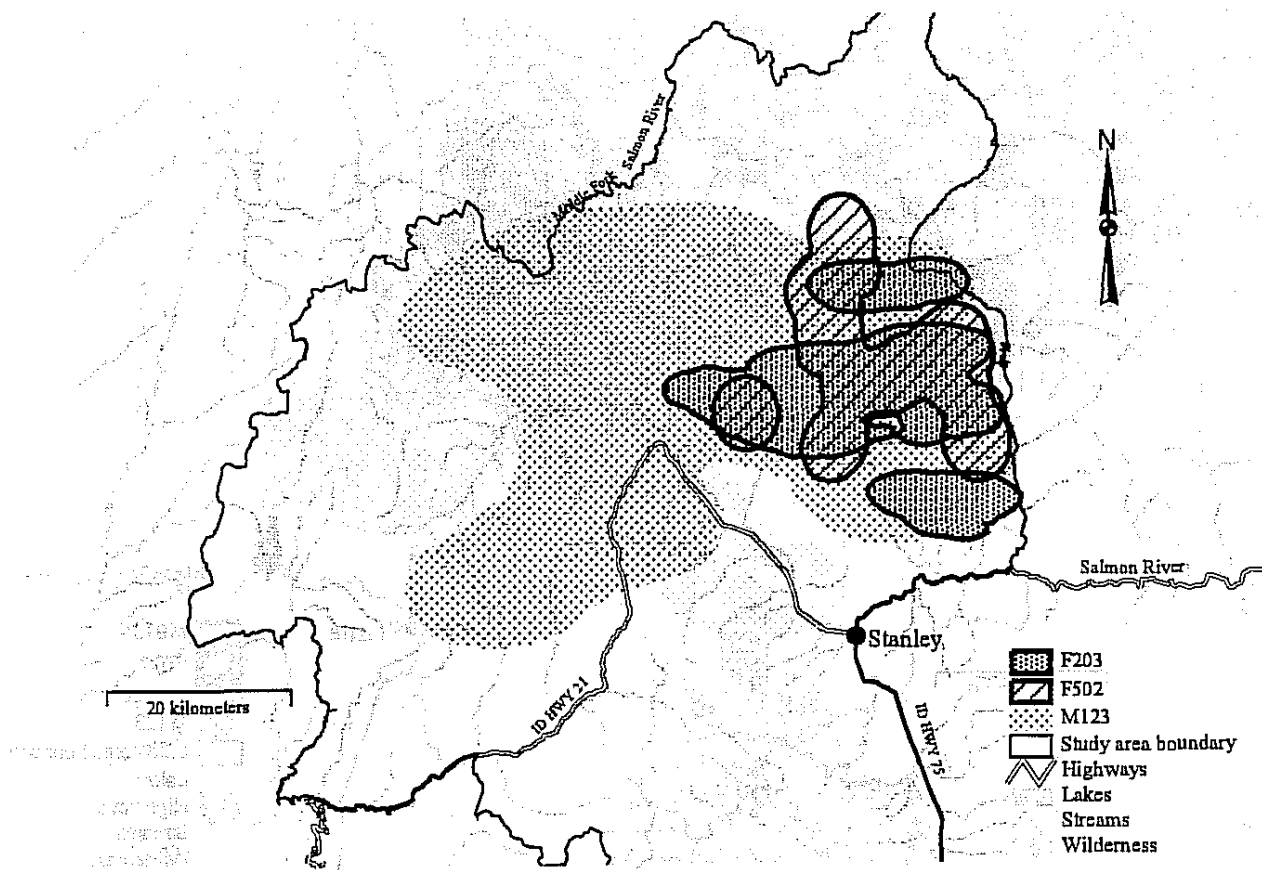


Fig. 2.6. Home ranges of adult wolverines male M123 and female F502, and subadult wolverine female F203 in central Idaho, 1993-1994. Temporal overlap only occurred from August to November 1993 for F502 and F203.

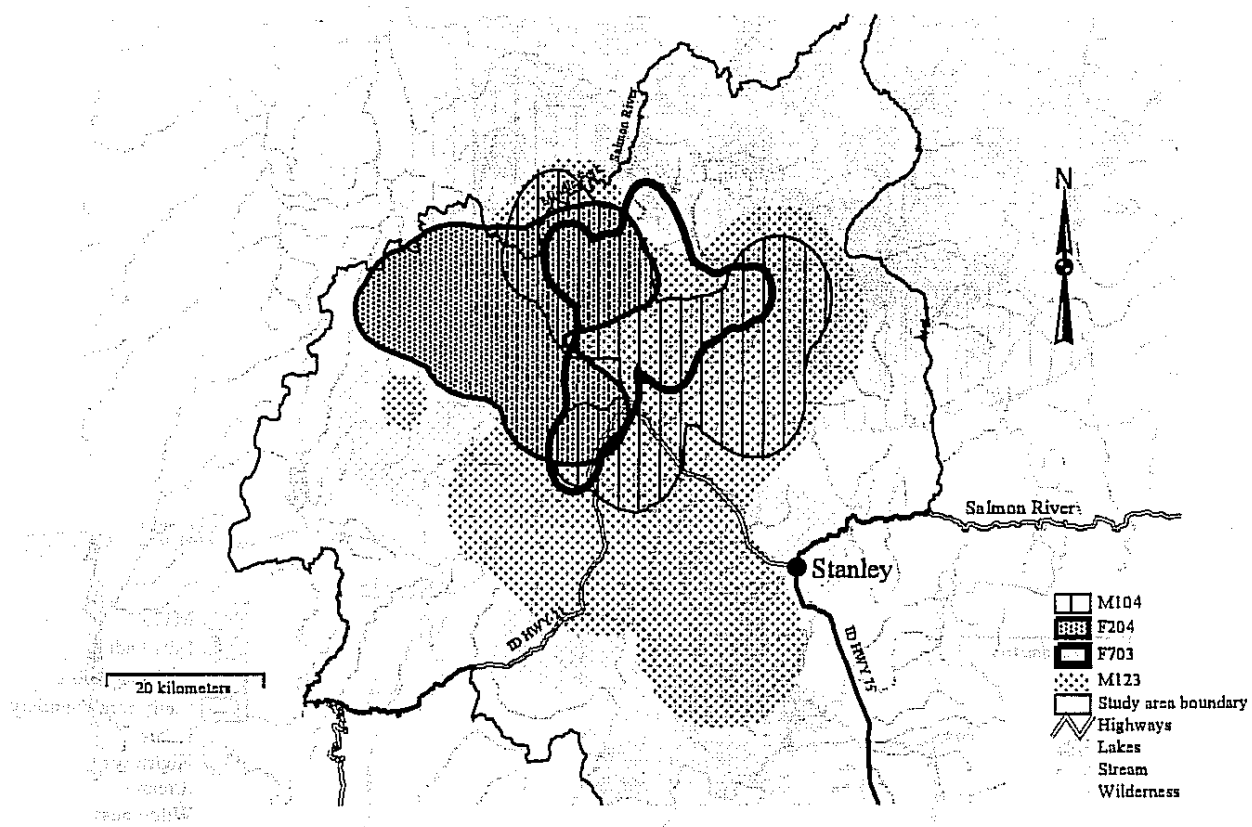


Fig. 2.7. Home ranges of adult wolverine male M123 and female F703, and subadult wolverine female F204 and male M104 in central Idaho, 1994-1994.

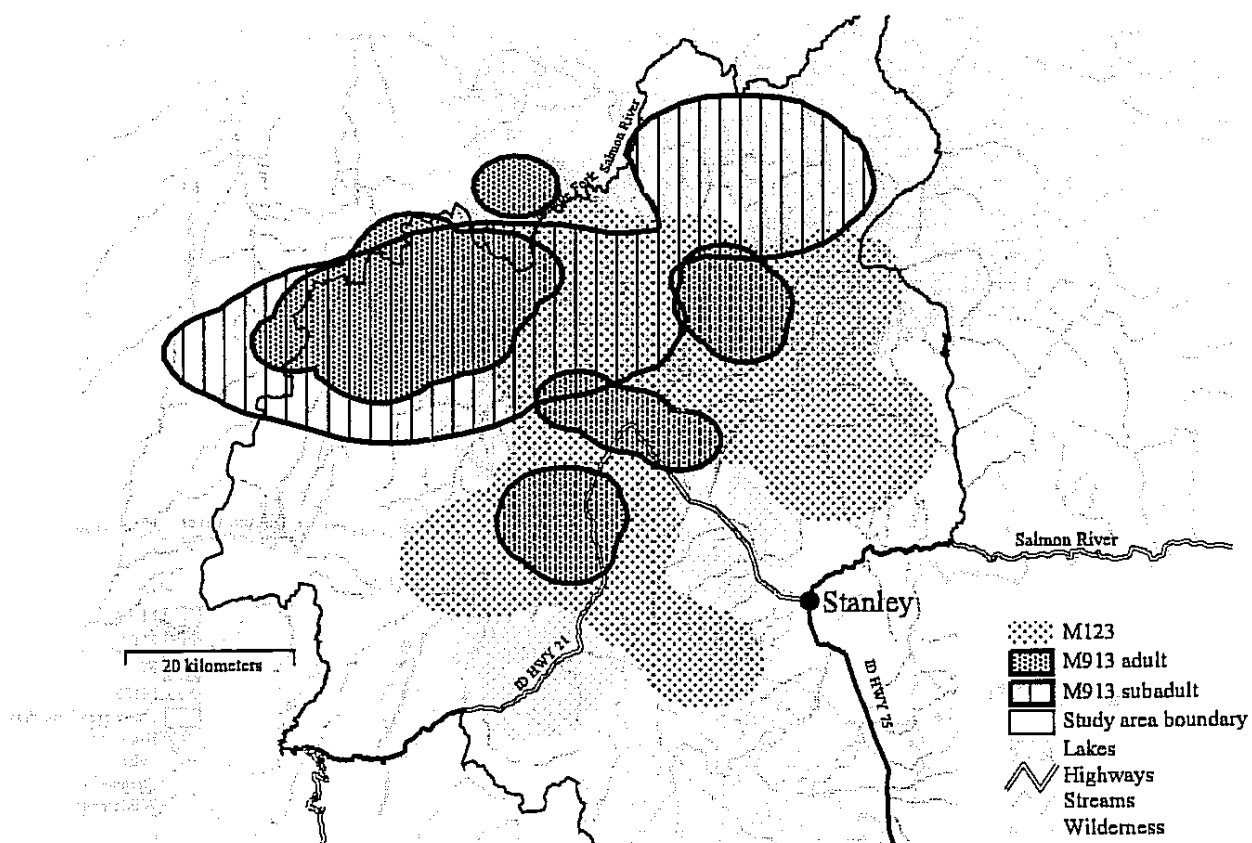


Fig. 2.8. Combined annual home ranges of adult male wolverine M123, and subadult and adult home ranges of male wolverine M913 in central Idaho.

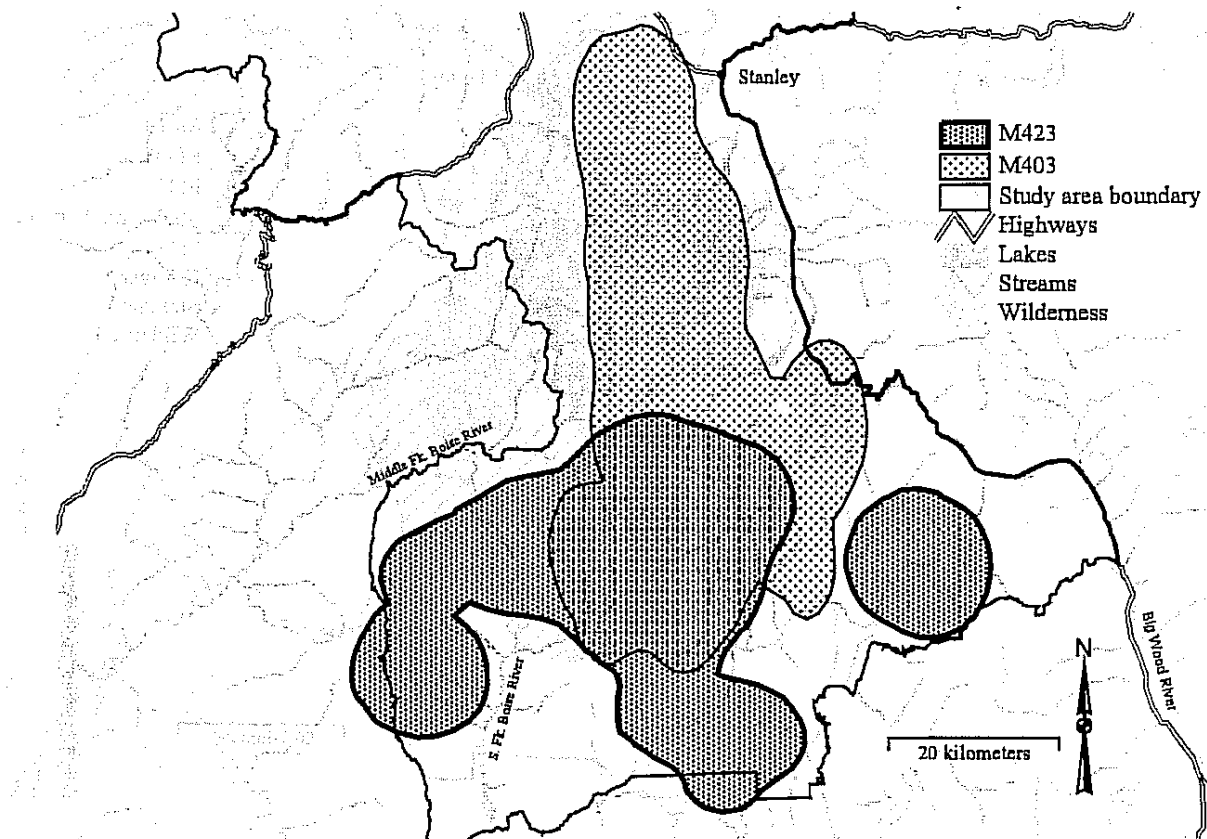


Fig. 2.9. Home ranges of adult male wolverine M403 and subadult male M423 in central Idaho, 1993-1994.

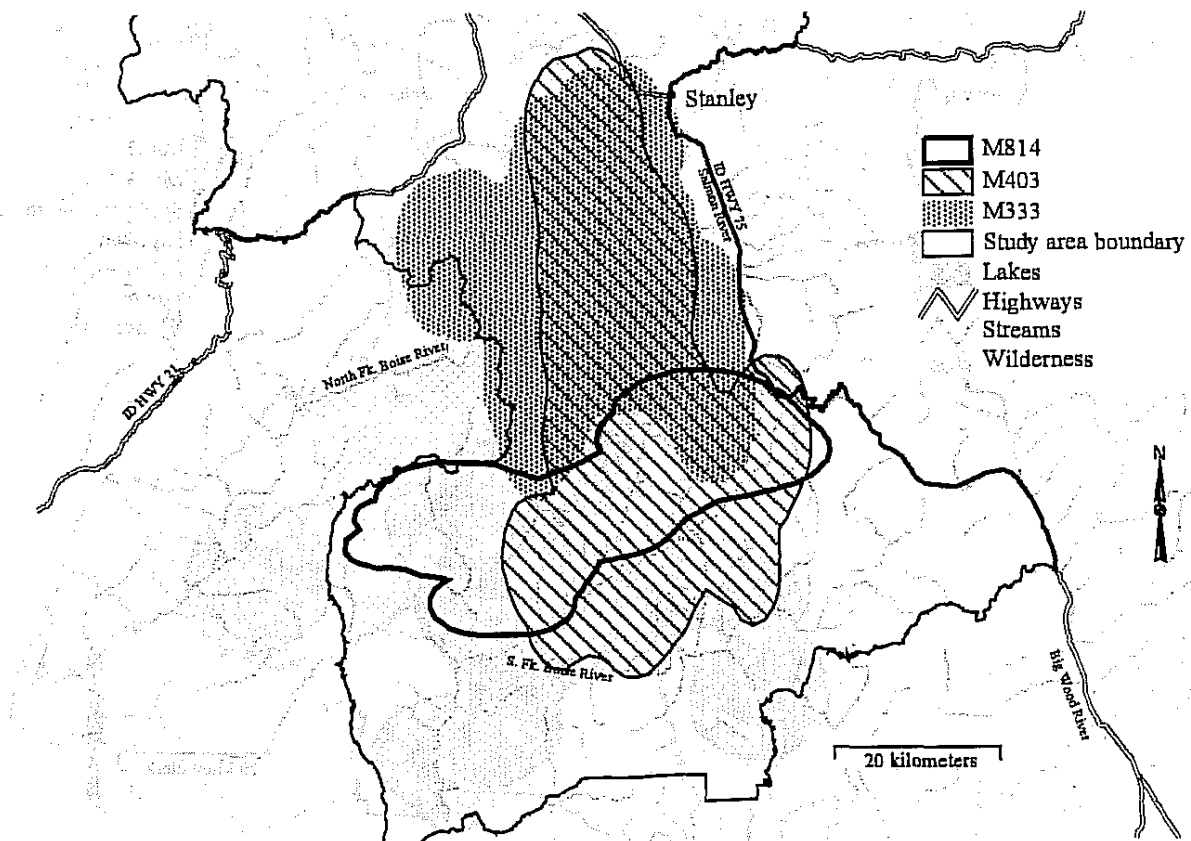


Fig. 2.10. Home ranges of adult male wolverines M403 and M333, and subadult male wolverine M814 in central Idaho, 1993-1995. The polygon for M403 is his 1993-1994 total home range. Polygons for M333 and M814 are 1994-1995 annual home ranges.

13 wolverines (Table 2.6). Seasonal elevation shifts occurred within a range of 1,578 m (range = 1,578-3,108 meters) for an average summer increase in elevational use of 154 m (Fig. 2.11).

DISCUSSION

Home Range Size

Five studies provide estimates of wolverine home range use from radio instrumented study animals (Hornocker and Hash 1981, Gardner 1985, Magoun 1985, Whitman et al. 1986, Banci 1987). Researchers focused primarily on home range size, stratified by sex and season. These studies also addressed home range overlap to investigate a postulated spacing pattern of intrasexual exclusion. Differences in area characteristics, and sampling and analysis techniques between these studies are likely responsible for some of the reported variation, although differences may indicate a naturally occurring diverse spatial and social character across the wolverine's range. Hatler (1989) noted several commonalities of spatial use apparent from previous works. Males have larger home ranges than females, females without kits have larger home ranges than accompanied females, and home range use appears to vary with season.

Prior to my study, the upper limit of reported wolverine home range size was under 1,000 km². Alaska wolverine researchers reported mean annual home range size for male wolverines at 535 km² (Whitman et al. 1986), 637 km² (Gardner 1985) and 666 km² (Magoun 1985), while Montana and Yukon male home ranges were somewhat reduced at 422 km² (Hornocker and Hash 1981) and 382 km² (Banci 1987), respectively. Female home

Table 2.6. Seasonal home range overlap and elevational use of wolverines in central Idaho, 1992-1995. Overlap measurements are based on seasonal home range estimates pooled among years. Percent overlap provides a measure of lateral shift, while elevation provides a measure of vertical shift in seasonal distribution.

ID	Age	Overlap (%) ^a	Mean elevation (meters) with confidence interval and probability of variation		
			$\bar{x}$ Summer	$\bar{x}$ Winter	Prob.
F602	A	65.5	2,310 $\pm$ 52	2,128 $\pm$ 60	0.003*
F703	A	37.7	2,444 $\pm$ 44	2,341 $\pm$ 51	0.005*
F822	A	40.7	2,566 $\pm$ 65	2,581 $\pm$ 114	0.804
F502	A	13.3	2,507 $\pm$ 76	2,426 $\pm$ 55	0.086
M123	A	61.9	2,334 $\pm$ 63	2,178 $\pm$ 68	0.001*
M403	A	59.1	2,384 $\pm$ 88	2,331 $\pm$ 110	0.447
M333	A	34.3	2,391 $\pm$ 157	2,216 $\pm$ 64	0.020*
F203	SA	35.7	2,417 $\pm$ 68	2,326 $\pm$ 50	0.040*
F204	SA		2,408 $\pm$ 115	2,079 $\pm$ 126	0.001*
M913	SA	30.4	2,199 $\pm$ 58	2,124 $\pm$ 78	0.117
M423	SA	47.7	2,323 $\pm$ 101	2,357 $\pm$ 82	0.595
M104	SA		2,242 $\pm$ 172	2,096 $\pm$ 132	0.157
M814	SA		2,354 $\pm$ 148	2,201 $\pm$ 179	0.170

^a Missing data indicates relocation sample size too small for seasonal home range estimation.

* Significant probability of seasonal variation ($P < 0.05$).

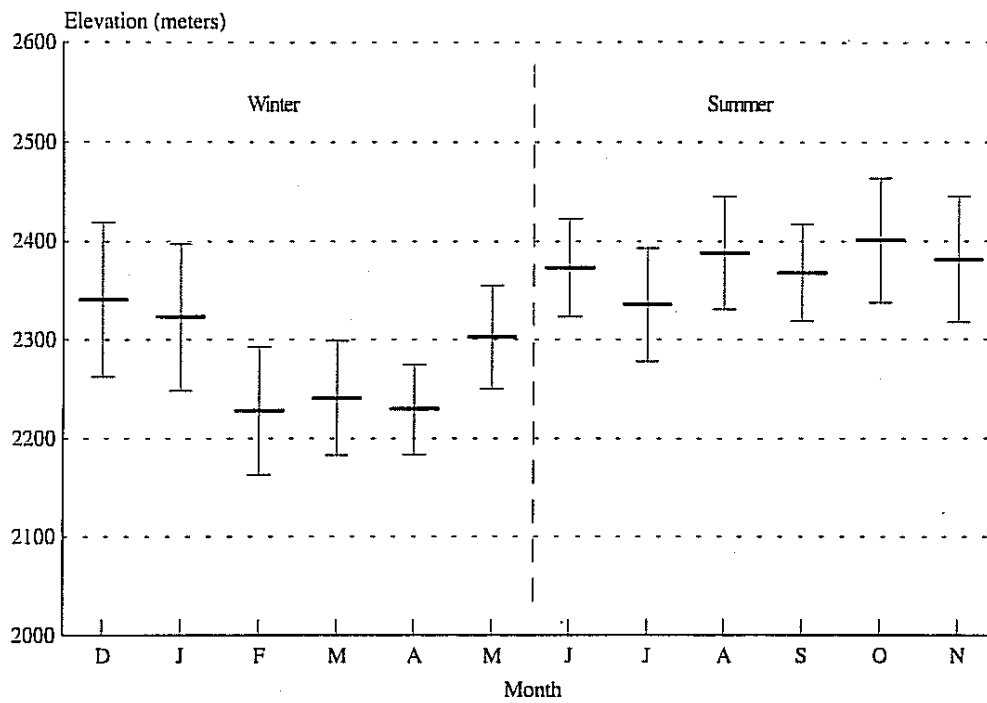


Fig. 2.11. Monthly mean elevational use with confidence intervals of wolverines in central Idaho, 1992-1995.

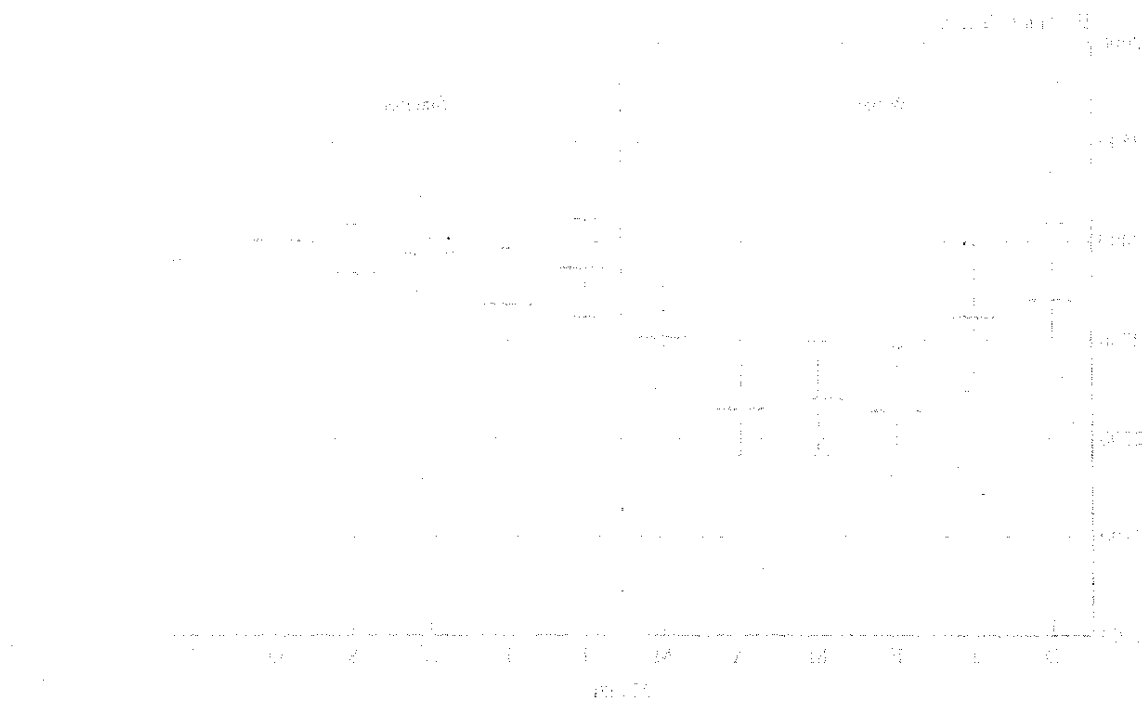


Figure 10. Relationship between the number of days (X-axis) and the number of days (Y-axis) for the data set shown in Figure 9.

ranges varied from 104 km² in Alaska (Magoun 1985) to 388 km² in Montana (Hornocker and Hash 1981), with 1 Montana female using a 963 km² home range.

Home range size is generally presumed inversely correlated with the availability of resources. Sandell (1989) based this relationship on the requirement of females, in non-cooperative species, to rear young by themselves, with reproductive success correlated with nutrition. This relationship has not been well studied in carnivores. Gittleman and Harvey (1982) suggest large geographic variation in home range size of African lion (*Panthera leo*) and red fox (*Vulpes vulpes*) in North America and Britain (Macdonald 1983) in relation to prey densities as evidence of this relationship. Minta (1992) reported large seasonal variation in home range size of male badgers (*Taxidea taxus*) in response to the spatial and temporal distribution of estrous females. Resources, in this instance were females rather than food, supporting the contention that food controls female dispersion while the spacing of males is tied to the distribution of females (reviewed in Gittleman and Harvey 1982, Macdonald 1983, Sandell 1989). Behavior and social constraints may influence a species response to variations in resource availability. Spatial adjustment related to food abundance appeared to be influenced by the presence of transients in Great Basin coyotes (*Canis latrans*) (Mills and Knowlton 1990). Gittleman and Harvey (1982) caution against inter-specific comparisons of ranging behavior of carnivores, due to variability in intra-specific behavior.

Food availability was not measured within any of the North American wolverine study areas, and the relationship between resource dispersion and home range size in wolverines is not known. Hornocker and Hash (1981) believed an abundant and consistent ungulate prey base in their study area explained higher estimates of wolverine density than estimates available for wolverine populations at higher latitudes. Ungulates appear to provide adequate

food for central Idaho wolverines. Defense of feeding sites was not apparent, while sharing of resources appeared common within kinship groups. Long daily movements in Idaho wolverines may reflect a widely dispersed, although not necessarily limited, food resource. Patchy dispersion of resources generally leads to increased home range size (Macdonald 1983) and may also lead to resource competition (Sandell 1989). Highly concentrated food resources may force breakdowns in established territory boundaries, altering the social system, and allowing individuals to exploit new opportunities (Lott 1991). Although this was not evident in my population, Yukon wolverines concentrated on spawning streams to take advantage of spawned out salmon (Banci 1987).

Gardner (1985) suggested home range size may be related to habitat and topography as well as food availability. Central Idaho wolverines appeared highly selective in choice of natal denning and kit rearing habitat. Females foraged 19 km from den sites indicating den site selection based on factors other than food availability. Krott (1959) believed the availability of suitable denning habitat may influence the size of wolverine territories. Even with adequate food, wolverines may not be resident without suitable denning habitat.

In social carnivores, group size rather than individual needs may dictate the spatial requirements of the species. Changes in food abundance may alter group size while territory size remains unchanged (Macdonald 1983). At higher densities, spotted hyena (*Crocuta crocuta*) were more gregarious and territorial while territory size remained unchanged (Kruuk 1972). Still, the territory must encompass an adequate foraging area to provide for the needs of all residents. Subadult wolverines in Idaho remained associated with their natal area until sexual maturity. Their presence was tolerated by resident adults and resources were commonly shared. Whether subadults are viewed as competitor or progeny is a function of

the derived social structure and will likely influence the spatial pattern. Macdonald (1983) suggests that to an extent which depends on their degree of relationship, the net cost of tolerance to the occupier's fitness is diminished in proportion to the benefit accruing to the interloper, if they are related. Large home ranges of Idaho wolverines may reflect the resource requirements of offspring with extended dependency needs in addition to the energetic requirements of the parent. The home range of F822 was nearly 50% smaller than the next largest home range of a reproductively mature female (F502, Table 2.1). Subjective aging suggested F822 was reproductively mature, while teat measurements placed her in the category of nullipary (see Reproduction and Table 1.2). Had she produced no kits during her lifetime, her small home range may reflect female spatial needs without the added energetic requirement of providing for offspring.

Seasonal Shifts in Distribution

Gardner (1985) reported seasonal shifts of wolverine elevational use in Alaska associated with the early summer emergence of ground squirrels at higher elevations and higher availability of carrion at lower elevations during winter months. Whitman et al. (1986) also reported seasonal elevational shifts of wolverine habitat use likely induced by changes in seasonal prey abundance. Elevational shifts were significant ($P < 0.05$) in 6 of 13 Idaho wolverines (Table 2.6), including 2 adult females, 2 adult males, and 2 subadult females.

Magoun (1985) and Banci (1987) theorized that increased movements of adult males during the spring-summer mating period may result in larger home ranges. Their assessment was based on limited home range data from Alaska (Gardner 1985); and movement data for wolverines from Montana (Hornocker and Hash 1981) and Alaska (Magoun 1985). Sandell (1989) suggested that home range size may increase as males compete for mates. Where

competition for mates is reduced, males need not roam widely in pursuit of mating partners, therefore lack of seasonal variability in home range size would be consistent with exclusive home range use (Sandell 1989). Idaho wolverines appeared to increase movements during the mating period (Table 3.2), consistent with data from Alaska (Magoun 1985) and Montana (Hornocker and Hash 1981), but my data were inadequate to measure variability in home range size of mating versus non-mating ranges.

Female wolverine accompanied by kits may display reduced home range size. Banci (1987) measured home ranges of 5 accompanied and 5 unaccompanied females and found home ranges of females with young 50% smaller than those of unaccompanied females. High variability in home range size of Idaho female wolverines made comparison difficult, although 1 female provided 3 years of reproductive data. In 1993, female F703 produced no kits, displaying a March through August home range nearly 2 times the size of home ranges within the same period in 1994 and 1995 when accompanied by kits (Table 2.2).

Home Range Overlap and Spatial Strategy

Exclusive home ranges develop in the presence of stable and evenly distributed food resources, whereas overlapping ranges are likely when the timing and spacing of available food varies (Sandell 1989). Where several exclusive female territories are encompassed within that of 1 male, female dispersion may control the spatial pattern of the male (Macdonald 1983). This pattern of intersexual overlap appears as one of the few spatial commonalities among previous wolverine studies, while degrees of intrasexual overlap varied considerably. Magoun (1985) found most resident female home ranges were maintained exclusive of other females with spatial separation most prominent during summer months. The other Alaska study (Gardner 1985) only found home range overlap within a single adult

and subadult male. Hornocker and Hash (1981) found no evidence of exclusive home range use and suggested that trapping harvest may have created behavioral instability in the population, allowing inadequate time for establishment of site tenure. Hornocker and Hash (1981) and Banci (1987) concluded that a lack of understanding of familial relationships in their wolverine populations made assessment of spatial relationships difficult.

Within the home range of adult male M123, resident juvenile wolverines remained closely associated to their mother's home range until separation in mid- to late August of their first year. As subadults they overlapped the home range of the resident male as well as their mother and siblings. In 2 cases subadults were found associating with a neighboring adult female, and a neighboring adult male. In both instances the adults were kin to the subadults.

Contact between juveniles and the adult male may have occurred early in the juvenile's life. In 1994, adult male M123 was located with adult female F703 in late May near weaning age of her 2 kits, although it was not determined if the kits were present. In April of 1995, M123 was located in a maternal den with F703. The female was later confirmed to have 2 kits that would have been approximately 7-weeks-old at the time of M123's visit to the den. Association at this early stage of juvenile development would suggest a familiarity between the adult male and female beyond that generally expected within a polygynous species. Ewer (1973) suggests that successful mating requires not only that male and female should meet but that they should be physiologically and behaviorally adjusted to each other. The dominance status of the resident male may provide him with what Eisenberg (1981) termed a "priority of access" to resident females resulting from established pair bonding, or as Eisenberg concedes, some female "choice" may be involved. A requirement of familiarity for mate pairing might lessen the need for the resident male to defend access to females. The male's reduction in

mating opportunities may be offset by increased kit survival resulting from his association with offspring.

III. MOVEMENTS AND DISPERSAL

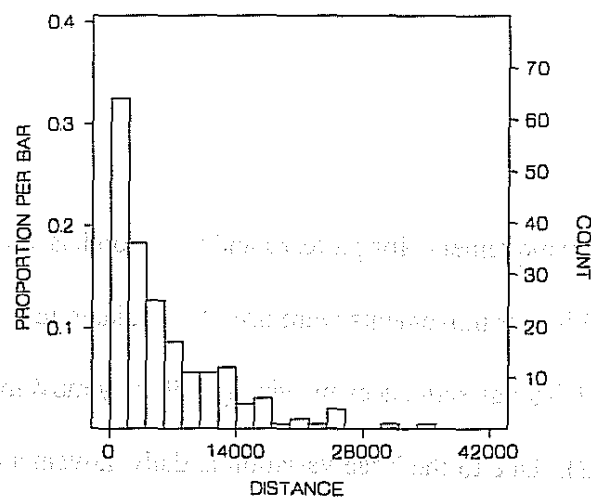
RESULTS

Movements

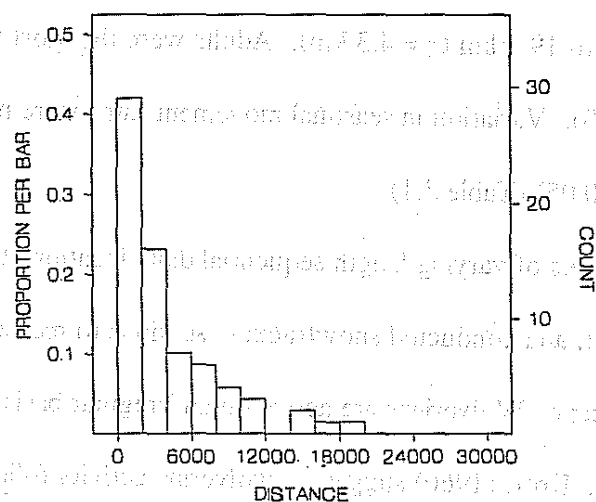
I analyzed daily movements for patterns and variation based on sex, age, and season. Only approximate 24-hour movements were used to eliminate underestimation. Daily relocations included 2-5 day sequences providing 219 daily movement distances (male $n = 116$, female $n = 103$). Due to the large variation in daily movements (Fig. 3.1), distances were log transformed for statistical analysis (Zar 1984). Data were not adequate to test for differences among years.

Daily movements of male wolverines ranged from 0 to 35.2 km ($\bar{x} = 7.6$ km), and were significantly greater than female movements ($F = 4.218$, $P = 0.041$). Females made daily movements of 0 to 19.8 km ($\bar{x} = 4.3$ km). Adults were the most variable age class ($F = 15.995$, $P = 0.000$). Variation in seasonal movement rates were not apparent within sex or age classes ($P > 0.05$) (Table 3.1).

I collected sets of varying length sequential daily locations to look for patterns in the rate of movement, and conducted snowtracking sessions to measure how wolverines moved across the landscape. Wolverines are active on an irregular basis (Krott 1960, Haglund 1966, Gittleman 1989). Krott (1960) suggested wolverine activity follows a somewhat continuous pattern of activity and rest cycling about every 3-4 hours, the pattern Idaho wolverines followed. Snowtracking revealed wolverines generally traveling a direct route with little meandering or apparent hunting or foraging behavior, with occasional stops to feed or rest.



Distance moved (m) males



Distance moved (m) females.

Fig. 3.1. Histograms of daily movement distances of wolverines in central Idaho, 1992-1995.

Table 3.1. Seasonal daily movements (meters) of wolverines in central Idaho, 1992-1995.

	Summer				Winter				Seasonal variation ¹
	Mean	Range	n	Confidence interval ¹	Mean	Range	n	Confidence interval ¹	
Adult Male	6,545	200-25,801	35	2,349-5,672	11,293	141-35,151	37	4,335-10,290	P = 0.051
Subadult Male	4,591	283-12,766	16	1,981-5,494	4,870	0-24,829	17	1,463-5,320	P = 0.678
Adult Female	3,434	0-16,184	42	1,330-2889	4,903	0-19,840	27	916-3,925	P = 0.965
Subadult Female	3,679	100-16,184	14	903-4,340	8,001	632-17,599	9	2,017-12,637	P = 0.101

¹ Confidence intervals and probability values based on lognormal distribution. Confidence intervals are back-transformed.

Through the study period, wolverines were snowtracked 32.4 km with snowtracking sessions defined by periods of movement between stopping points such as scent marks, foraging sites, investigative sites, or rest sites. Of 127 of these snowtracking sessions conducted from February 1993-April 1994, wolverine movement was subjectively described as "direct" in 101, or 80% of these sessions. Meandering movements generally occurred as individuals approached or investigated foraging sites. Field personnel commonly noted the traveling wolverine's lack of interest in sites that appeared to present potential food such as red squirrel (*Tamiasciurus hudsonicus*) middens or areas of concentrated varying hare (*Lepus americanus*) activity.

Dispersal

Four males moved distances ≥ 100 km (Figs. 3.2-3.4). Two dispersing males appeared to establish in new areas, while 2 returned to the study area. Dispersals were made by males believed to be, or confirmed as 2 years old. No females left the study area.

DISCUSSION

Movements

Wolverines in Yukon (Banci 1987) and Montana (Hornocker and Hash 1981) moved greater distances in summer than in winter. Seasonal variation in movement distances in Idaho wolverines was not significant ($P \geq 0.05$) (Table 3.1), although substantial variation was evident among adult males. Several long distance movements of adult males occurred during the mating period from February through June (Table 3.2). This seasonal variation was not evident in subadult males.

In several instances I noted that hunter's camps, trap lines, and bait stations were visited or investigated by study animals several times within and among years. Bait stations

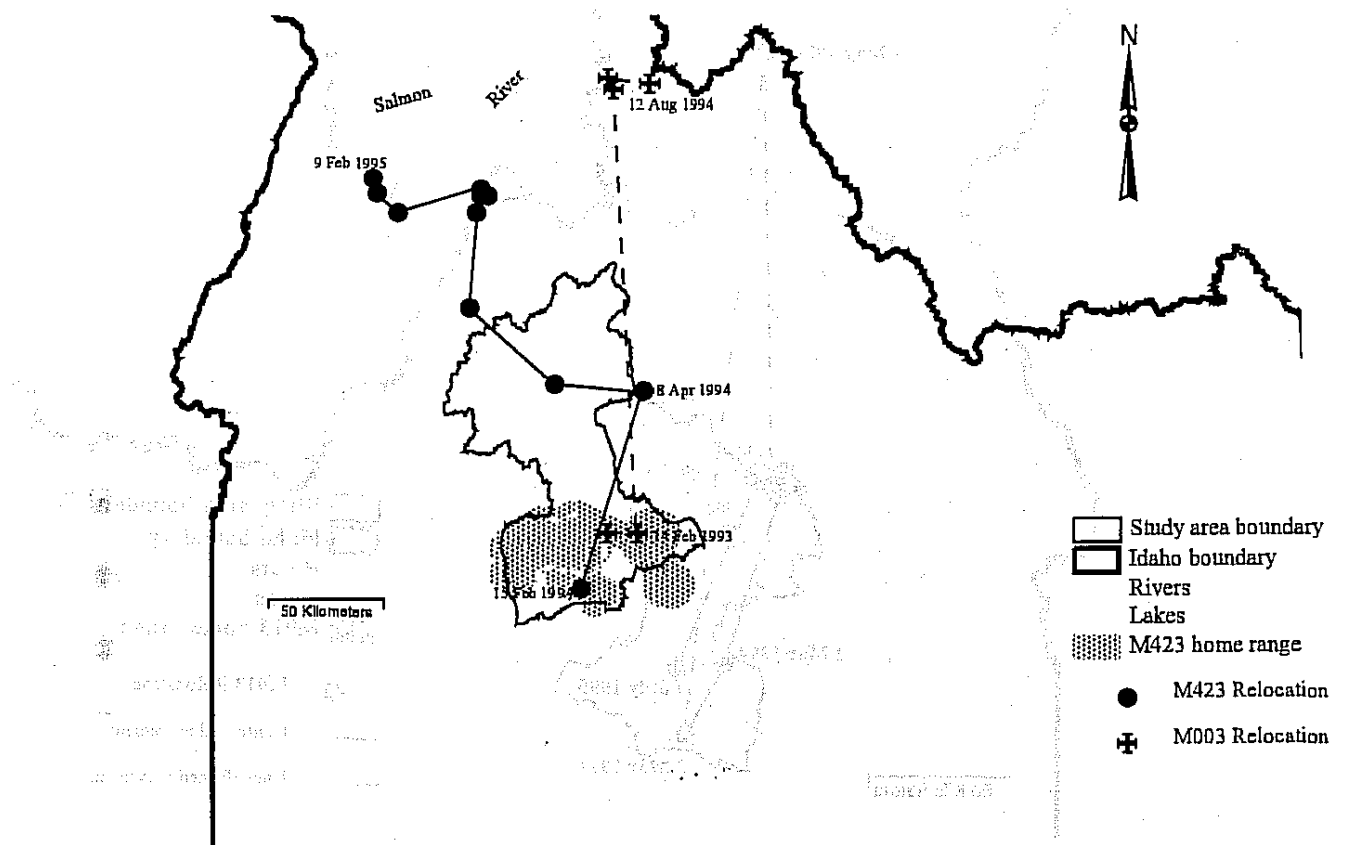


Fig. 3.2. Dispersal of male wolverines M423 and M003 in central Idaho, 1993-1995.

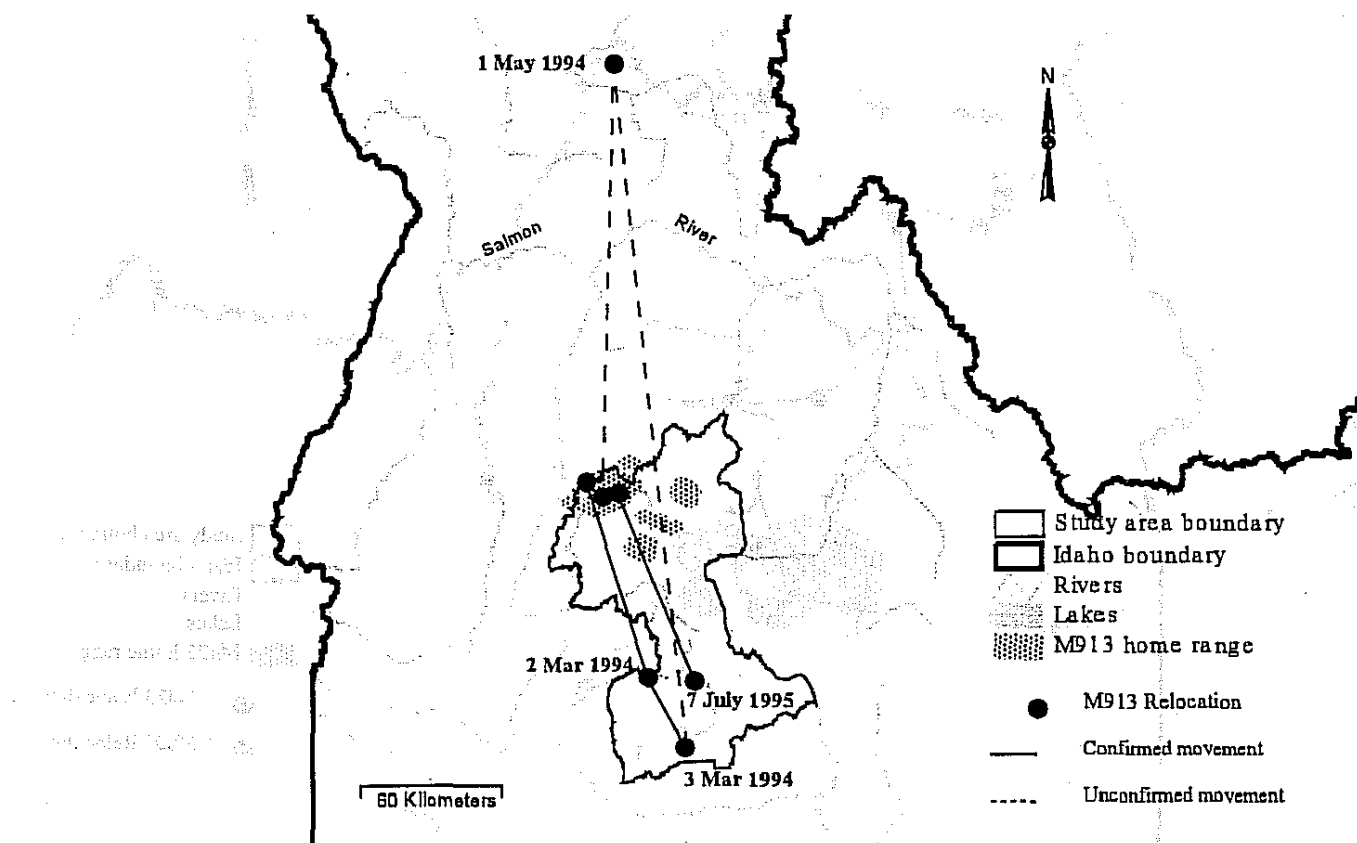


Fig. 3.3. Long distance movements of wolverine M913 in central Idaho, 1994-1995.

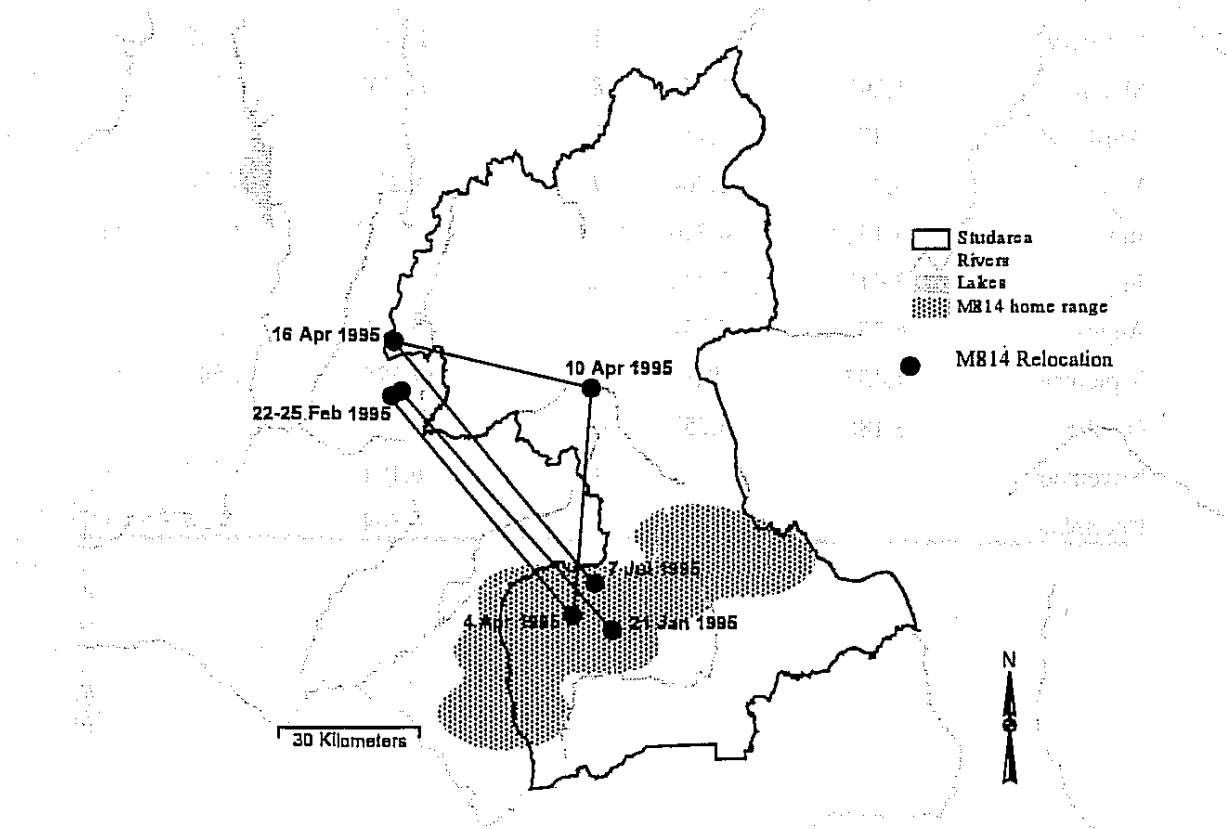


Fig. 3.4. Long distance movements of wolverine M814 in central Idaho, 1994-1995.

Table 3.2. Monthly mean daily movements of adult wolverines in central Idaho, 1992-1995.

Month	Adult Female			Adult Male		
	Mean Daily Movement (m)	SD	(n)	Mean Daily Movement (m)	SD	(n)
January	2,228	1,225	3			2
February			1	11,478	9,423	6
March	1,293	1,977	8	14,752	8,378	16
April	7,473	7,757	7			2
May	5,960	2,764	7	9,223	12,746	5
June	4,198	4,710	7	10,413	7,364	11
July	3,017	2,941	12			1
August	6,273	5,734	8	5,086	5,222	6
September	1,457	816	4	4,125	4,543	11
October	3,188	3,257	13			0
November			1	6,191	4,363	6
December			1	4,864	4,900	6

established in 1992 but abandoned in 1993 were visited by wolverines in 1993 and 1994. In 1992 I snowtracked a wolverine investigating marten trap boxes, along a trap line abandoned for the past 3 years (Gary Gadwa, Idaho Dep. of Fish and Game, pers. commun.). While snowtracking in 1993 and 1995 wolverines were found urinating on scent stations used in previous years. This revisiting of historical scent stations was also noted by Hornocker and Hash (1981).

Wolverines showed similar timing of their movements in successive years. Dates of recapture or revisits to traps for resident wolverines were closely timed. Male M123 was first captured on 8 April 1993. In 1994 and 1995 he was captured in this same trap on 9 April and 3 April, respectively. Female F885 was first contacted by remote camera photograph at the Mays Creek (SNF) trap on 8 April 1994. She was captured in this trap in 1995 on 10 April. These were the only dates she was documented visiting this trap.

I collected sets of daily relocations to see if movement patterns could be distinguished. Although inconclusive, these sequences suggest a pattern of movement comprised of a series of short distance localized movements interrupted by short duration long distance movements (Fig. 3.5). Individuals generally remained in an area for a short period of time, perhaps pressured by an adaptation to continually patrol along a network of foraging sites, revisiting sites which provide a high probability of resource presence. These may include trap lines, hunter camps, or livestock allotments providing carrion during winter months, or rodent habitations or ungulate calving or fawning areas during spring and summer months. Trap and bait sites became part of the individual's gleaning network. This may explain why resident wolverines, following established networks, only occasionally revisit trap sites, while inexperienced subadults frequent the sites. As suggested by Hornocker (pers.

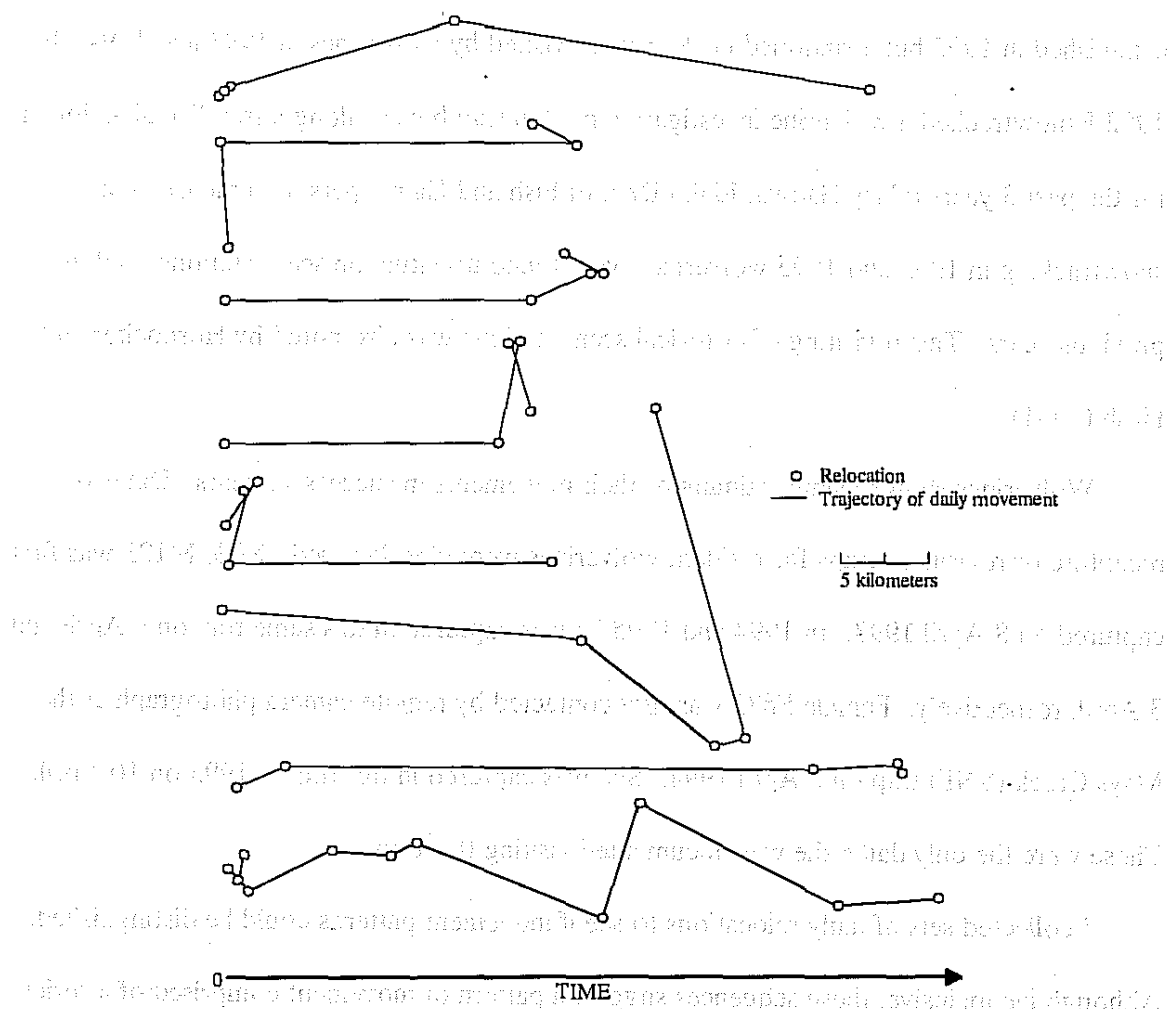


Fig. 3.5. Daily movement sequences for 8 wolverines in central Idaho, 1992-1995.

commun.) it may profit the wolverine to apportion its time between several foraging sites rather than remain on a particular site even though forage is still available, leaving the individual to rely on opportunity for the next meal. Scent-marking may play a role in maintenance of gleaned sites.

Movement records from 3 other studies documented long distance movements, but the relationship between simple movements and actual dispersal was unclear. Studies have described movements as little as 15 km as dispersal, and movements of over 300 km simply as movements. Gardner (1995) reported the longest movement distance on record for a wolverine was recorded by a trap capture of a 2-year-old male 378 km from its collaring location. Hornocker and Hash (1981) recommended a regional management approach based on movements of their study wolverines outside their study area, although they did not provide movement distances. Magoun (1985) reported a 300 km movement of an unknown age female. Idaho wolverines also traveled extended distances (Table 3.3) with 3 individuals traveling over 200 km in apparent dispersal attempts.

Dispersal

Emigration from the natal area usually assumes displacement of subadult individuals due to social pressure or partitioning of resources. Wolverine researchers have assumed the presence of a social mechanism for displacement of subadult and juvenile wolverines based on minimal evidence of conspecific aggression supplemented with records of long distance movements in young individuals. Magoun (1985) provided the most compelling evidence of possible dispersal in juvenile and subadult wolverines, reporting dispersal attempts related to movements of 100 km and 60 km in a 1-year-old male and female respectively. She also suggested dispersal attempts may occur in younger animals citing incidents of disappearance

Table 3.3. Movements that occurred outside of home ranges for wolverines in central Idaho 1992-1995. Distances are approximate measures from point of relocation to nearest boundary of 90% kernel home range.

ID	Date of movement	Approximate age (years) at movement	Distance moved (km)	Post-movement response or comment
M913	Mar 1994 ¹	2	100	disappeared for 67 days
M913	Apr 1994	2+	173	unconfirmed, returned to home range
M913	Apr 1995	3+	20	trap capture, returned to home range
M913	Jul 1995 ¹	3+	75	distribution shift
M423	Mar 1993	1	23	returned to home range
M423	Jun 1993	1+	45	returned to home range
M423	Aug 1993	1+	34	returned to home range
M423	Feb 1994	2		disappeared for 64 days
M423	Apr 1994 ¹	2+	168	dispersed - did not return to home range
M003	Feb 1994	2		disappeared for 484 days
M003	Jun 1995 ¹	3+	199	dispersed - did not return to home range
M814	Jun 1994	1+	18	returned to home range
M814	Jul 1994	1+	6	returned to home range
M814	Jan 1995	1+		disappeared for 32 days
M814	Feb 1995 ¹	2	49	returned to home range
M814	Feb 1995	2		disappeared for 39 days
M814	Apr 1995 ¹	2+	33	returned to home range
M814	Apr 1995 ¹	2+	59	returned to home range
M123	1993-1995	5+	<3	6 movements outside home range
M403	Jul 1993	3+	15	returned to home range
M403	1993-1994	3+	<3	3 movements outside home range
M333	Jun 1994	3+	6	returned to home range
M104	Apr 1995	14 months	5	returned to home range
M104	May 1995	15 months	5	returned to home range
F203	Mar 1994	13 months	9	returned to home range
F203	1993-1994	1+	<2	9 movements outside home range
F204	1994-1995	1+	<5	10 locations outside home range
F822	Feb 1993	adult	8	mortality site
F822	1992-1993	adult	<3	2 locations outside home range
F602	1992-1993	4+		0 movements outside home range
F502	1993	3+	<5	7 movements outside home range
F703	Jul 1993	3+	9	returned to home range
F703	1993-1995	3+	<6	7 movements outside home range

¹ Relocation data point not included in home range calculation.

of juvenile wolverines in the population. Banci (1987) suggested dispersal in her report of a subadult male that disappeared from her study area in December, most likely just prior to its second birthday. The long distance movement recorded by Gardner (1985) was also made by a 2-year-old male. He describes the movement of a second wolverine as dispersal although the animal only traveled 30 km.

The timing of dispersal attempts in my study animals was correlated with the onset of sexual maturation. All dispersal attempts were made by male study animals at least 2 years old. Emigration is energetically expensive, favoring individuals in optimal physical condition (Morse 1980). The development and perfection of techniques used in finding, capturing, and processing food items are not easily attained and may take considerable time to perfect (Morse 1980). Evidence of extended parental care within my study population is consistent with rearing strategies employed within high trophic levels, correlating with the difficulty of procuring food in unfamiliar areas, emigration energetics, and predation defense.

The longest confirmed movements by central Idaho wolverines were made by M423 and M003, both believed to be 2 years old, moving 204 km and 198 km respectively (Fig. 3.2). Male M423 was captured in March 1993 as a subadult and remained relatively localized within a 1,300 km² home range until disappearing in February 1994. He was relocated in April 1994, 91 km north of his last location. The following morning he was captured in one of my traps; a 24-hour movement of 39 km. From that point he traveled north, moving 50 km in the next 3 days and 41 km the following 2 days, appearing to localize near the South Fork of the Salmon River. He was last located in this area on 18 April 1994 at which time he again disappeared. He was relocated in August 1994, 8 km north of McCall, Idaho, 36 km west of his last location. He remained in this area, moving another 20 km north by early February

1995. This was my last location on M423, probably due to transmitter failure. Following the points of contact from his subadult home range, M423 traveled over 292 km.

Male M003 was believed to be older than subadult age at capture, although tooth wear suggested a relatively young individual. I only relocated him within the study area twice, losing contact in February 1993. Another researcher detected M003's signal in June 1994, in the Horse Creek drainage north of the Salmon River, 199 km north of his last location, and I subsequently confirmed his presence by telemetry and visual observation. I monitored him in this area until losing contact in August 1994, probably due to transmitter battery failure.

Male M913 was captured as a subadult in February 1993. In early March 1994, he moved south 116 km, moving 35 km in 1 day, then disappeared (Fig. 3.3). Another researcher detected M913's signal frequency in early May 1994, 294 km north of his last location, near the confluence of the Lochsa and Selway rivers. Fourteen days later, before the location could be confirmed, I located M913 back within his subadult home range. I lost contact with M913 in November 1994, most likely a result of transmitter failure. He was recaptured in the Iron Creek (SNF) trap in April 1995, 21 km southeast of his subadult home range. He was re-instrumented and relocated 5 days later in Sulphur Creek (BNF), within his subadult home range, 51 km NW of the trap location. In July 1995 he again traveled 95 km south into the South Fork of the Boise River where he remained through the study period. I monitored M913 from his subadult to well within his third year of life. He represents a nomadic behavior consistent with that expected of a transient male that did not establish a permanent home range. His presence within his subadult home range appeared stable with only minimal contact with neighboring resident male M123. No other adult male wolverines were contacted within his home range. In April 1995, I located M913 in association with F204, a

sibling, within the core of his home range. This was my last location for M913 in his home range.

Male M814 was captured in April 1994 and aged by tooth wear and pelage character as a subadult. He remained relatively localized through 1994 within his subadult home range. In late January 1995 he disappeared for 32 days until relocated 60 km NW near Scott Peak (BNF) in late February (Fig. 3.4). In April 1995, he was located 59 km north of his home range within the South Fork Payette River (BNF). He returned to his subadult home range in July where he remained through the study period.

The return of M814 and M913 to their areas of origin may suggest their status as transients in the population. Dispersal carries a high risk of starvation or predation and data on the fate of dispersing individuals are scarce. Camenzind (1978) suggested that nomadic coyotes, while not breeders themselves, function as a reproductive reservoir for the local population.

No subadult or adult females made movements greater than 9 km from their home range boundaries (Table 3.3). Three subadult females were monitored. Female F803 died within her natal home range as a subadult, female F203 died within her natal home range at 2 years of age, and monitoring was continuing on 19-month-old female F204 within her natal.

IV. BEHAVIOR AND SOCIAL ORGANIZATION

Denning

Fennoscandian studies provide the majority of data on winter denning habits of wolverine. Pulliainen (1968) presented the characteristics of 31 reproductive dens in Finland. Eighty-one percent of dens occurred on bare, rocky hillsides of mountain slopes near or above timberline, while 6 dens were located in lower elevation spruce and pine peat-bogs. Most of 28 dens in Norway were situated above timberline in deep snow near cliff areas (Myrberget 1968). The general structure of dens in both studies was the same. Den entrances were located in soft snow near trees or rocks, with a vertical tunnel extending 1-5 meters to ground level. Lateral tunnels extended for up to 50 meters along the ground surface. In most cases, wolverine kits were found at ground level on bare soil.

Limited data are available on wolverine denning habits in North America. Rausch and Pearson (1972) described 3 dens in Alaska. Two were above timberline in snow filled ravines while the third was found in an abandoned beaver house. Magoun (1985) provided data on the natal dens of 2 females in tundra habitat of northwest Alaska. She described entrance tunnels extending <2 meters beneath the snow surface accessing den systems of up to 50 m in length.

All authors agree that use of reproductive dens begins from early February to late March. In some cases, females may use multiple dens prior to kit weaning. Why dens become unsuitable is not well understood. Fennoscandian studies were based on data collected from wolverine hunters rather than radio instrumented animals, so it was not always known if dens were the actual birthing sites. Idaho wolverines abandoned natal dens as early

as 10 March moving kits through a series of maternal dens until weaning. Females in arctic Alaska remained at a single den until late April or early May and did not appear disturbed by the presence of human observers (Magoun 1985). Magoun (1985) felt that den abandonment was probably forced by snow melt. Fennoscandian studies report den abandonment as a common response to human disturbance. Finland wolverine hunters emphasized that pursuit of a pregnant female may result in use of "exceptional" places as birthing sites (Pulliainen 1968). Myrberget (1968) mentions 4 instances of den abandonment due to human disturbance and suggests that secondary dens may be less suitable. My data is consistent with this. My first direct contact with denning females did not occur until late April and resulted in immediate den abandonment. Females had made several den changes prior to first contact with field personnel, but we were unaware of any disturbance, other than the circling aircraft, that might have induced earlier den abandonment. Ewer (1972) suggests that moves may occur in response to den parasites, or attempts by the female to deter predators from locating the den. The latter hypothesis seems more likely given the female's tendency to make lengthy foraging forays from the den site. Avoidance of predators may also explain the selection of den sites far removed from foraging areas.

The denning habitat used by 2 marked females and 1 unmarked female in Idaho was specific to subalpine talus habitats. The availability of talus communities throughout Idaho may define limitations for wolverine reproductive potential. When viewed in conjunction with potential displacement and disturbance of denning females by winter recreational activities of humans, denning habitat may be a limited and critical component of wolverine habitat.

Localized behavior of females in late February suggested natal denning. Location of the natal den was determined by searching for a concentration of tracks radiating from a site in of

localized activity. The site was confirmed as the natal den once the presence of kits was confirmed. Aging of kits by tooth eruption aided in confirming timing and location of parturition. Once the female moved the kits from the natal den, subsequent pre-weaning den sites were classified as maternal dens. Although other activities such as foraging and resting commonly occurred at these sites, maternal dens were defined by the presence of the kits. Maternal den sites were usually comprised of multiple dens.

Post-weaning dens were classified as rendezvous sites by Magoun (1985). These differed from maternal dens in that kits were not necessarily confined to a specific site. Rendezvous sites were oftentimes defined by a localized area rather than a specific den and appeared to function in providing security for the kits in the female's absence. Although resting may occur at all den sites, resting sites are not always associated with subnivian excavations or talus sites commonly used as dens. Resting sites usually occurred along travel routes or near foraging sites.

Natal Dens.--Dens associated with the birth of kits were identified for 2 females. Den site selection and post-partus movements for females F502 and F703 were similar. Both individuals selected den sites associated with large boulder talus (individual rock size greater than 2 m diameter) in subalpine cirque basins above 2,500 m elevation. Natal dens were located in isolated talus sites that were less than 100 m wide and surrounded by trees, as opposed to the more expansive and exposed talus generally characterizing glacial cirques. Den entrances had a north or north-easterly aspect. Natal dens in Finland were primarily north facing (Pulliainen 1968) while most Norway dens lay in terrain facing south (Myrberget 1968). Parturition occurred about 20 February for F502 in 1993, and 23 February for F703 in 1994. Timing of parturition for F703 in 1995 was not determined although localization at the

den was first noted on 16 February. The natal den and 1 of the maternal dens used by F703 in 1994 were re-used by her in 1995.

Females accessed natal dens by tunneling through snow into the natural chambers and passage-ways created by the talus. The depth of snow at the time of den use was not determined but it most likely exceeded 2 m. The site of parturition could not be identified, although it did not appear to have occurred within the snow layer. Substantial vegetation caches were present in both natal dens, but evidence of use by wolverines was not present. In 10 of 28 dens in Norway, young laid on branches while in the remainder of cases they were found on the ground or bare snow (Myrberget 1968). In all reported cases in the Finland study (Pulliainen 1968), kits were found lying on bare ground. The natal den site used by F502 in 1993 was accessed by a single entrance, whereas 3 entrances were present at the natal den site used by F703 in 1994 and 1995. It was not determined if the entrances led to common chambers.

Maternal Dens.--Maternal den sites for the 2 females were comprised of 16 individual dens at 6 sites (Figs. 1.4,1.5) Ten of the dens were located in talus while 6 were associated with fallen trees. Female F502 used 4 maternal den sites (Fig. 1.4). Three dens at the Fish Lake site were situated at the base of an exposed, northeasterly facing talus slope, and were inaccessible to us. Two of 3 Knapp Lakes dens were snow-tunnel excavations on exposed talus, while the third followed the trunk of a standing mature spruce. The 3 dens appeared to have been used in sequence with the initial use at the spruce associated den, which was not excavated. The first talus den entered beneath a slight snow cornice on the exposed face of the talus slope. On the day prior to excavation of this site, F502 was located in the den which provided direction to the resting chamber. The following day, F502 moved to the third den

site 330 m south. The second den was excavated 2.2 m vertically from the surface of the snow to a talus chamber approximately 1 m in diameter. The chamber was lined with a bed of forbs and grass; most likely the winter cache of rodents or pika (*Ochotona princeps*). The wolverine's presence from the previous day was not evident. The third den accessed the talus face at the base of a large hump in the snow, most likely the result of a snow covered boulder. This den also was not excavated. F502 was last located at the Knapp Lakes den complex on 14 April. Her abandonment of the site likely resulted from disturbance of the area by field personnel.

The fourth maternal den site used by F502 was located on 26 April at 2,447 m elevation in the mixed conifer habitat of Summit Creek (CNF). The den complex involved 3 separate dens associated with fallen trees in a relatively flat opening in the timber approximately 15 m across. The entrance tunnels accessed natural chambers created by the root mass of a fallen tree and the horizontal stems of 2 others. On the day of discovery of the den complex, F502 and her kits abandoned the dens although she remained in the Summit Creek drainage until 3 May.

Female F703 used 6 individual dens at the Soldier Lakes maternal den site, 5 of which were located in exposed talus and 1 in the cavity under a leaning tree. The sites were visited for excavation and mapping on 22 April, 20 days after F703 had abandoned the site. Two of the talus dens appeared to have had the majority of use as evidenced by wolverine tracks, staining of the snow, scats, and blue grouse (*Dendragapus obscurus*) remains. As with the natal dens, snow tunnels excavated by the female accessed the natural cavities within the boulder talus. On 24 April field personnel visited the Avalanche Chute den presently in use by F703. The den was located in a spruce-fir riparian area under snow covered fallen trees at the

base of an avalanche chute. There appeared to be 2 entrances, each located at the root-mass of 2 fallen trees. The chamber of the den in use by F703 was located under a point where the 2 logs crossed, 22 m from the farthest entrance. The den was observed from 300 m until mid-afternoon when F703 exited the den and discovered my snowshoe tracks. A later investigation of her tracks found that she had followed my tracks to within 20 m of our observation location. Within an hour of discovering our presence, she returned to the den and exited carrying a kit in her mouth. She carried the kit into the trees in a direction opposite our location and returned 30 minutes later, collected a second kit, and left in the same direction. A flight over the area the following day revealed she had returned to the den, although she was not subsequently relocated at the site.

On 16 February 1995, F703 relocated at the Chicken Creek natal den. The site was in use until late March (Fig. 1.5). She moved directly to the Avalanche Chute maternal den in early April showing no interest in the Soldier Lakes maternal den site used the previous year. None of the 1995 dens were visited by field personnel.

Prey remains were common in and around dens in Finland and Norway (Myrberget 1968, Pulliainen 1968). In 1 Finland wolverine den, hunters found 2 reindeer (*Rangifer rangifer*), 39 almost whole willow grouse (*Lagopus lagopus*), 32 wings of willow grouse, and the head of a hare (*Lepus timidus*) (Pulliainen 1968). While no prey remains were found at either of the Idaho natal den sites, prey remains were common at maternal dens. Idaho wolverines traveled up to 17.9 km from maternal dens to forage. Finland wolverine hunters found wolverines bringing food to dens from as far as 20 km (Pulliainen 1968).

Rendezvous sites.--I identified 4 rendezvous sites used by F502 and kit F203, and 6 sites used by F703 and kits M104 and F204. Five of the sites were talus and 5 were coniferous

riparian. Talus sites occurred in subalpine cirques within concentrated patches of large boulder talus similar to sites used as natal and maternal dens, but they were not necessarily associated with snow. Riparian sites occurred within lower slope spruce/fir riparian areas. Only 3 of the riparian sites were visited. All were characterized by a mesic, dense shrub and regenerating conifer understory associated with multiple layered timber downfall.

F502 was first found separated from her kit, F203, on 15 July 1993. F203 was located in talus above Valley Lakes (CNF) while her mother was 8 km to the south. F502 returned to the kit that evening and they left the area. On 3 other occasions from early to mid-August, F203 was left alone in non-talus associated coniferous habitats. Although F203 was active at the sites, she remained localized until the return of her mother. On 6 August her telemetry signal was monitored from 1345-2000 hours (the time of return of F502). Her level of activity was judged by changes in the amplitude of the telemetry signal. The signal suggested she was active on 16 of 29 telemetry readings. The third coniferous rendezvous site occurred within a mixed conifer stand on the lower third of a slope but it was not visited by field personnel. F502 and F203 were last located together on 11 August.

Only 2 of 6 rendezvous sites used by F703 and kits M104 and F204 were associated with coniferous riparian areas. On 27 July, 1994, F703 left the kits in the Lola Creek (CNF) drainage. The kits remained together through the early day, separating in early afternoon. M104 remained localized throughout the afternoon while F204 moved about the area. She walked onto my position at 1600 hours, observed me and rapidly moved away. I observed her moving through the timber deadfall 1 hour later at which time the telemetry signals suggested the 2 kits were together. I attempted to locate their hiding spot but was unable to do so in the heavy deadfall. F703's telemetry signal was detectable within the drainage but she did not

return to the kits before I left the area. The kits were relocated together on 3 August, 5.7 km from the Lola Creek site, and on 21 August, 16.8 km from the Lola Creek site but were not relocated with their mother subsequent to the Lola Creek location. Separation of the kits and their mother may provide opportunity for the adult female to contact and mate with the resident male. Although following the apparent separation of F703 and her kits, on 21 August, F703 was located 0.5 km from resident male M123. The kits were separated by 5.4 km but they were only 3.1 and 2.5 km from their mother.

Resting sites.--This classification assumes that resting was the primary function of a particular site or den. Many resting sites were associated with foraging activities either in close proximity or within the general locale of prey remains. Resting sites were non-specific and are described as "exposed" if the site was afforded no overhead cover other than natural vegetation, or "sheltered" if the site occurred within a snow, rock, or log den. Twenty-six sites were considered as resting sites. Nineteen were exposed, appearing as either depressions in the snow or forest floor duff; 14 were located directly at the base of a tree, and 13 were at or near prey remains. Seven of 26 sites were sheltered; 3 in snow dens, 1 in a hollow log, and 3 associated with rock. Three of the sheltered sites were near prey remains.

Related activities.--The importance of olfaction as a sensory tool of the wolverine is never more evident than during winter. Numerous excavations were common in areas of localized activity, such as maternal dens or foraging sites. Nine sites were investigated near F502's Summit Creek maternal den, with prey remains evident at only 3. At the Elk Lake (CNF) foraging site used by M123 and F203, there were 13 excavations with prey remains at only 2. At 2 of these sites were imprints of a wolverine rostrum in the wall of the dig. This aggressive olfactory exploration is probably evidence that these dead-end excavations are

either the result of the wolverine searching for previously cached food or investigation of a scent. At an "investigative" site in Crystal Creek (CNF) a coffee can containing lard lay on the snow surface near numerous holes and shallow trenches dug in the snow by a pair of wolverines. At a site near the Emma Creek trap a wolverine excavated an egg carton and sardine can from under 2 m of snow.

Dens may provide thermal advantage to wolverines in winter and cool environments in summer. Pulliainen (1968) suggested the insulative value of snow may protect kits from hypothermia during periods of the mother's absence. During investigation of talus dens used during summer, I noted a substantial gradient between the ambient temperature, and the temperature within the dens. I learned to key on isolated point flows of cool air radiating from the talus in searching for scats and prey remains at summer rendezvous sites. No measurements of the temperature gradient were taken. Temperature also appeared to influence summer movements of Montana wolverines (Hornocker and Hash 1981).

Food Habits

I analyzed 95 scat and 22 foraging site collections. Thirty-five percent of collections were associated with natal and kit rearing dens of 2 adult females. Seventy-two percent of the samples were collected in winter months.

Ungulates, both wild and domestic, were the most common food item, representing 45.8% of all occurrences (Table 4.1). Ungulates comprised 44.4% of summer and 46.3% of

Table 4.1. Species and item incidence within scat and foraging site collections for wolverine in central Idaho, 1992-1995.¹

Species	Summer (n = 33)		Winter (n = 84)	
	Number of occurrences	% of collections	Number of occurrences	% of collections
Unidentified Cervidae	8	24.2	27	32.1
Elk (<i>Cervus elaphus</i>)	7	21.2	15	17.9
Mule deer (<i>Odocoileus hemionus</i>)	4	12.1	6	7.1
Moose (<i>Alces alces</i>)			2	2.4
Mountain Sheep (<i>Ovis canadensis</i>)			1	1.2
Domestic cow (<i>Bos bos</i>)	5	15.2	14	16.7
Domestic horse (<i>Equus</i> sp.)			4	4.8
Marten (<i>Martes americana</i>)	1	3.0	3	3.6
Weasel (<i>Mustela</i> sp.)			1	1.2
Striped skunk (<i>Mephitis mephitis</i>)	2	6.0	7	8.3
Wolverine (<i>Gulo gulo</i>) ²	16	48.5	12	14.3
Coyote (<i>Canis latrans</i>)			6	7.1
Black bear (<i>Ursus americanus</i>)	1	3.0	1	1.2
Varying Hare (<i>Lepus americanus</i>)	1	3.0	4	4.8
Porcupine (<i>Erethizon dorsatum</i>)	1	3.0	1	1.2
Marmot (<i>Marmota</i> sp.)	3	9.0	1	1.2
Beaver (<i>Castor canadensis</i>)			6	7.1
Red squirrel (<i>Tamiasciurus hudsonicus</i>)			1	1.2
Ground squirrel (<i>Spermophilus</i> sp.)	2	6.1		
Flying squirrel (<i>Glaucomys sabrinus</i>)			1	1.2
Chipmunk (<i>Tamias</i> sp.)			1	1.2
Unidentified Sciurid	4	12.1	8	9.5
Vole (<i>Microtus</i> sp.)	1	3.0	3	3.6
Mouse (unidentified Cricetidae)			8	9.5
Deer mouse (<i>Peromyscus maniculatus</i>)			4	4.8
Shrew (<i>Sorex</i> sp.)	3	9.0	1	1.2
Unidentified Bird	1	3.0	2	2.4
Grouse (<i>Bonasa</i> sp./ <i>Dendragapus</i> sp.)			2	2.4
Blue grouse (<i>Dendragapus obscurus</i>)			1	1.2
Unidentified fish			1	1.2
Egg shell fragments	2	6.1	3	3.6
Unidentified insect	2	6.1	5	6.0
Ant	2	6.1	1	1.2
Unidentified vegetation	15	45.5	27	32.1
Conifer needles or cone seeds	1	3.0		
Lichen			5	6.0
Unidentified grass	6	18.2	5	6.0
Woody debris	6	18.2	1	1.2
Soil	2	6.1		
Plastic mesh	2	6.1		
Fabric	3	9.0	3	3.6
Gravel				

¹ Elk, mule deer, mountain sheep, fish, and beaver were available at study trap sites during winter months.² Wolverine presence in scats was detected only in hair samples and was most likely incidental to pelage grooming.

winter occurrences (Fig. 4.1). Small mammals (all rodents and lagomorphs) were the second most common item occurring at 20.7%. Carnivore species comprised 20.1% of occurrences with marten, skunk (*Mephitis mephitis*), and black bear present in small numbers in both summer and winter collections. Vegetative items comprised 25.6% of occurrences with conifer needles making up 80.8% of the vegetative sample. Insects, primarily ants, occurred at 5.9%, while soil and gravel, and man-made plastics and fibers were present at 6.4% and 1.9% respectively.

Ewer (1973) described the wolverine as a polyphagous mustelid. Wolverines would probably not persist in the absence of ungulate populations, and evidence suggests at least a seasonal reliance on local rodent abundance (Magoun 1985, Gardner 1985, Banci 1987). The wolverine is capable of taking large ungulates as live prey (Myrberget 1968, Pulliainen 1968, Magoun 1985) but ungulate presence in the wolverine diet most likely results from scavenging (Hornocker and Hash 1981, Magoun 1985, Gardner 1985, Banci 1987). Ungulate use by wolverines at higher latitudes was more prevalent during months associated with migrating caribou (*Rangifer tarandus*) or local moose populations (Magoun 1985, Gardner 1985). Ground squirrels were most prevalent in late winter and spring diets in arctic Alaska (Magoun 1985) and southcentral Alaska (Gardner 1985) while snowshoe hare contributed the highest proportion of any single species to the wolverine's diet in Yukon (Banci 1987). Vegetation has been reported in the diet of wolverines but it may be consumed incidental with prey rather than in lieu of prey (Banci 1987).

Elk, mule deer, and moose were present in my study area throughout the year, although their availability to wolverine varied with seasonal shifts in ungulate distribution. Most elk and deer move to lower elevation winter habitats within the Middle Fork of the Salmon

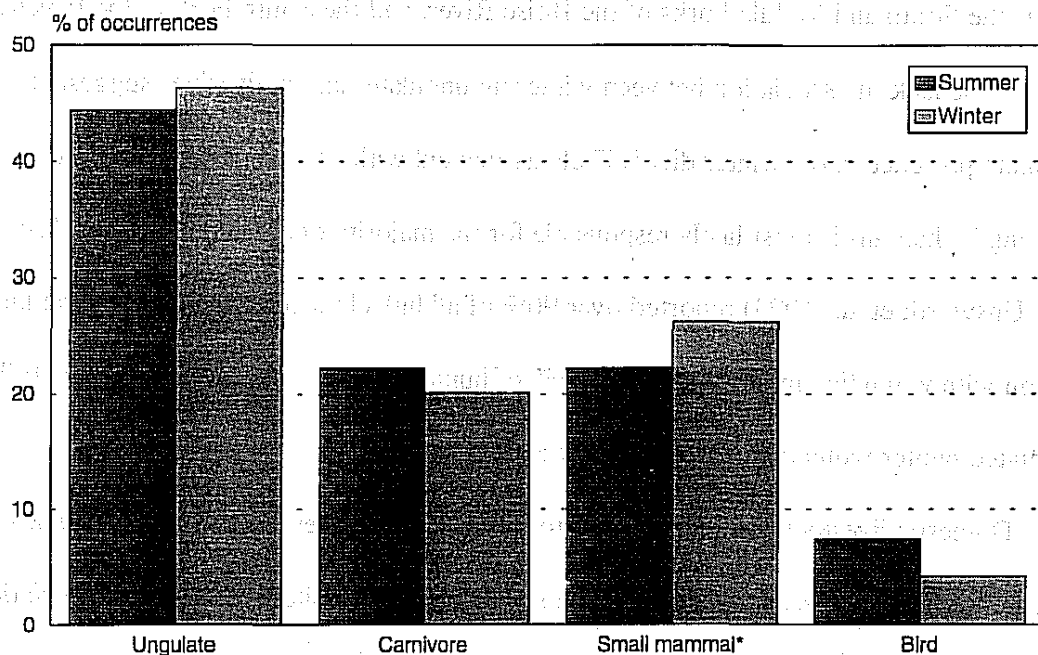


Fig. 4.1. Seasonal frequency of occurrence of 4 major prey groups in wolverine scats collected in central Idaho, 1992-1995. Percent occurrence based on proportion of each prey item to total animal occurrences in foraging collections. *Small mammal category includes Rodentia and Lagomorpha.

River, the South and Middle Forks of the Boise River, and the South Fork of the Payette River. The lack of association between wintering ungulates and wolverines suggests that ungulate presence in the winter diet is likely associated with non-winter ungulate mortality. Hunting by humans is most likely responsible for the majority of elk and deer mortality during fall. Unsworth et al. (1993) reported over 90% of all bull elk deaths occurred during hunting season with wounding mortality equaling 7% of hunter harvest. Leptich and Zager (1991) estimated hunter wounding loss of cow elk at 27%.

Domestic livestock also contributed to the wolverine's diet. Horse and domestic cow occurred in 13.4% of scats. Neither were used as bait at trap sites. Cattle, grazing National Forest livestock allotments, occasionally die, as do horses used during the hunting season.

Two incidents of food caching were documented. A coyote carcass was found in a snow excavation 0.4 m deep and 25 cm in diameter. Claw marks on the wall of the excavation suggested it was not a natural depression. The carcass had not been covered. The cache was located at the base of a talus area used extensively by adult male M123 and subadult female F203. Three of 6 scats collected at the site contained coyote hair. Male M333 cached remains of fish bait, collected from one of my trap sites, in 2 uncovered shallow excavations at a foraging site 300 m from the trap.

Five species of sciurids were present in collections comprising 16.7% of total occurrences. Marmot (*Marmota* sp.) and chipmunk (*Tamias* sp.) were found in winter collections indicating these prey species were either cached prior to hibernation or captured in hibernacula. Wolverines in Magoun's (1985) winter study area used ground squirrels cached prior to hibernation. Incidence of marmot in wolverine scats from Montana led Hornocker and Hash (1981) to speculate that wolverines may be searching out marmot winter

hibernacula. In March 1992 I found female F822 in a cirque basin above 2,700 m elevation investigating sites where marmots had tunneled through snow to the surface.

Foraging behavior.--Snowtracking indicated wolverines spent most of their time in direct movement rather than hunting. Wolverine rarely investigated tracks of potential prey, although they commonly investigated tracks of wolverines and other carnivores. I documented no evidence of wolverines pursuing or capturing live prey.

Evidence of winter foraging was commonly associated with snow excavations.

Exceptions were investigations of trap lines, foraging at trap sites, and prey remains within natal and maternal dens. Fox and coyote sign was normally associated with wolverine tracks at winter carcass foraging sites making it difficult to determine which species first discovered and exposed the carcass. Wolverine rarely remained at foraging sites for extended periods but would oftentimes return to a site. In 1993 and 1994, wolverines excavated elk hides and bones at a hunter camp. The camp was used by adult male M123 and subadult female F203 in 1994 as a foraging and resting site. In January 1994, adult female F703 and subadult male M913 remained near a moose carcass for 3 days. The carcass was partially consumed and, although neither was relocated at the site subsequent to their visit, wolverine tracks were found on subsequent visits to the site. In March 1994, adult female F703 was located at a site she and her subadult offspring F803 had used on the same day 1 year earlier. The lower portion of this drainage, approximately 2 km below the wolverine locations, supported a small population of wintering elk. Six study animals were located near this site during winter months. Elk bones were found near this site in the summer of 1993.

Banci (1987) reported that consumption of trap bait by wolverines is rare, most likely due to capture stress. My study animals generally consumed at least a portion of the trap bait

possibly suggesting our box trap design (Copeland et al. 1995) is less stressful to trapped wolverines. Four individuals remained near traps for extended periods of time (Table 1.1). Adult female F822 was photographed by remote camera 16 times at the Beaver Creek (SNF) trap in December and January of 1992-1993. I believe her dependence on trap baits was attributable to her poor physical condition. The compulsive use of trap baits by adult male M333 appeared to be based more on convenience than necessity. He became skilled at obtaining hanging baits by chewing through ropes suspending the baits and appeared able to lift trap lids to escape. In 1993 he was captured once and photographed 3 additional times at 2 traps within the home range of M123. In 1994 and 1995 his distribution shifted to the south (see Spatial and Temporal Distribution of the Study Population) where he was captured in 3 different traps a total of 6 times. During a 4-day period in April 1994, M333 visited the Iron Creek (SNF) trap daily from which he dragged bait to a site 300 m from the trap. Inexperience at foraging may have prompted 2 subadults to remain near trap baits resulting in 18 recaptures of these individuals (Table 1.1).

Females with kits traveled extensive distances in search of food. In March 1993, F502 left a well worn trail in the snow to an elk carcass 3.9 km from her natal den (Fig. 1.4). The elk carcass had been frequented by canids and possibly other wolverines. F502 had excavated an extensive snow den 100 m from the carcass but the purpose of the den was undetermined. In March 1994, adult female F703 was captured in a trap 12.2 km from her maternal den. When my field assistant opened the trap to release her, F703 attempted to take the trap bait with her. In 1995, while using the same maternal den, she was recaptured once and photographed by remote camera twice at this same trap. In April 1994, she was located 15.4 km from her maternal den where she fed on an elk carcass.

Insect foraging sites were used by 2 study animals. In July 1993, I observed adult female F602 rolling rocks and tearing into rotting logs at the base of a talus area. In a distance of 200 m, she rolled 38 rocks and tore into 6 logs. Ants were present at many of the sites and occurred at 3.4% in scats. In July 1994, while ground tracking subadult female F203, I observed numerous displaced rocks and several disturbed logs along her trail.

Social Organization

The spatial structure for the wolverine and its closest sympatric relatives, the marten and fisher, appears to follow a pattern of intrasexual territoriality (Ewer 1973, Powell 1979, Magoun 1985, Arthur et al. 1989, Banci and Harestad 1990). However, the internal reproductive and resource partitioning structure driving such a spatial pattern is less apparent.

References on ecology, habitat use, and spatial characteristics depict this group as solitary, based on an apparent lack of gregarious or aggregate behavior occurring outside of mating and kit rearing periods. Sociality in these species has received much less attention than has spacing. Too often, and largely in the absence of supporting data, solitary is considered contrary to social (Sandell 1989). Buskirk and Ruggiero (1994) reported over 26 published accounts of home range and no reported accounts of parental care behavior in marten. They suggest parental care likely does not occur; consistent with a pattern for polygamous carnivores. Direct acts of parental care such as food regurgitation, grooming, or playing may not be evident for this group of species, but as suggested by Kleiman and Malcolm (1981) and Ewer (1973), paternal care does not necessarily require direct association; indirect acts of polygamous males, such as resource acquisition, maintenance, and defense, may also increase survivorship of young by providing for the future needs of the female.

Excluding association of females with kits up to 6 months old, pairing or grouping of wolverines was verified 30 instances (Table 4.2). On 2 occasions groups of 3 individuals were noted. All interactions between adult males and younger wolverines occurred with juveniles and subadults between 7-14 months of age.

Adult male M123 and juvenile female F204 were the most gregarious, with each interacting with 4 other individuals (Table 4.3). Twenty-four interactions involved juveniles and/or subadults interacting with their mother (21%), the resident male (46%), or as sibling pairs (33%). Juveniles associated more often with the resident male than with siblings or their mother, while subadults associated more often with siblings and their mother than with the resident male (Fig. 4.2).

In February 1993, I snowtracked 2 wolverines traveling together near 2 of my traps located on the east boundary of adult female F703's home range. On 12 February subadult male M913 was captured and remote camera photographs revealed a second wolverine at the trap. Subadult female F803 was captured in a nearby trap 2 days later. On 22 February, F703 moved 24.7 km from the west side of her home range to the vicinity of F803's capture site. F803 remained near the trap after being captured through 24 February, and was located near her mother twice during that period. From 26 February-3 March, F803 and F703 returned to the west side of F703's home range where they were located together twice. F803 returned to her initial capture site and was recaptured in the trap on 6 March. Her sibling, M913, had localized approximately 25 km north of his capture site, and north of F703's home range, subsequent to his initial capture. Between 4 March and 7 March he returned 30.4 km,

Table 4.2. Age and sex stratification of association for wolverines in central Idaho, 1993-1995. Adult female-juvenile pairs only include interactions occurring later than September 1st of juvenile birth year.

Pair	Number of Pairings	Comments
Adult male - Adult male	1	resident/transient association
Adult male - Adult female	3	includes breeding and non-breeding period
Adult female - Adult female	0	
Adult male - Subadult female	7	includes 1 out-year sibling pair ¹
Adult male - Subadult male	0	
Adult male - Juvenile female	2	
Adult male - Juvenile male	3	
Adult female - Subadult	5	all parent-offspring pairs
Adult female - Juvenile	4	all out-year sibling pairs ¹
Siblings	4	all in-year sibling pairs ²

¹ "Out-year" describes siblings born in different years.

² "In-year" describes siblings born in the same year.

Table 4.3. Association data for wolverines in central Idaho, 1993-1995. Values are percent of relocations in which pairing occurred. Data were standardized by dividing number of pairings by number of relocation attempts in which both individuals were located (Morgan et al. 1974).

	M123	F703	M913	F803	F203	M104	F204
M123							
F703	4.5						
M913		3.3					
F803		20.0	27.3				
F203	11.8						
M104	11.5				11.1		
F204	7.7		5.3		4.2	4.8	

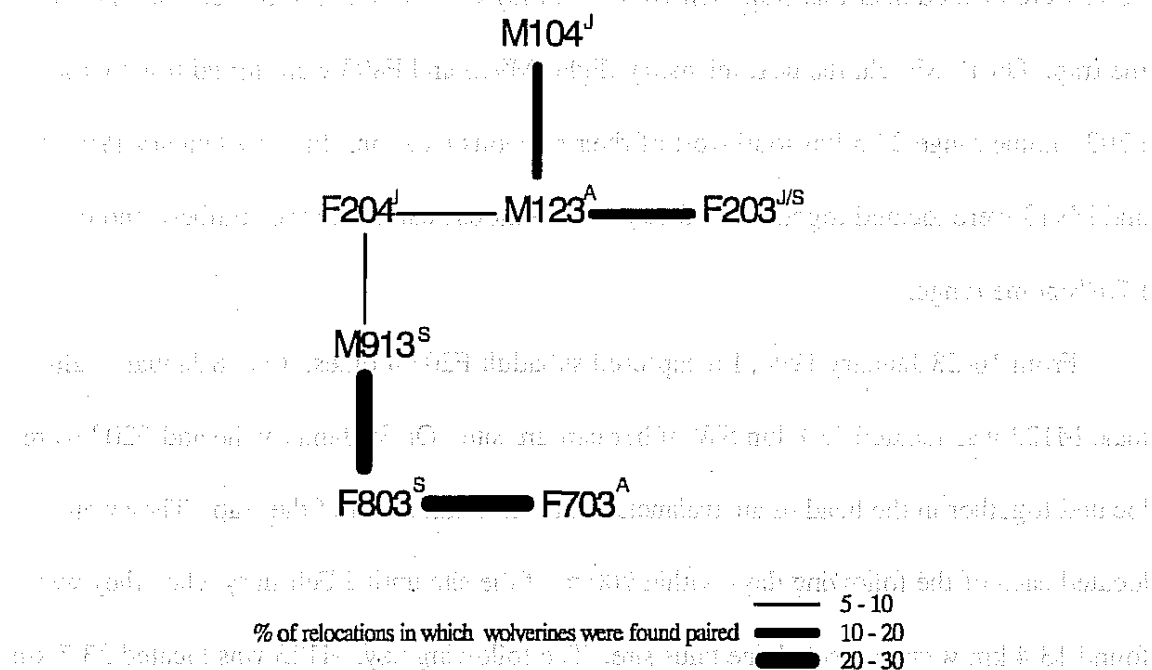


Fig. 4.2. Maximum spanning tree of closest associates (Morgon et al. 1974) for wolverines in central Idaho, 1993-1995. Identification numbers denote male (M) and female (F) study animals. Superscript denotes resident adult (A), subadult (S), or juvenile (J).

to his initial capture site, and was recaptured on 7 March. Later that day, both M913 and F803 were located near that trap. On 10 March they were found together 22.9 km north of the trap. On 19 March, the next telemetry flight, M913 and F803 were found together in F703's home range 23.5 km southwest of their previous location. In early January 1994, F703 and M913 were located together for 3 days near a moose carcass in the southern end of F703's home range.

From 16-28 January 1994, I recaptured subadult F203 4 times. On 28 January, adult male M123 was located 13.8 km SW of her capture site. On 30 January, he and F203 were located together in the head of an avalanche chute 15.9 km north of the trap. They were located each of the following days within 700 m of the site until 2 February when they were found 13.4 km west at a subalpine talus site. The following day, M123 was located 23.7 km farther west while F203 moved 9.8 km south. They were found together 3 additional times during the winter: on 20 February, they were observed together running across an open slope; on 7 March, together in a snow den; and on 2 April at a complex of dens at the base of a talus area (see Denning). On 23 December, as an adult, F203 was located in her home range with M123 and juvenile male M104.

The 1994 kits of F703 may have associated with M123 at an early age. On 3 May, 1994, M123 and F703 were located together on 2 consecutive days 1.7 km north of her avalanche chute maternal den (Fig. 1.5). The next documented contact between M123 and 1 of F703's kits also occurred in this area nearly 5 months later on 28 September when M123 and juvenile F204 were located together 2.4 km from the 3 May location. This site had also been used on 16 August by F204's brother, M104. The reuse of the site by both kits may be evidence that the kits were present at the 3 May meeting of M123 and F703.

We first found juveniles M104 and F204 separated on 21 August. Although they were commonly found with other local wolverines, they were not relocated with their mother (F703) through the remainder of the study. From mid-October to mid-January, the juveniles were found together 3 times, with M123 4 times, and with neighboring female F203 3 times. On 18 October, M123 and F204 were together on the west side of F703's home range. On 3 November they were in the same area and were joined by M104. On 22 November, M123 and M104 had moved 28.5 km east into the home range of adult female F203. F203 was found 3 km from their location. F203 was likely a half-sister to juveniles M104 and F204. The following 2 telemetry flights on 8 and 19 December found M104 and F203 together. On 29 December they were again together and had been joined by M123, thereby bringing together a group representing 3 generations. On 4 January 1995, both M123 and M104 had returned 25 km to the west side of F703's home range. M123 rejoined juvenile F204 while M104 was located 2.6 km away. By 20 January M104 and F204 had returned to F203's home range and were located with her. F204 subsequently settled in the area west of her mother's home range and within the home range of M913. On 16 April, F204 and M913 were located together. She remained in M913's home range through the study period while he moved 95 km into the southern portion of the study area.

F703 produced kits in 1995 in the same natal and maternal den complex as the previous year. On 4 April I located M123 and F703 together in the maternal den. Her kits would have been approximately 7 weeks old. On 8 May 2 kits were observed with F703.

The assemblage of immature individuals, and their continued association with resident kin, may define a basal level of social grouping for central Idaho wolverines. While evidence of delayed dispersal may appear unique, occurrence of males near denning females is not.

Magoun (1985) found males near females and kits on several occasions, although she felt the association was likely related to breeding. Wolverine hunters in Finland commonly found evidence of male wolverine activity near dens in March and April (Pulliainen 1968). Haglund (1966) also described the extended presence of a male wolverine near a den in Sweden.

The length of the parental care period correlates positively with the difficulty of foraging technique (Morse 1980), which may necessitate the development of social behavior. The evolution of sociality has most often been attributed to increased foraging efficiency (Moehlman 1983) and is generally identified with group living; a condition which Kleiman and Malcolm (1981) believe may have fostered the evolution of male parental behavior. While interaction between resident adults and immature wolverines may be incidental, it appears functional in kit learning and development (association often occurred at foraging sites and immature wolverines commonly returned to those sites). The tolerance of the resident male to the subadults' extended presence may have adaptive significance. Perpetuation of the genotype may be enhanced by the resident male tolerating, and even cooperating in the rearing of offspring, rather than competing with them, especially in the context of the low reproductive potential that appears to be inherent in the wolverine. Few offspring are produced, and age related variation in foraging skills observed in Idaho wolverines suggest these skills may develop slowly.

Presence of the resident male near maternal dens, and in association with pre-weaning age kits, implies sociality and familiarity between mated pairs. As argued by Kleiman and Malcolm (1981), in some cases a female may prefer a male who invests in parental care over one who deserts. The establishment of social bonds might provide the male with preferential access to females thereby decreasing the need for mating competition and spatial defense.

Scentmarking

Wolverines were snowtracked for 54.4 km during 30 snowtracking sessions in which 91 marks were recorded. Marks included urine (61), scat (18), scratches on trees (4), bites on trees (3), and unidentified substances (5). Urine marks occurred on objects, including live trees (either saplings or at the base of larger trees), stumps, or humps in the snow, 54 times. The remaining marks were deposited on the snow surface and did not appear related to any object. Scratching or biting of tree bark and limbs was not always associated with other marks.

Frequency of marking was highly variable among individual wolverines. On 24 March 1993, while traveling through the home range of resident adult male M123, male M333 left no urine marks in 5.1 km. On the same day in 1994, while traveling through his own recently established home range, M333 left 9 urine marks in 3.1 km. Inhibition of scent-marking while in a neighbor's territory has been shown in foxes (Macdonald 1979) and wolves (Rothman and Mech 1979). On 2 occasions, individuals urine-marked stations used the previous year.

Traditional use of scentmarks appears common in some canids (Rothman and Mech 1979, Macdonald 1979) and was noted by Koehler et al. (1980) in Montana wolverines.

Scent-marking posture, particularly as it relates to urination, appears to have social significance in some carnivores. Amongst coyotes the frequency of raised leg urination (RLU) as opposed to squat urination (SQU) varies with the individuals age and sex (Macdonald 1985). RLUs were also more often associated with traveling in coyotes than were SQUs (Wells and Bekoff 1981). Peters and Mech (1975) reported that SQUs were commonly associated with solicitous interactions while only high ranking individuals show RLUs. Raised leg urination appears to be uncommon in wolverine. Snow-track impressions at urination sites

suggested that when marking near large objects, such as trees, wolverines backed-up and squatted near the base of the tree, or would either climb a short distance up the tree or stand on hind legs against the tree and urinate. On small objects such as sapling trees, limbs, or humps in the snow, wolverines squatted over the object to urinate. Wolverine would occasionally stand on hind legs against a sapling and broadcast urinate which could give an impression of RLU. Magoun (1985) reported witnessing RLU by a male wolverine, and evidence of another incident where RLU appeared to be the only method of broadcast. Remote camera photographs of wolverines urine-marking traps show that individuals would occasionally place a raised leg on the object to be marked, giving the impression of RLU although a squatting posture was always evident.

Common to all mustelids is a pair of anal sacs (Pocock 1921). Haglund (1966) and Pulliainen and Ovaskainen (1975) suggest that anal gland marking may function in wolverine territoriality while others contend its use is primarily a fear-defense mechanism (Krott 1959, Ewer 1973, Long 1987). Koehler et al (1980) described all scentmarks associated with Montana wolverines as "musk", making no mention of urine marks. Although urine was the primary marking substance in arctic Alaska, Magoun (1985) suggested that the ventral gland and anal sacs were probably used for scent-marking. In Idaho, musking (evacuation of the anal glands) was common in traps and usually occurred during attempts at immobilization. Attempts to manually express contents of the anal sac for collection usually found the sac empty. Contrary to Krott's (1959) description of wolverine anal sac secretion as "very smelly", field personnel found the odor mild and non-offensive. Musking had little effect on field personnel and may not have always been noted. Both anal musking and urination are associated with raised-tail posturing in wolverine (Clint Long pers. commun.). When released

from traps, wolverines always left with an elevated tail. Of 5 collections of scentmarks of unidentified origin, only 1 smelled similar to the odor of anal sacs.

Limited behavioral evidence suggests the presence of abdominal scent glands in some mustelids. Erlinge et al. (1982) describe anal drag and body rubbing in the stoat (*Mustela erminea*), the latter of which refers to the rubbing of the abdominal surface. While both the fisher and marten are commonly referenced in the use of abdominal rubbing (Hall 1926, Markley and Bassett 1942, Powell 1982, Pulliainen 1982), I found no reference to any observations of this behavior. Long (1987) described abdominal rubbing as the second most common marking method, following urination, in captive wolverines. Magoun (1985) observed wolverines in Alaska performing rocking motions while straddling tussocks but she could not determine whether the marking involved ventral or anal rubbing.

The wolverine has several mechanisms of marking at its disposal and all are likely functional in communication. Others have suggested function in locating cached food (Magoun 1985), in maintaining temporal separation (Koehler et al. 1980), and in alarm and defense (Krott 1959, Long 1987). The functionality of scent-marking in navigation and orientation, social integration, reproduction, and territoriality has received substantial attention in many carnivores (reviewed in Eisenberg and Kleiman 1972, Stoddart 1980a, Stoddart 1980b, Brown and Macdonald 1985), however, it has not been well investigated in wolverine. Leyhausen (1965) noted that attention is commonly focused on repulsive forces within animal territories and that little attempt has been made to study counteracting forces and modes of behavior that allow a population of solitary individuals to maintain contact with each other. Information regarding aspects of identity, as well as clues to an animal's sex, is likely contained in many carnivore odors and is probably key to wolverine locating each other

and spatially orienting themselves (Macdonald 1985). The frequency of interaction by as few as 10 wolverines in an area of nearly 2,000 km² seems too great to have occurred by chance.

Behavior

Field work provided only limited opportunity to observe wolverine behavior. Although several attempts were made to track and monitor wolverine activities, wolverines were rarely unaware of the observers presence. When startled, wolverines rapidly left the site with little opportunity for observation. When a wolverine's initial detection of human presence was less abrupt, individuals commonly searched the air for scent, occasionally standing on hind legs to do so, and often vocalized before leaving an encounter. A raised tail posture always was characteristic of alarm.

During attempts to capture kits, females were strongly solicitous of young. While in pursuit of a family group, the female would respond to kits falling behind by stopping to wait, standing on hind legs to view kits, or by returning to them. Females did not confront field personnel during kit capture and handling but they continually circled the processing site, promptly returning to the kits once humans had left. In March 1994, F703 was recaptured in the Shake Creek trap 15 km from her maternal den. F703 responded to attempts to release her by lunging aggressively at field personnel.

Trapped wolverines reacted to human presence with various posturing displays.

Response was not predictable for individuals at recaptures although females were generally more aggressive than males. Wolverines were generally subdued while field personnel were present at traps, often vocalizing in response to loud sounds or disturbance of the trap. When the trap lid was raised during immobilization attempts, wolverines normally confronted the opening with an opened mouth growl or quick lunge and snort but they rarely attempted

escape and usually retreated to the rear of the trap. When presented with the jab stick, used for immobilization, wolverines responded by either biting or attempted to control the stick by pushing it aside or pressing it to the floor of the trap with a front foot. On his first capture, subadult male M913 reacted to immobilization attempts by presenting his ventral surface in an apparent submissive posture. Several individuals, including 2 adult males and a subadult female, responded with a lowering of the head and shoulders followed by a rubbing motion similar to the commonly observed behavior of a dog rubbing its shoulders, neck, and back on some odoriferous site on the ground. Wolverines displaying this posture would occasionally roll completely on their back pushing themselves with hind feet, often exposing their ventral surface. This behavior often culminated with the individual lying relatively motionless on its side. Trapped individuals commonly redirected aggression by biting and clawing at trap bait.

Most interactions between animal pairs involve a signal or display from one individual which in some way modifies the behavior of another (Krebs and Davies 1981). Fox (1975) suggested that increasing complexity of the visual display repertoire in canids is correlated with increasing sociability. Signals evolve from selection pressures which increase their effectiveness in altering the behavior of reactors (Krebs and Davies 1981). Interpreting the functionality of wolverine posturing may be less important than recognizing its presence as suggestive of sociability.

V. HABITAT USE

RESULTS

Random use of 6 cover types was tested for 13 wolverines (Table 5.1). Comparison of habitat use to availability suggested that wolverines did not select cover types or aspect at random.

Montane coniferous forest types constituted 66.0% of available habitat and accounted for 70.2% of wolverine relocations (Table 5.2). There was an inverse relationship between seasonal use of Douglas-fir and lodgepole pine, with Douglas-fir preferred in summer and lodgepole pine favored in winter (Table 5.2). Shrub/grass and ponderosa pine constituted smaller proportions of female than male home ranges (Table 5.1) which probably reflects the wide-ranging behavior of males. Subadult (F204, M814, M913) home ranges contained higher proportions of shrub/grass types than those of adult's (Table 5.1). Wolverines were located in openings, defined as any break in the canopy resulting in an observable change in understory composition, on 34% of relocations and were located in burned areas 34 times. Three wolverines were located in logging areas, 1 in an old clearcut and 2 near active sales.

When cover types were combined into 6 types, the 3 levels of analysis produced similar results (Table 5.3). A significant preference for rock habitats was evident in summer and montane coniferous forest types in winter (Table 5.3). Rock was used more than all other cover types in summer with preference most evident at level 2 (Table 5.3). Montane coniferous forest types were used more than all other types in winter, but use was not significantly different ($P > 0.05$) than parks in level 1 and 2, or parks and mixed alpine in level 3 (Table 5.3). Rock types were avoided during winter at all 3 levels (Table 5.3). Use

Table 5.1. Cover type classification and pooling for habitats in central Idaho wolverine project study area, 1995.

COVER CLASS	FIRST POOLING	SECOND POOLING
Urban	(deleted)	(deleted)
Agriculture	(deleted)	(deleted)
Foothills grasslands		
Mesic upland shrub	Shrub/Grass	Shrub/Grass
Xeric shrub		
Broadleaf forest (<i>Populus</i> sp.)		
Ponderosa pine	Ponderosa pine	Ponderosa pine
Mixed xeric forest		
- ponderosa pine		
- juniper (<i>Juniperus</i> sp.)		
Lodgepole pine	Lodgepole pine	
Douglas-fir/lodgepole pine	Douglas-fir/lodgepole pine	
Douglas-fir		
Mixed mesic forest	Douglas-fir	
- Douglas-fir		Montane coniferous forest
- Engelmann spruce		
Mixed subalpine forest	Mixed subalpine forest	
- subalpine fir		
- Douglas-fir		
- Engelmann spruce		
Subalpine fir	Subalpine fir	
Montane parklands and subalpine meadows	Montane parklands and subalpine meadows	Montane parklands and subalpine meadows
Mixed alpine forest (whitebark pine)	Mixed alpine forest	Mixed alpine forest
Mixed barren (< 15% forest, shrub, or herbaceous cover)		
Exposed rock	Rock	Rock
Snow		
Water	(deleted)	(deleted)
Cloud	(deleted)	(deleted)
Cloud shadow	(deleted)	(deleted)

Table 5.2. Percentage cover type composition pooled for 13 wolverines within 3 scales of use and availability in central Idaho. Level 1: within merged 99% home range polygons, Level 2: within individual 99% home ranges, Level 3: within individual core home ranges.

LEVEL 1						
Cover type	Available	Use-Summer		Use-Winter		
		Mean	SD	Mean	SD	
Lodgepole pine	14.86	9.95	8.71	18.82	9.25	
Douglas-fir/lodgepole pine	8.97	9.84	9.06	18.29	12.50	
Mixed subalpine forest	11.78	13.60	8.31	14.25	10.34	
Subalpine fir	10.25	12.42	6.75	12.93	6.25	
Douglas-fir	22.82	16.79	12.60	12.02	6.61	
Mixed alpine forest (whitebark pine)	4.91	9.25	7.73	6.88	8.15	
Parklands and subalpine meadows	6.55	6.45	5.88	6.63	4.37	
Shrub/grass	12.77	4.49	5.58	4.16	5.71	
Exposed rock/barren	5.45	16.39	9.76	3.16	5.55	
Ponderosa pine	1.64	0.80	2.00	2.87	3.84	

LEVEL 2						
Cover type	Available		Use-Summer		Use-Winter	
	Mean	SD	Mean	SD	Mean	SD
Lodgepole pine	13.46	3.37	9.95	8.71	18.82	9.25
Douglas-fir/lodgepole pine	12.54	5.47	9.84	9.06	18.29	12.50
Mixed subalpine forest	13.73	5.12	13.60	8.31	14.25	10.34
Subalpine fir	12.55	2.70	12.42	6.75	12.93	6.25
Douglas-fir	18.32	7.92	16.79	12.60	12.02	6.61
Mixed alpine forest (whitebark pine)	6.41	4.19	9.25	7.73	6.88	8.15
Parklands and subalpine meadows	7.38	1.94	6.45	5.88	6.63	4.37
Shrub/grass	8.35	3.91	4.49	5.58	4.16	5.71
Exposed rock/barren	6.30	4.73	16.39	9.76	3.16	5.55
Ponderosa pine	0.98	0.94	0.80	2.00	2.87	3.84

LEVEL 3						
Cover type	Available		Use-Summer		Use-Winter	
	Mean	SD	Mean	SD	Mean	SD
Lodgepole pine	12.77	4.67	9.32	9.07	21.86	14.03
Douglas-fir/lodgepole pine	12.26	6.43	9.36	9.23	16.50	14.39
Mixed subalpine forest	13.48	6.41	12.93	8.48	13.16	9.72
Subalpine fir	13.74	4.13	11.50	6.17	14.22	9.97
Douglas-fir	17.61	9.71	17.88	14.90	10.73	9.32
Mixed alpine forest (whitebark pine)	7.64	6.21	8.84	7.10	5.91	7.48
Parklands and subalpine meadows	7.86	2.37	6.62	6.40	6.49	6.78
Shrub/grass	6.19	4.77	4.27	5.25	4.75	7.06
Exposed rock/barren	7.74	7.46	18.49	11.95	3.03	4.39
Ponderosa pine	0.73	0.81	0.80	2.26	3.36	4.67

Table 5.3. Cover type ranking matrices for wolverines in central Idaho based on comparing proportional habitat use from all relocations to habitat available within merged 99% kernel home range polygon for all wolverines (Level 1); proportional habitat use from all relocations to availability within individual 99% home ranges (Level 2); and proportional habitat use from relocations within core home ranges to availability within individual core home ranges. Signs in the matrix represent greater (+) or lesser (-) use between cover type pairs; a triple sign represents significant deviation from random at $P < 0.05$. Ranks are descending from cover type of highest use based on number of positive signs within a cover type (Aebischer et al. 1993). Cover type abbreviations: shb-grs = shrub/grass, p-pine = ponderosa pine, montane = montane coniferous forest, alpine = mixed alpine, parks = montane parklands and subalpine meadows, rock = exposed rock/barren.

$\chi^2 = 48.45$, 5 df, $P = 0.000$

LEVEL 1 - SUMMER						
	shb-grs	p-pine	montane	alpine	parks	rock
shb-grs		+	-	-	-	---
p-pine	-		---	---	---	---
montane	+	+++		-	+	---
alpine	+	+++	+		+	-
parks	+	+++	---	---		---
rock	+++	+++	+++	+	+	
Rank						

$\chi^2 = 28.30$, 5 df, $P = 0.000$

LEVEL 1 - WINTER						
	shb-grs	p-pine	montane	alpine	parks	rock
shb-grs		-	---	-	-	+
p-pine	+		---	---	---	+
montane	+++	+++		+++	+	+++
alpine	+	+	---		+	+
parks	+	+	-	+		+++
rock	---	---	---	---	---	
Rank						

$\chi^2 = 31.93$, 5 df, $P = 0.000$

LEVEL 2 - SUMMER						
	shb-grs	p-pine	montane	alpine	parks	rock
shb-grs		+	-	-	-	---
p-pine	-		-	---	---	---
montane	+	+		-	+	---
alpine	+	+++	+		+	-
parks	+	+++	-	-		---
rock	+++	+++	+++	+	+++	
Rank						

$\chi^2 = 27.14$, 5df, $P = 0.000$

LEVEL 2 - WINTER						
	shb-grs	p-pine	montane	alpine	parks	rock
shb-grs		-	---	-	-	+
p-pine	+		---	-	-	+
montane	+++	+++		+++	+	+++
alpine	+	+	---		-	+
parks	+	+	---	+		+
rock	-	-	---	-	-	
Rank						

of ponderosa pine and shrub/grass types ranked low at all levels and seasons, although both were used more than rock during winter in Levels 1 and 2, with only ponderosa used more than rock at level 3.

Northerly aspects were preferred in both summer and winter. North aspects were used significantly more ($P < 0.05$) in summer than all other aspects except northwest and east (Table 5.4). North and northwest aspects were used significantly more ($P < 0.05$) than southeast during winter, with no other detectable differences in aspect use.

DISCUSSION

Hornocker and Hash (1981) found 70% of wolverine use in medium to scattered timber. Southcentral Alaska wolverines preferred spruce (*Picea* sp.) during winter and rocky areas during summer (Gardner 1985). Male wolverines in Yukon preferred coniferous habitats in winter and avoided alpine talus in summer (Banci 1987). Whitman et al. (1986) found forest types were avoided by wolverines during summer in south-central Alaska.

Preference for higher elevation habitats during summer may be related to the availability of prey species (Gardner 1985, Whitman et al. 1986) or human avoidance (Hornocker and Hash 1981) while lower elevational forest types commonly associated with wild ungulates likely provide the highest carrion availability. Banci (1985) felt that low rodent availability in subalpine habitats in Yukon may have accounted for avoidance of these areas by male wolverines.

Montana wolverines were reluctant to cross openings such as clearcuts or burned areas (Hornocker and Hash 1981). Idaho wolverines commonly crossed natural openings and areas with sparse overstory such as burned areas, meadows, or open mountain-tops. Eight wolverines were relocated in burned areas at least once. M913 was located 15 times in 4

Table 5.4. Aspect ranking matrices for wolverines in central Idaho based on comparing proportional use of aspect from all relocations to availability of aspects within individual 99% home ranges. Signs in the matrix represent greater (+) or lesser (-) use between aspect pairs; a triple sign represents significant deviation from random at $P < 0.05$. Ranks are descending from cover type of highest use based on number of positive signs within a cover type (Aebischer et al. 1993).

$\chi^2 = 23.28$, 7 df, $P = 0.002$

SUMMER									
	N	NE	E	SE	S	SW	W	NW	Rank
N		+++	+	+++	+++	+++	+++	+	7
NE	---		+	+	+++	+	-	+	5
E	---			+	+	+	-	+	3
SE	---	-	-		-	-	-	-	0
S	---	---	---	+		---	---	---	1
SW	---	-	+	+	+		---	+	4
W	---	+	+	+	+	+++		+	6
NW	-	-	-	+	+	-	-		2

$\chi^2 = 42.06$, 7 df, $P = 0.007$

WINTER									
	N	NE	E	SE	S	SW	W	NW	Rank
N		+	+	+++	+	+	+	+	7
NE	-		+	+	+	+	+	-	5
E	-	-		+	+	+	+	-	4
SE	---	-	-		+	-	+	---	2
S	---	---	---	---		---	---	---	0
SW	-	-	-	+	+		+	-	3
W	---	---	---	---	+	+		+	1
NW	-	+	+	+++	+	+	+		6

different burned areas over 2 years. In September 1992, I ground tracked F602 as she traveled through the still smoldering County Line Fire (BNF) burn area. In July 1994 I observed M913 following a group of >20 elk through an area that had burned 2 years prior. During his subadult year, M913 was relocated 7 times in an old burn devoid of overstory.

Extirpation of the wolverine through the eastern provinces of Canada and the midwestern U.S. most likely coincided with the westward advancement of civilization (Banci 1994). Throughout its North American range, the wolverine occupies a wide variety of habitats, although the character of wolverine habitat most readily apparent is its isolation from the presence and influence of humans. Habitat used by the wolverine, such as vegetative communities that support a prey base and landscape features suitable for denning habitat, may be as useful for their isolation as for their other attributes. As such, what is viewed as wolverine habitat may define what is available more than, or as much as, what is preferred.

Hatler (1989) commented that no particular habitat components can presently be singled out specifically for wolverines, and added that reduction of wilderness "refugia" through access and alienation for timber and mineral extraction may be the greatest threat to local population viability. The wolverine has persisted in southwestern Alberta despite extirpation elsewhere in the province largely because of the presence of large refugia in the form of National Parks (Banci 1994).

The discovery of fossil wolverine remains in cold desert environments of southern Idaho (White et al. 1984) may characterize the species' adaptability. Overharvest and displacement by humans may have forced the wolverine out of lowland habitats now altered by agriculture and urban development, and into the more isolated tracts of its present day distribution. The absence of wolverines from historical ranges may be related to human activity as much as

from reductions in habitat. As transient wolverines (usually young dispersing individuals) attempt to colonize or travel through areas of human habitation, their probability of survival may be low.

VI. SUMMARY AND MANAGEMENT RECOMMENDATIONS

Summary

This study established presence and described morphology, ecology, spatial characteristics, and social organization of a wolverine population in central Idaho. Wolverine body mass was smaller while morphology and pelage characteristics were consistent with distribution-wide traits. Individuals established site tenure and were spatially segregated within sexes. Spatial requirements were the largest recorded for the species with male home ranges averaging 1,522 km² and female home ranges averaging 384 km². Population density was estimated at 1 wolverine/198 km². Three of 6 reproductively mature females produced kits during the study period for a reproductive rate of 0.86 kits/female/year. Females selected subalpine cirque habitats for natal and kit rearing dens and were sensitive to human disturbance during kit rearing. One female produced 3 litters in 4 years using the same natal den in consecutive years. Foraging sites were shared with association most prevalent between the resident adult male and sexually immature resident offspring. Offspring did not disperse until sexual maturation with 2 males dispersing over 185 km. Seven study animals died over the course of the study with 50% of the mortality attributed to predation. Subalpine rock habitats were preferred during summer and montane coniferous forest habitats were preferred during winter. Carrion related food items comprised 46% of the diet and were used in similar proportion during both summer and winter.

Management Recommendations

In the United States, wolverines may be harvested only in Alaska and Montana. Outside of these areas a lack of basic information on wolverine distribution and habitat requirements has resulted in little management beyond administrative protection. Hatler (1989) suggested that appropriately responsive management will require a better knowledge of the nature, extent, and correlates of wolverine occurrence. Zielinski and Kucera (1996) argued that distributional surveys are essential to the generation of habitat-relations models, in the evaluation of land-use changes and the effects of human density and disturbance. Surveys should focus on determining occurrence and may include snowtracking surveys or remote camera bait surveys (Zielinski and Kucera 1996). Winter aerial surveys of potential denning habitat may provide an alternative to ground methods. Female wolverine in Idaho located reproductive dens on northerly aspects in isolated subalpine talus cirques. These sites generally lacked overstory canopy allowing snow trails of females traveling to and from the natal den to be visible from aircraft.

Protection of natal denning habitat from human disturbance is critical for the persistence of wolverine in Idaho. The clear association between wolverine presence and refugia may be strongly linked to a lack of available natal denning habitat outside protected areas. Idaho wolverines selected specific natal and kit rearing habitat and responded negatively to human disturbance near these sites. Technological advances in over-snow vehicles and increased interest in winter recreation has likely displaced wolverines from potential denning habitat and will continue to threaten what may be a limited resource.

Vegetative characteristics appear less important to wolverines than physiographic structure of the habitat. Montane coniferous forests suitable for winter foraging and summer

kit rearing may only be useful if connected with subalpine cirque habitats required for natal denning, security areas, and summer foraging. In addition, these habitats must be available during the proper season. Subalpine cirque areas important for natal denning may be made unavailable by winter recreational activities. Conversely, high road densities, timber sales, or housing developments on the fringes of subalpine habitats may reduce potential for winter foraging and kit rearing and increase the probability of human-caused wolverine mortality.

A close relationship exists between wolverine and ungulate presence. Ungulate carrion is a primary food item, and activities that decrease large mammal populations may negatively affect carrion availability. Excessive hunter harvesting and loss of ungulate wintering areas (Banci 1994) as well as displacement of ungulate populations due to excessive timber harvest and urbanization may adversely impact wolverines. Ungulate wounding mortality from hunting and livestock losses on public grazing allotments most likely provides a consistent carrion source. Management practices that reduce the presence and opportunity for carrion availability may impact wolverine foraging success.

Refugia may be most important in providing availability and protection of reproductive denning habitat. Life history requirements of the wolverine are tied to the presence and stability of ecosystems lacking broad scale human influence. Dispersing wolverines in Idaho traveled over 200 km following routes across isolated subalpine habitat. Habitat alteration may isolate subpopulations increasing their susceptibility to extinction processes.

VII. LITERATURE CITED

- Aebischer, N. J., P. A. Robertson, and R. E. Kenwood. 1993. Compositional analysis of habitat use from radio-tracking data. *Ecology* 74:1313-1325.
- Ackerman, B. B., F. A. Leban, M. D. Samuel, and E. O. Garton. 1990. User's Manual for Program Home Range. Second Ed. Tech. Rep. 15, For. Wildl. and Range Exp. Stn., Univ. Idaho, Moscow. 80pp.
- Adams, M. G. 1980. Odour-producing organs of mammals. *Symp. Zool. Soc. Lond.* 45:57-79.
- Addison, E. M., and B. Boles. 1978. Helminth parasites of the wolverine *Gulo gulo* from the District of Mackenzie, Northwest Territories, Canada. *Can. J. Zool.* 56:2241-2242.
- Allredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manage.* 50:157-165.
- Arthur, S. M., W. B. Krohn, and J. R. Gilbert. 1989. Home range characteristics of adult fishers. *J. Wildl. Manage.* 53:674-679.
- Bachman, D., G. Gadwa, and C. Groves. 1990. A winter survey for wolverines (*Gulo gulo*) on the Sawtooth and Challis National Forests, Idaho. Challenge Cost Share Rep. to Sawtooth and Challis Natl. For., Idaho Dep. Fish and Game, Boise. 29pp.
- Banci, V. A. 1982. A bibliography on the wolverine Gulo gulo. Research, Minist. of Environ. and For. IWIFR-9. Victoria, B.C. 53pp.
- _____. 1987. Ecology and behavior of wolverine in Yukon. M.S. Thesis, Univ. British Columbia, Vancouver. 178pp.
- _____, and A. S. Harestad. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. *Ann. Zool. Fenn.* 25:265-270.
- _____, and _____. 1990. Home range and habitat use of wolverines *Gulo gulo* in Yukon, Canada. *Holarctic Ecol.* 13:195-200.
- _____. 1994. Wolverine. Pages 99-127 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, eds. The scientific basis for conserving forest carnivores, American marten, fisher, lynx and wolverine in the western United States. USDA For. Serv. Rocky Mt. For. and Range Exp. Stn., Gen. Tech. Rep. RM-254, Fort Collins, Colo.
- Banks, W. J. 1981. Applied veterinary histology. Williams and Wilkins, Baltimore Md. 540 pp.

- Becker, E. F. 1991. A terrestrial furbearer estimator based on probability sampling. *J. Wildl. Manage.* 55:730-737.
- Boles, B. K. 1977. Predation by wolves on wolverines. *Can. Field-Nat.* 91:68-69.
- Brown, R. E., and D. W. Macdonald, editors. 1985. *Social odours in mammals*. Vol. 2. Clarendon Press, Oxford, England. 882pp.
- Burkholder, B. L. 1962. Observations concerning wolverine. *J. Mammal.* 43:263-264.
- Buskirk, S. W., P. F. A. Maderson, and R. M. O'Conner. 1986. Plantar glands in North American mustelidae. Pages 617-622 in D. Duvall, D. Müller-Schwarze, and R. M. Silverstein, ed. *Chemical signals in vertebrates IV*. Plenum Press, New York, N.Y.
- _____, and L. F. Ruggiero. 1994. American marten. Pages 7-30 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, eds. *The scientific basis for conserving forest carnivores, American marten, fisher, lynx and wolverine in the western United States*. USDA. For. Serv. Rocky Mt. For. and Range Exp. Stn., Gen. Tech. Rep. RM-254, Fort Collins, Colo.
- Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 in M. Bekoff, ed. *Coyotes: biology, behavior, and management*. Academic Press, New York, N.Y.
- Conover, W. J. and R. L. Iman. 1976. Rand transformation as a bridge between parametric and nonparametric statistics. *Am. Statistician* 35:124-133.
- Copeland, J. P., E. Cesar, J. M. Peek, C. E. Harris, C. D. Long, and D. L. Hunter. 1995. A live trap for wolverine and other forest carnivores. *Wildl. Soc. Bull.* 23:535-538.
- Dagg, A. I., and C. A. Campbell. 1974. Historic changes in the distribution and numbers of wolverine in Canada and the northern United States. Ottawa, Can. Wild. Serv. 21pp.
- Davis, W. B. 1939. *The recent mammals of Idaho*. Caxton Printers, Caldwell, Id. 400pp.
- de Monte, M. and J. J. Roeder. 1990a. Histological structure of the abdominal gland and other body regions involved in olfactory communication in Pine martens (*Martes martes*). *Z. Säugetierk.* 55:425-427.
- _____, and _____. 1990b. Les modalités de communication chez la martre (*Martes martes*). *Mammalia* 54:11-22.
- Dieterich, R. A. 1981. Alaskan wildlife diseases. Inst. of Arct. Biol., Univ. of Alaska, Fairbanks. 524pp.

- Eisenberg, J. F., and D. G. Kleiman. 1972. Olfactory communication in mammals. Pages 1-32 in R. F. Johnston, P. W. Frank, and C. D. Michener, eds. Ann. rev. of ecol. and syst., Vol. 3. Ann. Rev. Inc., Palo Alto, Calif.
- _____. 1981. The mammalian radiations. Univ. Chicago Press. 509pp.
- Erlinge, S., M. Sandell, and C. Brinck. 1982. Scent marking and its territorial significance in stoats, *Mustela erminea*. Anim. Behav. 30:811-812.
- Erlinge, S., and M. Sandell. 1986. Seasonal changes in the social organization of male stoats, *Mustela erminea*: an effect of shifts between two decisive resources. Oikos 47:57-62.
- Ewer, R. F. 1973. The Carnivores. Cornell University Press. Ithaca, N.Y. 494pp.
- Fox, M. W. 1975. Evolution of social behavior in canids. Pages 429-459 in M. W. Fox, ed. The wild canids - Their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Company, New York, N.Y. 508pp.
- Gardner, C. L. 1985. The ecology of wolverines in southcentral Alaska. M. S. Thesis, Univ. Alaska-Fairbanks. 82pp.
- Gill, D. 1978. Large mammals of the Macmillan Pass area, Northwest Territories and Yukon. Rep., AMAX Northwest Mining Co. Ltd., Vancouver, B.C. 58pp.
- Gittleman, J. L. 1989. Carnivore group living: comparative trends. Pages 183-208 in J. L. Gittleman, ed. Carnivore behavior, ecology, and evolution. Cornell Univ. Press, Ithaca, New York. 620pp.
- _____, and P. H. Harvey. 1982. Carnivore home-range size, metabolic needs, and ecology. Behav. Ecol. Sociobiol. 10:57-63.
- Gorman M. L., and B. J. Trowbridge. 1989. The role of odor in the social lives of carnivores. Pages 57-88 in J. L. Gittleman, ed. Carnivore behavior, ecology, and evolution. Cornell Univ. Press, Ithaca, N.Y. 620pp.
- Grinnell, G. B. 1920. As to the wolverine. J. Mammal. 1:182-184.
- Groves, C. 1987. Distribution of the wolverine (*Gulo gulo*) in Idaho, 1960-1987. Nongame and Endangered Species Program Report, Idaho Dep. Fish and Game, Boise. 24 pp.
- _____. 1988. Distribution of the wolverine in Idaho as determined by mail questionnaire. Northwest Sci. 62:181-185.

- _____, and G. Gadwa. 1989. Status survey for wolverines (*Gulo gulo*) on the Sawtooth National Forest and adjacent areas. Challenge Cost Share Rep. to Sawtooth Natl. For., Idaho Dep. Fish and Game, Boise. 49pp.
- Haglund, B. 1966. De stora rovdjurens vintervanos. *Viltrevy* 4:245-283.
- Hall, E. R. 1926. The abdominal skin gland of *Martes*. *J. Mammal.* 7:227-229.
- Hatler, D. F. 1989. A wolverine management strategy for British Columbia. *Wildl. Bull.* ISSN 0829-9560; no. B-60, Wildl. Branch, Minist. of Environ., Victoria, B.C. 124pp.
- Hawley, V. D., and F. E. Newby. 1957. Marten home ranges and population fluctuations. *Ibid.* 38:174-184.
- Hayne, D. W. 1949. Calculation of size of home range. *J. Mammal.* 30:1-18.
- Heinemeyer, K. S. 1988. Temporal dynamics in the movements, habitat use, activity, and spacing of reintroduced fishers in northwestern Montana. M.S. Thesis, Univ. Montana, Missoula. 158pp.
- Hickman C. P., Sr., C. P. Hickman, Jr. and F. M. Hickman. 1974. Integrated principles of zoology. The C. V. Mosby Com., St. Louis. 1,025pp.
- Holland, G. P. 1949. A revised check list of the fleas of British Columbia. *Proc. Entomol. Soc. B.C.* 45:7-14.
- Hornocker, M. G. and H. S. Hash. 1981. Ecology of the wolverine in northwestern Montana. *Can. J. Zool.* 59:1286-1301.
- _____, J. P. Messick, and W. E. Melquist. 1983. Spatial strategies in three species of Mustelidae. *Acta Zool. Fenn.* 174:185-188.
- Iverson, J. A. 1972. Basal metabolic rate of wolverines during growth. *Norw. J. Zool.* 20:317-322.
- Kelly, B. T. 1991. Carnivore scat analysis: an evaluation of existing techniques and the development of predictive models of prey consumed. M.S. Thesis, Univ. of Idaho, Moscow. 200pp.
- Kleiman D. G., and J. R. Malcolm. 1981. The evolution of male parental investment in mammals. Pages 347-387 in D. J. Gubernick and P. H. Klopfer, eds. *Parental care in mammals*. Plenum Press, New York, N.Y.

- Koehler, G. M., and M. G. Hornocker. 1979. A winter survey of threatened, endangered, and status undetermined species in north Idaho. U.S. Fish and Wildlife Service Rep., Portland, Org. 30pp.
- _____, _____, and H. S. Hash. 1980. Wolverine marking behavior. *Can. Field-Nat.* 94:339-341.
- Krebs, J. R., and N. B. Davies. 1981. An introduction to behavioural ecology. Sinauer Assoc., Inc., Sunderland, Mass. 292pp.
- Krott, P. 1959. Der Vielfrass (*Gulo gulo* L. 1758). *Monogr. Wildsäuget.* 13:1-159.
- _____. 1960. Ways of the wolverine. *Nat. Hist.* 69:16-29.
- Kruuk, H. 1972. The spotted hyena: a study of predation and social behavior. Univ. Chicago Press. 335pp.
- Leptich, D. J., and P. Zager. 1991. Road access management effects on elk mortality and population dynamics. Pages 126-131 in A. G. Christensen, L. J. Lyon, and T. N. Lonner, compilers. *Proc. elk vulnerability symp.*, Montana State Univ., Bozeman.
- Leyhausen, P. 1965. The communal organization of solitary mammals. *Symp. Zool. Soc. Lond.* 14:249-264.
- Liskop, K. S., R. M. S. F. Sadleir, and B. P. Saunders. 1981. Reproduction and harvest of wolverine (*Gulo gulo*) in British Columbia. Pages 469-477 in J. A. Chapman and D. Pursley eds. *Worldwide furbearer conference proceedings*, Frostburg, Md.
- Long, C. D. 1987. Intraspecific communication of the wolverine. Page 13 in B. Townsend ed. *Abstracts of the Fourth Northern Furbearer Conference*. Alaska Dep. Fish and Game, Juneau.
- Lott, D. F. 1991. *Interspecific variation in the social systems of wild vertebrates*. Cambridge Univ. Press. 238pp.
- Luna, L. G. 1992. *Histopathologic methods and color atlas of special stains and tissue artifacts*. American Histolabs Inc., Gaithersburg, Md. 766p.
- Macdonald, D. W. 1979. Some observations and field experiments on the urine marking behaviour of the red fox, *Vulpes vulpes*. *Z. Tierpsychol.* 51:1-22.
- _____. 1983. The ecology of carnivore social behavior. *Nature* 301:379-384.
- _____. 1985. The carnivores: order Carnivora. Pages 619-722 in R. E. Brown and D. W. Macdonald, ed. *Social odours in mammals*. Vol 2. Oxford Univ. Press, New York, N.Y.

- Magoun, A. J. 1985. Population characteristics, ecology and management of wolverines in northwestern Alaska. Ph.D. Thesis, Univ. Alaska, Fairbanks. 197 pp.
- _____. 1987. Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. Can. Field Nat. 101:392-397.
- Markley, M. H., and C. G. Bassett. 1942. Habits of captive marten. Am. Midl. Nat. 28:604-616.
- Mead, R. A., M. Rector, G. Starypan, S. Neirinckx, M. Jones, and M. N. DonCarlos. 1991. Reproductive biology of captive wolverines. J. Mammal. 72:807-814.
- _____, M. Bowles, G. Starypan, and M. Jones. 1993. Evidence for pseudopregnancy and induced ovulation in captive wolverines (*Gulo gulo*). Zoo Biol. 12:353-358.
- Mills, S. L., and F. F. Knowlton. 1990. Coyote space use in relation to prey abundance. Can. J. Zool. 69:1516-1521.
- Minta, S. C. 1992. Tests of spatial and temporal interaction among animals. Ecol. Appl. 2:178-188.
- Moehlman P. D. 1983. Socioecology of silverbacked and golden jackals (*Canis mesomelas* and *Canis aureus*). Pages 433-453 in J. F. Eisenberg and D. G. Kleiman, eds. Advances in the study of mammalian behavior. Special Pub. No. 7, Am. Soc. Mammal.
- Morgan B. J. T., M. J. A. Simpson, J. P. Hanby, and J. Hall-Craggs. 1974. Visualizing interaction and sequential data in animal behaviour: theory and application of cluster-analysis methods. Behaviour 56:1-43.
- Morse D. H. 1980. Behavioral mechanisms in ecology. Harvard Univ. Press, Cambridge. 383pp.
- Conservation Data Center. 1994. Rare, threatened, and endangered plants and animals of Idaho. Third ed. Idaho Dep. Fish and Game, Boise. 39pp.
- Myrberget, S. 1968. Jervens ynglehi [The breeding den of the wolverine, *Gulo gulo*.] Fauna (Oslo) 21:108-115.
- Pengelly, W. L. 1951. Recent records of wolverines in Idaho. J. Mammal. 32:224-225.
- Peters, R. and L. D. Mech. 1975. Scent-marking in wolves. Am. Sci. 63:628-637.
- Pocock, R. I. 1914. On the feet and external features of the Canidae and Ursidae. Proc. Zool. Soc. Lond. 1914:914-941.

- _____. 1921. On the external characters and classification of the Mustelidae. Proc. Zool. Soc. Lond. 1921:803-807.
- Powell, R. A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. Z. Tierpsychol. 50:153-165.
- _____. 1982. The fisher. Life history, ecology, and behavior. Univ. of Minnesota Press. 217pp.
- Pulliainen, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. Ann. Zool. Fenn. 5:338-344.
- _____, and P. Ovaskainen. 1975. Territory marking by a wolverine (*Gulo gulo*) in northeastern Lapland. Ann. Zool. Fenn. 12:268-270.
- _____. 1982. Scent marking in the pine marten (*Martes martes*) in Finnish Forest Lapland in winter. Z. Säugetierk 47:91-99.
- Quick, H. F. 1953. Wolverine, fisher, and marten studies in a wilderness region. Trans. N. Amer. Wildl. Conf. 18:513-532.
- Rausch, R. L. 1959. Studies on the helminth fauna of Alaska. J. Parasitol. 45:465-484.
- Rausch, R. A., and A. M. Pearson. 1972. Notes on the wolverine in Alaska and the Yukon territory. J. Wildl. Manage. 36:249-268.
- Rothman, J., and L. D. Mech. 1979. Scent marking in lone wolves and newly formed pairs. Anim. Behav. 27:750-760.
- Rubenstein, D. I., and R. W. Wrangham. 1986. Socioecology: origins and trends. Pages 3-20 in D. I. Rubenstein and R. W. Wrangham, eds. Ecological aspects of social evolution. Princeton Univ. Press.
- Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. J. Anim. Ecol. 54:711-719.
- Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164-182 in J. L. Gittleman, ed. Carnivore behavior, ecology, and evolution. Cornell Univ. Press, Ithaca, N.Y. 620pp.
- Schaller, G. B. 1972. The Serengeti lion: a study of predator-prey relations. Univ. Chicago Press, Chicago. 480pp.
- Seidensticker, J. C., IV, M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho primitive area. Wildl. Monogr. 35:1-60.

Shaffer, M. L. 1987. Minimum viable populations; coping with uncertainty. Pages 69-86 in M. E. Soulé, ed. Viable populations for conservation. Cambridge Univ. Press, Cambridge.

Stoddart M. D. 1980a. The ecology of vertebrate olfaction. Chapman and Hall, New York, N.Y. 234pp.

_____, editor. 1980b. Olfaction in mammals. Symp. Zool. Soc. Lond. 45. 363pp.

Swingland, I. R., and P. J. Greenwood. 1984. Animal movement: approaches, adaptations, and constraints. Pages 1-5 in I. R. Swingland and P. J. Greenwood, eds. The ecology of animal movement. Clarendon Press, Oxford.

Unsworth J., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of northcentral Idaho. J. Wildl. Manage. 57:495-502.

Van Zyll de Jong. 1975. The distribution and abundance of the wolverine (*Gulo gulo*) in Canada. Can. Field-Nat. 89:431-437.

Wells, M. C., and M. Bekoff. 1981. An observational study of scent marking in coyotes, *Canis latrans*. Anim. Behav. 29:332-350.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, Calif. 383pp.

White J. A., H. G. McDonald, E. Anderson, and J. M. Soiset. 1984. Lava blisters and carnivore traps. Spec. Pub. Carnegie Mus. Nat. Hist. 8:241-256.

Whitman, J. S., W. B. Ballard, and C. L. Gardner. 1986. Home range and habitat use by wolverines in southcentral Alaska. J. Wildl. Manage. 50:460-463.

Wright, P. L., and R. Rausch. 1955. Reproduction in the wolverine, *Gulo gulo*. J. Mammal. 36:346-355.

Zar, J. H. 1984. Biostatistical analysis. Second ed. Prentice-Hall, Inc. Englewood Cliffs, N.J. 718pp.

Zielinski W. J., and T. E. Kucera, eds. 1996. American marten, fisher, lynx, and wolverine: survey methods for their detection. USDA For. Serv., Pac. Southwest Res. Stn., Gen. Tech. Rep. PSW-GTR-157. 163pp.