

AN ABSTRACT OF THE THESIS OF

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Title: Resource Partitioning by Bobcats and Coyotes in a  
Coniferous Forest

Abstract approved: Redacted for privacy  
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Bobcats (Felis rufus) and coyotes (Canis latrans) were studied in Oregon's Cascade Range between October 1982 and June 1984. Objectives were to describe population characteristics of an exploited bobcat population and to determine patterns of habitat use, movements, and food habits of both species in order to describe partitioning of spatial, vegetational, and food resources on the study area.

Bobcat densities were low (0.04 bobcats/km<sup>2</sup>). Breeding rates and mean litter size increased with age up to 3.5 years; for adults, mean values were 82% and 2.29 kittens/litter, respectively. Survival rates averaged 0.53 annually. Home ranges averaged 34.2 km<sup>2</sup> (harmonic mean model) and did not differ between sexes. No difference between proportional availability and use of slope classes was detected. South-southeasterly aspects were used significantly more frequently than expected. No macrohabitat selection by bobcats was detected, although some selection for microhabitats was evident by season and activity.

Bobcats moved an average of 10.0 km/24 h period; movements were arrhythmic, and males moved further than females during all seasons. Bobcats fed regularly on snowshoe hares (Lepus americanus), black-tailed deer (Odocoileus hemionus), and a variety of rodents.

Home range sizes of coyotes differed between sexes (males  $\bar{x} = 138.3 \text{ km}^2$ , females  $\bar{x} = 30.9 \text{ km}^2$ ; harmonic mean model). Coyotes exhibited significant selection for flat ground and southerly aspects. Although coyotes did not exhibit macrohabitat selection, microhabitat selection was pronounced. Coyotes moved an average of 16.2 km/24 h period, and activity patterns varied from diurnal to nocturnal by season. Fruit, rodents, black-tailed deer, and snowshoe hares were eaten.

Resource partitioning between bobcats and coyotes relied on differences in use of available habitats. Seasonal overlap in use of slope, aspect, and habitat by both species was minimal during winter, when overlap in diets was greatest. Because of the low degree of distributional overlap during winter (16 to 23%), coefficients of competition were lower during the winter than in any other season, whether calculated as multiplicative (15 to 17%) or additive (58 to 59%) values.

**Resource Partitioning by Bobcats and Coyotes  
in a Coniferous Forest**

by

**Dale E. Toweill**

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## PREFACE

This research was funded by the Oregon Department of Fish and Wildlife, whose primary objectives were to obtain baseline ecological and harvest information on bobcat populations in Oregon's Cascade Range. Accordingly, allocations of resources and manpower were made to emphasize data collection on bobcats throughout the study. Data collection on coyotes received lesser priority, resulting in some deficiencies, most notably in sample size of monitored animals. The dimensions of the study area, which provided an adequate sample of bobcats, limited the number of coyotes available for study.

This thesis was prepared in the form of four manuscripts to be submitted for publication. The first of these deals with bobcat ecology, the next two with coyote ecology, and the last presents a synthesis of research completed. A range of supporting data is presented in the Appendix.

RESOURCE PARTITIONING BY BOBCATS  
AND COYOTES IN A CONIFEROUS FOREST

INTRODUCTION

One of the fundamental questions of ecological theory concerns the way different species within an ecosystem can coexist in an environment within which essential resources are limited. Partitioning of resources and adaptations to ensure an adequate supply of all requirements essential for continued existence are believed a fundamental force in driving the evolution of species, leading to formulation of species "niches." Any time the niche of 2 species overlaps too greatly, competition should eventually lead to the extirpation of 1 according to ecological theory.

Bobcats and coyotes both function primarily as predators in the upper portions of the food web in many complex ecological systems. In addition, both of these species are carnivores having approximately equal body size, home range requirements, diet, and metabolic needs (Gittleman and Harvey 1982). Despite these similarities, obviously they must have some mechanisms by which they partition resources since they coexist in a wide variety of habitats over much of North America. This study was designed in order to derive a basic understanding of what resource partitioning methods may be employed in the Cascade Range of western Oregon.

Prerequisite to an understanding of resource partitioning among bobcats and coyotes was an understanding of the ecology of these species in managed forests of the western Cascade Range. Accordingly, results of this study are presented in 3 chapters, the first dealing with ecology of bobcats, the second with ecology of coyotes, and the third dealing with the question of resource partitioning between them. Each of the chapters is written as a separate essay in publication-style format (Chapter 2 contains 2 such essays). This format was selected to allow the reader to selectively review the material, and to provide a ready format for dissemination of the material to a larger audience through publication.

## CHAPTER ONE

## ECOLOGY OF BOBCATS IN THE CASCADE MOUNTAINS OF WESTERN OREGON

The bobcat (Felis rufus) is among the most widespread of all North American predators, with populations in all of the contiguous 48 states, except Delaware, and the southern Canadian provinces (Deems and Pursley 1978). Until recently the low economic value of bobcat pelts and difficulties in working with bobcats had precluded research in many portions of its range. In 1972 use of Compound 1080 (a highly effective toxicant used in coyote control) was discontinued on public lands, which resulted in increased coyote populations. At about the same time, there was a shift in world fur garment markets toward use of feline furs, which resulted in a dramatic increase in pelt prices and hunting and trapping pressure. As a result of these factors, bobcat populations are believed to have declined after 1972 (Nunley 1978). Public concern for felid species and the lack of baseline ecological data resulted in inclusion of bobcats in Appendix II of the Convention in International Trade in Endangered Species (CITES) agreement in 1976. With inclusion of the bobcat in the CITES agreement, states were required to

demonstrate that trapping to provide bobcat pelts for international trade would "not be detrimental to the survival of the species." Data requirements were stringent, and many investigations into bobcat ecology were begun nationwide.

Information on bobcat populations in coniferous forest habitats has not been previously reported, although the extensive coniferous forests of the Pacific Northwest have long supported harvests of 2,000 to 3,000 bobcats annually. The only published information on bobcats in this region was an investigation of bobcat food habits from Oregon's Coast and Cascade Ranges (Nussbaum and Maser 1975). This study was designed to examine the ecology of an exploited bobcat population in Oregon's Cascade Range to evaluate bobcat management practices and hypotheses advanced by Bailey (1981) concerning bobcat social organization.

#### STUDY AREA

The study area (43° 55' N, 122° 30' W) included approximately 310 km<sup>2</sup> of the Willamette National Forest, 55 km east of Eugene in Oregon's Cascade Mountain range. Topography was abruptly dissected by stream courses along the North Fork of the Middle Fork Willamette River at an elevation of about 500 m. Canyon walls were steep, rising about 250 m from the river to the edge of Christy Flat on the north and about 500 m to a dividing ridge on the south. Christy Flat was a relatively level plateau

ranging in elevation from 850 to 920 m and was sharply dissected by a number of small drainages. To the north and east of Christy Flat lay a complex system of ridges ranging from 920 to 1,500 m in elevation.

Climate was typical of western Cascade maritime areas with mild, wet winters and warm, dry summers. Days with precipitation averaged about 160 per year, and precipitation averaged about 150 cm annually (Lahey 1979). January mean minimum temperature averaged about  $-1^{\circ}\text{C}$ , while July mean maximum temperature averaged about  $27^{\circ}\text{C}$ ; annual extreme temperatures ranged from about  $-18^{\circ}\text{C}$  to  $38^{\circ}\text{C}$ . Mean annual snowfall averaged about 163 cm, and the latest date with 150 cm of snow usually occurred in late March (Lahey 1979).

The study area was within the western hemlock (Tsuga heterophylla) vegetation zone (Franklin and Dyrness 1973). Logging, reforestation, and forest fires led to dominance of Douglas-fir (Pseudotsuga menziesii) over most of the area. The region is characterized by extensive stands of Douglas-fir and climax stands of western redcedar (Thuja plicata). Grand fir (Abies grandis), Pacific silver fir (Abies amabilis), western yew (Taxus brevifolia), and western white pine (Pinus monticola) occur commonly. Understories are dominated by creambush oceanspray (Holodiscus discolor) on dry sites, Pacific rhododendron (Rhododendron macrophyllum) and Cascade hollygrape (Berberis nervosa) on intermediate sites, and swordfern (Polystichum munitum) and Oregon oxalis (Oxalis oregana) on wet sites (Franklin and Dyrness 1973).

The impacts of past management practices on the study area were extensive, so that the area was very unlike pristine forest. Habitats identified, descriptions of each, and extent on the 279 km<sup>2</sup> (68,837 acre) core study area follow:

**Large Sawtimber:** Stands of trees, typically dominated by Douglas-fir or western redcedar, having average diameters > 50 cm dbh. Crown cover varied. The limited amount of old-growth forest that occurred on the study area was included in this vegetation class, which occurred on 131 km<sup>2</sup> (47%) of the core study area.

**Closed Sapling Pole Sawtimber:** Stands of Douglas-fir or mixed conifers with trunks averaging 2 to 50 cm dbh and having a crown canopy cover  $\geq$  60%. Characteristically, these stands were areas clearcut 25 to 50 years earlier, or areas subjected to selective harvest of sawtimber within the previous 10 to 25 years. This vegetation class occurred on 55 km<sup>2</sup> (20%) of the study area.

**Open Sapling-Pole:** Stands of trees averaging 2 to 50 cm dbh and a crown canopy cover < 60%. Although this vegetation class was dominated by regenerating stands of Douglas-fir, areas of recent selective harvest of sawtimber and hardwood riparian vegetation were also included. This class occurred on 25 km<sup>2</sup> (9%) of the study area.

**Dense Shrub:** Shrub stands with crown canopy closure  $> 40\%$  and tree stands averaging  $< 2$  cm dbh with crown canopy closure  $> 40\%$  for trees  $> 1.5$  m high. Stands in this class typically were clearcut Douglas-fir stands 5 to 15 years post-harvest that were not treated with herbicides following timber harvest. Most tree stands in this category were stands of regenerating Douglas-fir, while shrub stands in this category typically were dominated by rhododendron. This vegetation class occurred on  $61 \text{ km}^2$  (22%) of the study area.

**Sparse Vegetation:** A mixed classification ranging from grass-forb stands to shrub stands with  $\leq 40\%$  crown cover and heights  $\leq 1.5$  m and stands having trees  $\leq 1.5$  m tall. Stands in this class typically represented either natural meadows (above or below timberline) or sites of recent clearcut activity, particularly if timber harvest was followed with herbicide treatment. This vegetation class occurred on  $6 \text{ km}^2$  (2%) of the core study area.

**Non-habitats:** A mixed class including water, soil, rock, or bare soil, which occurred on  $1 \text{ km}^2$  ( $< 1\%$ ) of the core area.

The entire study area lays within the managed forest, so that all of the habitats described above were thoroughly intermingled in small patches. The effect of past harvest practices was to create a "fine-grained" environment in terms of habitats described.

## METHODS

### Capture and Tagging

Bobcats were live-trapped using Victor and Blake & Lamb 1.75 coil-spring traps placed near bait or scent attractants. Traps were modified to prevent injury to bobcats by padding the trap jaws or adding extension chains or drags. In addition, 29 box-type livetraps featuring live-bait cages in one end were employed, using domestic rabbits as attractors. All traps were checked at least once daily throughout the period of capture efforts. Trapping was conducted through all seasons of the year except late spring and early summer, to avoid stressing female bobcats during the late pregnancy or post-partum period. In addition to live-trapping, bobcats were regularly captured with trained hounds.

Captured bobcats were restrained with a spring-loaded Ketch-All Noose (Ketch-All Equipment Co., San Diego, CA) and anesthetized with ketamine hydrochloride injected intramuscularly at an estimated dosage of approximately 25 mg/kg body weight. Treed bobcats were injected with ketamine hydrochloride from hypodermic darts fired from a .50 caliber Pneu-Dart rifle. At time of capture, sex of each animal was determined, and each was equipped with a radio-transmitter collar, weighed, measured, and examined for evidence of trap injury and general physical condition. Each ear was marked with a numbered metal fingerling tag, and each animal was placed in a quiet, shaded area to

recover from the effects of the anesthetic. Field personnel left the area only after the animal had gained sufficient body control to move away from the capture site.

### Monitoring

Radio-transmitter equipped bobcats were monitored using portable, hand-held 4-element yagi antennas and radio receivers built by AVM Instrument Co., Inc. (Model LA-12) and Telonics, Inc. (Model TR-2 with scanner). Field tests indicated average accuracy in determination of true bearing to be  $\pm 3^\circ$ . Bobcat locations were determined by triangulation following a series of directional bearings recorded by one or more observers. Each animal's position was determined from a distance of 500 m or less whenever possible, using 3 or more directional bearings, and was assigned grid unit of 1 ha<sup>2</sup> using Universal Transverse Mercator (UTM) system markings on 1:24,000 scale orthophoto-quadrangle maps.

Monitoring of radio-equipped bobcats featured both "scanning" and "focal animal" approaches (Lehner 1979). "Scanning" consisted of locating each individual animal 3 to 7 times/week. These data were used to calculate home range size and to evaluate macrohabitat selection. "Focal animal" monitoring consisted of locating an individual animal sequentially once every 15-minute period in bouts of 6 - 12 h conducted around the clock. Focal animal monitoring of each bobcat encompassed at least one 24 h

diurnal period every season. Focal animal data were used to investigate macrohabitat selection and movements of bobcats during seasonal and diurnal periods.

All data were summarized monthly and seasonally, with seasons designated as follows: winter--January 1 through March 31, spring--April 1 through June 30, summer--July 1 through September 30, and fall--October 1 through December 31.

### **Carcass Evaluations**

Skulls and reproductive tracts were collected from trappers in western Oregon. A lower canine tooth was extracted from each skull of bobcats killed in a four-county (Lane, Linn, Douglas, and Marion) area surrounding and including the study area. Teeth were sent to Matson's Microtechnique, Milltown, Montana, for age determination (Crowe 1972). Female reproductive tracts were preserved in 70% ethyl alcohol; ovaries were sectioned and corporal bodies enumerated, and uteri were cleared through progressive dehydration in ethyl alcohol and immersion in methyl salicylate. Following clearing, embryo implantation sites (placental "scars") were identified and enumerated to determine the number of embryos implanted.

### **Food Habits**

Scats were collected from the study area almost daily from 15 October 1982 through 30 June 1984. Each scat was labeled and air-dried prior to separation and identification of prey

remains. Prey items in a portion of the scats were separated from undigested residues as collected, but bones were separated from most scats using a weak solution of NaOH to digest the associated conglomerate (Degn 1978). Samples of hair were removed from scats prior to NaOH digestion for comparison with hair keys (Mayer 1952, Stains 1958, Adorjan and Kolenosky 1969) to aid in prey species identifications. Food items were identified by comparison with skeletal materials in the vertebrate museum of the Department of Fisheries and Wildlife, Oregon State University, Corvallis.

Because of difficulties in identifying bobcat and coyote scats (Murie 1954), each scat collected was subjected to a three-part identification procedure. At time of collection, each scat was identified to species based on physical characteristics, odor, and associated "sign"; identified to species using criteria of color, texture, and odor at time of analysis; and finally a portion of each scat was subjected to thin-paper chromatography for identification of bile acid residues present (Johnson et al. 1979, Major et al. 1980, and Johnson et al. 1984). Thin-paper chromatography was used to derive final identification of scats where other data were not definitive.

#### Data Analysis

Bobcat densities were estimated from the maximum number of bobcats known to occur on the core study area at fixed points in time during this study. Crude harvest density of bobcats was

calculated as number of bobcats harvested divided by harvest area, based on trapper reports from a contiguous four-county area which included the study area. Similarly, bobcat sex ratios were calculated based on all bobcats captured on the study area and on all bobcats of known sex harvested from a contiguous four-county area. Age structure of the population, age-specific pregnancy rates, and mean litter size were determined from harvested bobcats. Survival rates were determined for monitored bobcats using a conventional life-table approach (Caughley 1977:93) and mean daily survival rates of radio-equipped animals. Mean daily survival rates of radio-equipped bobcats were calculated by:

$$\hat{s} = [(x - y) / x]^n$$

where  $x$  = sum of days within the period when monitored bobcats were known to be alive,  $y$  = sum of mortalities recorded among monitored bobcats, and  $n$  = number of days in the monitor interval (Trent and Rongstad 1974).

Home ranges of bobcats were calculated using the harmonic mean model (Dixon and Chapman 1980) at a 95% utilization level and the minimum convex polygon model (Southwood 1966). Other methods and utilization level values were calculated for purposes of comparison (see Appendix Table 29). All calculations were made using Program Home Range (Samuel et al. 1983). Because the minimum convex polygon model is sample size dependent (Jennrich and Turner 1969), home range estimates using this model were based on leveling of an area/observation curve.

The extent of overlap among minimum polygon home ranges was measured as the coefficient of static overlap (Macdonald et al. 1980, Voight and Tinline 1980). This value, calculated as the area used in common divided by the total home range area of the animals under examination, can range from 0 (no area in common) to 1.00 (the entire home range within the range of another animal) and was not reflexive, i.e., overlap of "A" on "B" did not equal overlap of "B" on "A."

Aspects of bobcat social organization were inferred from the distribution and degree of overlap of home range areas, location of bobcat scent stations, and contacts between individuals.

A resource map of the area was developed through the Earth Remote Sensing Laboratory at the University of Washington, using multispectral scanner (MSS) reflectance data obtained via LANDSAT satellite. The 64 reflectance values obtained from digitized data were analyzed to provide a resource map featuring 6 major vegetation class (described above), 6 categories of slope (none, 1 to 10%, 11 to 20%, 21 to 30%, 31 to 40%, and over 40%), and 9 categories for aspect (none, NNE--0 to 45°, ENE--46° to 90°, ESE--91° to 135°, SSE--136° to 180°, SSW--181° to 225°, WSW--226° to 270°, WNW--271° to 315°, and NNW--316° to 360°). Identification and verification of all groupings were accomplished by aerial photointerpretation and ground truth verification, and lineprinter maps were produced at 1:24,000 (7.5 minute) scale to provide an overlay of U.S.G.S. topographic coverage.

Habitat selection by bobcats was examined on two levels: macrohabitat and microhabitat selection (second- and third-order selection as defined by Johnson 1980). Analysis of third-order selection was based on habitats within minimum convex polygon home ranges and specific point locations. Selection or avoidance of habitats was determined following the approach of Neu et. al. (1974), after chi-square analysis led to rejection of the null hypothesis that seasonal observations followed an "expected" occurrence pattern derived from relative frequency of habitats determined from LANDSAT data. Necessary assumptions for use of this approach are that (1) animals have opportunity to select any available habitat, and (2) observations are collected in a random, unbiased manner. Because of the low number of habitats identified and their degree of interspersion throughout the study area, bobcats had opportunity to exhibit habitat selection from any point within their home range between locations. This technique is conservative, owing to use of Bonferroni normal statistics, and has been shown to perform well when numbers of habitats and animals are small and numbers of locations large (Alldredge and Ratti 1986). Analysis of macro- and microhabitat selection were based on total and seasonal data; analyses of microhabitat selection were further examined by activity and photoperiod.

Differences in timing and extent of bobcat activity were tested using the non-parametric Wilcoxon matched-pairs signed ranks test (Siegel 1956). Seasonal diets were compared using the

equation of Horn (1966) to derive diet overlap values, which ranged from 0 (no overlap) to 1 (identical diets). This index, modified from Morista (1959), is calculated as:

$$C(\lambda) = 2 \sum_{i=1}^s x_i y_i / (\sum_{i=1}^s x_i^2 + \sum_{i=1}^s y_i^2)$$

Average size of prey items eaten by bobcats was calculated, based on the average adult weight of the prey species eaten and its frequency of occurrence in the bobcat diet. The sum of species values was divided by the number of kinds of prey eaten to derive average prey size. Average adult weights of mammals used in these calculations were taken largely from Maser et al. (1981); weights for mammals not reported by them were estimated from recorded weights of specimens on deposit at Oregon State University. Mammal nomenclature follows Jones et al. (1982), and plant nomenclature follows Garrison et al. (1976).

## RESULTS

Carcasses of 737 bobcats harvested during the 1983-84 season were analyzed, and comparable data were extracted from harvest summaries for the 1982-83 (Trainer, pers. comm.) and 1984-85 seasons. In addition, 15 bobcats were captured 28 times on the study area as a result of 12,011 trap-nights and 412 hours of pursuit by hounds (Table 1 and Appendix Table 27). Of these, 13 bobcats were radio-equipped and relocated 7 to 199 times over periods encompassing 15 to 620 days, for a total of 1,041 daily relocations. An additional 630.5 hours of intensive monitoring, during which individual bobcats were relocated at 15-minute intervals, were conducted to obtain more detailed data on activity and habitat use.

### Demographic Characteristics

Sex and Age Structure--The sex ratio of bobcats harvested from the four-county area in 1983-84 was 1.2 males per female ( $n = 737$ ), which differed significantly from equality ( $\chi^2 = 6.46$ ,  $p < 0.025$ ). However, the sex ratio of bobcats harvested in this same area in 1982-83 (1.1 males per female;  $n = 630$ ) and in 1984-85 (1.1 males per female;  $n = 191$ ) did not differ from equality ( $\chi^2 = 0.406$ ,  $p > 0.5$ , and  $\chi^2 = 0.634$ ,  $p > 0.6$ , respectively). Similarly, the sex ratio for all western Oregon bobcats did not differ significantly from equality in the 1983-84 sample (1.1 males/female;

Table 1. Summary data for bobcats monitored, 1982-1984.

| Bobcat No. | Sex | Age              | Days Monitored | No. of Locations |            | Home Range           |                            |
|------------|-----|------------------|----------------|------------------|------------|----------------------|----------------------------|
|            |     |                  |                | Daily            | Successive | Polygon <sup>a</sup> | Harmonic Mean <sup>b</sup> |
| 1          | F   | Ad               | 620            | 177 <sup>d</sup> | 243        | 29.6                 | --- <sup>c</sup>           |
| 2          | F   | Ad <sup>e</sup>  | 17             | 7                | 0          | --                   | --                         |
| 3          | F   | Juv              | 16             | 11               | 0          | --                   | --                         |
| 4          | M   | Ad <sup>f</sup>  | 92             | 84               | 0          | 7.8                  | 12.1                       |
| 5          | M   | Ad <sup>g</sup>  | 34             | 30               | 0          | --                   | --                         |
| 6          | F   | Ad               | 25             | 23               | 0          | --                   | --                         |
| 7          | F   | Ad               | 508            | 193 <sup>h</sup> | 632        | 39.3                 | 60.6                       |
| 8          | M   | Ad               | 485            | 199              | 654        | 37.6                 | 58.4                       |
| 9          | F   | Juv <sup>i</sup> | 17             | 17               | 0          | --                   | --                         |
| 10         | F   | Ad               | 489            | 177 <sup>h</sup> | 649        | 25.2                 | 33.4                       |
| 12         | M   | Ad <sup>j</sup>  | 157            | 47               | 200        | 29.4                 | 33.4                       |
| 13         | F   | Ad               | 306            | 68               | 232        | 6.8                  | 7.2                        |
| 14         | F   | Juv              | 17             | 8                | 53         | --                   | --                         |

a Min. convex polygon model (Southwood 1966).

b Harmonic mean model (Dixon and Chapman 1980) at 95% utilization distribution.

c Not available; ellipse did not close.

d Three points excluded for home range calculation.

e Killed illegally 7 Nov 1982; age 2.5 years.

f Killed by predator 5 Apr 1983; age 2.0 years.

g Killed by predator following handling injury 10 Feb 1983; age 2.5 years.

h One point excluded for home range calculation.

i Killed by coyote 14 Mar 1983; age 0.5 years.

j Harvested by trapper 28 Jan 1983; age 6.5 years.

$\chi^2 = 3.14$ ,  $p > 0.05$ ). (Harvest data for the 1983-84 season are presented in Appendix Table 31.)

Harvest rates were not uniform through the December-January season for either males ( $\chi^2 = 27.6$ ,  $p < 0.005$ ) or females ( $\chi^2 = 19.2$ ,  $p < 0.005$ ). Both sexes became increasingly vulnerable to harvest from December through January, but the difference in the ratio of males to females in the harvest did not differ significantly ( $p > 0.05$ ) by 2-week periods (Table 2).

The percentage of kittens in the harvest ranged from 19 to 26% (1982-83: 19%; 1983-84: 22%; and 1984-85: 26%). The kitten cohort in the harvest sample was typically smaller than the yearling cohort taken the following year, indicating that kittens were underrepresented in the harvest. Slightly over 50% of the bobcats in each sample were of breeding age (2.5 years or older), which remained remarkably consistent among years (1982-83: 53%, 1983-84: 59%, and 1984-85: 52%). Bobcats 10.5 years and older accounted for 2% of the harvest sample each of the 3 seasons. The oldest bobcat harvested in the 1983-84 season was a 13.5 year-old male; 2 females and 2 males each 12.5 years old were also recorded.

Natality--Natality rates were determined from examination of 133 female reproductive tracts from the 1983-84 harvest season. None of 26 female kittens, 5 of 18 (28%) female yearlings, and only 14 of 27 (52%) two-year-old female bobcats showed evidence

Table 2. Percent of harvest by sex during two-week intervals of the 1983-84 bobcat harvest season in Douglas, Lane, Linn, and Marion Counties, Oregon.

| Sex      | N          | Interval    |             |             |             |
|----------|------------|-------------|-------------|-------------|-------------|
|          |            | Dec. 1-15   | Dec. 16-31  | Jan. 1-15   | Jan. 16-31  |
| Males    | 403        | .186        | .201        | .258        | .356        |
| Females  | <u>334</u> | <u>.179</u> | <u>.207</u> | <u>.281</u> | <u>.333</u> |
| Combined | 737        | .183        | .204        | .268        | .346        |

of breeding activity. Breeding rate increased annually until bobcats reached 3.5 years; the breeding rate for adults was 82%. The mean litter size likewise increased with age, from 2.00 ( $\pm$  1.22) kittens for 1.5 year old bobcats ( $n = 5$ ) to 2.07 ( $\pm$  0.83) for 2.5 year-olds ( $n = 14$ ) and 2.29 ( $\pm$  0.67) for animals 3.5 years and older ( $n = 51$ ).

Survival Rates---Age specific survival rates of harvested bobcats were calculated using a composite life table with the zero frequency estimated from fecundity rates (Caughley 1977:93), equal representation of the sexes at birth, and a zero rate of increase in the population assumed. Data were entered as a sample of the dying, since harvest mortality was assumed a major portion of total mortality. Only females in the harvest were used in calculations. Females harvested in 1982-83, 1983-84, and 1984-85 were pooled to reduce the influence of annual variation in harvest, and all values were then adjusted to reflect a cohort of 1,000 females (Table 3).

Age-specific survival rate estimates for bobcats aged 3.5+ years averaged 0.678. However, it must be noted that the life table approach requires certain assumptions that these data may not meet, namely that the population sampled be a (1) stationary population, with (2) a stable age distribution, and that (3) all individuals have equal likelihood of representation in the sample. Our data are insufficient to evaluate the extent of departure from the first two assumptions, but they do indicate significant departure from the assumption

Table 3. Composite life table for bobcats, based on actual numbers of females harvested from Douglas, Lane, Linn, and Marion Counties, Oregon. Data were pooled from harvest samples obtained in 1982-83, 1983-84, and 1984-85 seasons.

| Class        | $d_x$<br>(Obs.) | $l_x$<br>(Est.)   | $m_x^a$ | $l_x m_x$   | Adjusted <sup>b</sup> |       |               | $s_x$ |
|--------------|-----------------|-------------------|---------|-------------|-----------------------|-------|---------------|-------|
|              |                 |                   |         |             | $l_x$                 | $d_x$ | $l_x m_x$     |       |
| 0.0          | --              | 1005 <sup>c</sup> | 0       | 0           | 1.000                 | 0.273 | 0             | 0.726 |
| 0.5          | 175             | 731 <sup>d</sup>  | 0       | 0           | 0.726                 | 0.173 | 0             | 0.760 |
| 1.5          | 168             | 556               | 0.280   | 155         | 0.552                 | 0.167 | 0.155         | 0.697 |
| 2.5          | 136             | 388               | 0.538   | 208         | 0.385                 | 0.135 | 0.2075        | 0.649 |
| 3.5          | 86              | 252               | 0.939   | 236         | 0.250                 | 0.085 | 0.2352        | 0.658 |
| 4.5          | 65              | 166               | 0.939   | 155         | 0.165                 | 0.064 | 0.1549        | 0.608 |
| 5.5          | 44              | 101               | 0.939   | 94          | 0.100                 | 0.043 | 0.0942        | 0.564 |
| 6.5          | 14              | 57                | 0.939   | 53          | 0.056                 | 0.013 | 0.0532        | 0.754 |
| 7.5          | 16              | 43                | 0.939   | 40          | 0.042                 | 0.015 | 0.0401        | 0.627 |
| 8.5          | 6               | 27                | 0.939   | 25          | 0.026                 | 0.005 | 0.0252        | 0.777 |
| 9.5          | 5               | 21                | 0.939   | 19          | 0.020                 | 0.004 | 0.0196        | 0.761 |
| 10+          | 16              | 16                | 0.939   | 15          | 0.015                 | 0.015 | 0.0149        | 0.000 |
| <b>TOTAL</b> | <b>731</b>      |                   |         | <b>1005</b> |                       |       | <b>1.0000</b> |       |

a Product of (breeding rate) x (mean litter size) / 2 to yield females produced/female.

b Adjusted to a cohort of 1,000 animals.

c Estimated from age-specific breeding rates and litter sizes (sum of unadjusted  $l_x m_x$  values).

d Sum of  $d_x$  values.

that all individuals have equal likelihood of representation in the sample, as evidenced by the underrepresentation of the kittens and yearlings in the harvest. Mean daily survival rates for radio-equipped bobcats also were calculated. Mean daily survival rates (95 percent confidence intervals in parentheses) for bobcats ranged from 0.74 (0.41-0.94) to 1.000 on a quarterly basis, and averaged 0.53 (0.23-0.81) annually (Table 4). Male survival rates were much lower than those of females monitored.

Five (36%) of the 14 bobcats monitored were known to have died during this study. Of these, 2 losses (14%) were human-related (1 bobcat killed illegally by a deer hunter, and 1 taken legally by a trapper), and 3 (21%) were predator-related (1 bobcat killed by a coyote, Canis latrans, and 2 by unknown predators, either coyote or cougar, Felis concolor). Contact was lost with 3 other bobcats during this study--2 with functional collars that disappeared on days when houndsmen were known active within their home ranges, and 1 that escaped its radio-collar but which apparently remained healthy within its home range, as bobcat "sign" was located regularly within its home range area until termination of this study. If the 2 bobcats that disappeared and which were believed harvested were included as mortalities, the annual survival rate for both sexes would have been 0.41 (0.16-0.70). Of the 5 bobcats that survived through the study, 1 was captured by a trapper and released during the 1983-84 season; addition of this animal as a mortality would have further reduced the estimated annual survival rate to

Table 4. Mean seasonal survival rates for monitored bobcats, as calculated by the method of Trent and Rongstad (1974). Values in parentheses are 95% confidence intervals.

| Sex     | N  | Total Survival Days | Total Mortalities | Seasons          |                  |           |                  | Annual Survival  |
|---------|----|---------------------|-------------------|------------------|------------------|-----------|------------------|------------------|
|         |    |                     |                   | Jan - Mar        | Apr - Jun        | Jul - Sep | Oct - Dec        |                  |
| Males   | 4  | 787                 | 3                 | 0.53 (0.10-0.93) | 0.61 (0.06-0.99) | 1.000     | 1.000            | 0.25 (0.02-0.75) |
| Females | 9  | 2,094               | 2                 | 0.88 (0.44-1.00) | 1.000            | 1.000     | 0.82 (0.34-0.99) | 0.71 (0.42-0.96) |
| Both    | 13 | 2,881               | 5                 | 0.74 (0.41-0.94) | 0.90 (0.54-1.00) | 1.000     | 0.870            | 0.53 (0.23-0.81) |

0.36 (0.14-0.64). Two of the 5 bobcats known alive on the study area at the end of field activities were known harvested by trappers in the 1984-85 trapping season, and 2 more were taken in the 1985-86 season. At best, only 1 of the 15 bobcats known alive on the study area survived 2 years after the conclusion of research (see Appendix Table 28).

Density--Harvest density (number of bobcats reported harvested by trappers from the four-county area) was 0.028 bobcats/km<sup>2</sup> in 1983-84. By comparison, crude density of bobcats known to occur on the study area during the study period was 0.060 bobcats per km<sup>2</sup>. Maximum known density of bobcats on the study area occurred during January 1984, when ranges of 3 adult males, 4 adult females, 1 female kitten, and 2 uncollared adults of unknown sex were known on the 279 km<sup>2</sup> study area. Thus maximum density was 0.04 bobcats/km<sup>2</sup>. Minimum known density occurred in January 1983, when at least 8 bobcats (3 adult males, 3 adult females, 1 female kitten, and 1 adult of unknown sex) were known on the study area, for a minimum density of 0.03 bobcats/km<sup>2</sup>. However, additional bobcats may have occurred on the area at that time. These figures include large expanses of habitat not occupied by bobcats, except possibly as occasional transients. Bobcat density in fully-occupied habitats, as occurred in western portions of the study area, was 0.09 bobcats/km<sup>2</sup>.

## Social Organization

Home Range Size--Thirteen bobcats were equipped with radio-transmitter collars and were located from 7 to 199 times during monitoring periods which ranged from 15 to 620 days (see Appendix Table 28). The amount of area added to minimum polygon home ranges as additional locations were added declined to less than 5% at about 15 locations per individual (see Appendix Fig. 10). Based on this finding, a minimum of 15 locations were required for calculation of seasonal home ranges. A minimum of 40 daily locations over a period of at least 90 days was required for calculation of total home range area. Home ranges calculated using the minimum convex polygon model averaged about 65% of the area estimated by the harmonic mean model at a 95% utilization interval (Table 1). Home range calculations based on other utilization intervals and methods are presented in Appendix Table 29. Minimum convex polygon home range areas did not show much disparity in home range size between male ( $\bar{x} = 24.9 \text{ km}^2$ ; range = 7.8 to 37.6  $\text{km}^2$ ) and female bobcats ( $\bar{x} = 25.2 \text{ km}^2$ ; range = 6.8 to 39.3  $\text{km}^2$ ). Values for home ranges calculated using the harmonic mean model ranged more widely, from 12.1 to 58.4  $\text{km}^2$  for males ( $\bar{x} = 34.6 \text{ km}^2$ ) and from 7.2 to 60.6  $\text{km}^2$  for females ( $\bar{x} = 33.8 \text{ km}^2$ ). The minimum convex polygon model was most useful as a mapping technique as it conformed more closely to the areas actually utilized or avoided by bobcats on a fine scale than the harmonic mean model. The

harmonic mean model provided a more accurate and statistically reliable indicator of actual utilization.

Home ranges of bobcats fluctuated seasonally. Male home range areas were largest during the spring but became progressively smaller during the summer, fall, and winter (Table 5). Female home ranges were largest during the summer, contracted during fall and winter, and began expanding in the spring (Table 5). Home ranges of males were significantly larger than those of females home ranges during all seasons ( $\chi^2 = 17.1$ ,  $p < 0.05$ ).

Home Range Distribution--Home ranges of bobcats were not distributed evenly on the study area (Fig. 1). Although every bobcat on the study area was believed to have been captured and monitored, large tracts of apparently suitable habitat remained unoccupied throughout the study, and several home ranges were not reoccupied following death of resident animals. Considerable overlap of bobcat home ranges occurred near the western boundary of the study area, where 5 adults (2 males and 3 females) lived throughout most of the study (Fig. 1). The basic pattern of home range overlap featured home ranges of males alternating with home ranges of females. For example, moving from southwest to northeast during fall 1983, the home range of male 12 included Hamner, McKinley, Chalk, and Christy Creek drainages; that of female 7 included Chalk and Evangeline Creek drainages; male 8 utilized Evangeline and Billy Creek drainages; and female

Table 5. Seasonal home range areas of male and female bobcats in km<sup>2</sup> as estimated by minimum convex polygon and harmonic mean (95% utilization distribution level) home range models. Numbers of individuals monitored per season are indicated in parentheses.

| Sex     | Method        | Season   |          |          |          |
|---------|---------------|----------|----------|----------|----------|
|         |               | Winter   | Spring   | Summer   | Fall     |
| Males   | Min. Polygon  | 11.6 (4) | 21.1 (1) | 17.1 (2) | 14.0 (2) |
|         | Harmonic Mean | 12.1 (4) | 22.2 (1) | 9.4 (2)  | 8.1 (2)  |
| Females | Min. Polygon  | 9.8 (8)  | 12.2 (3) | 15.6 (3) | 12.4 (4) |
|         | Harmonic Mean | 10.4 (8) | 11.2 (3) | 14.7 (3) | 6.5 (4)  |

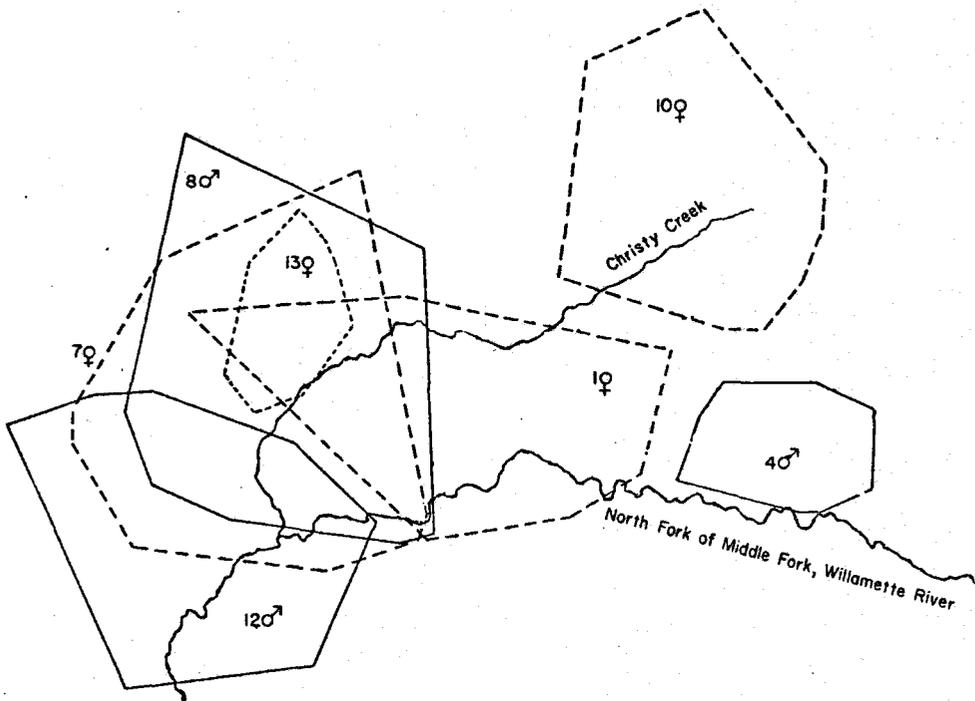


Figure 1. Location of minimum convex polygon home ranges of bobcats on the study area. Solid lines denote home ranges of males and dashed lined denote home ranges of females.

13 utilized upper portions of Billy Creek and Perdue Creek drainages. All of these drainages ran from the northwest to the southeast, and all 4 bobcat home ranges extended from ridgetop to the bottom of the main drainage (Fig. 1). The home range of another adult female (bobcat 1) lay to the west, primarily across Christy Creek, from below the mouth of Evangeline Creek to well above the mouth of Perdue Creek. Even though home ranges exhibited a high degree of overlap (Fig. 1), the areas where overlap occurred between bobcats of the same sex were not frequently used by either animal. (An exception occurred with female 13, believed to have been a kitten of female 7 within whose home range she lived.) The coefficient of static overlap for concurrently occupied home range areas was least ( $\bar{x} = 0.09$ ) for male home ranges on other males and greatest ( $\bar{x} = 0.22$ ) for female home ranges on those of males (Table 6).

Social Organization--Known contacts between bobcats were rare during this study. Use of areas of home range overlap usually occurred by a single individual only when the area in common was otherwise vacant. Because of the dense vegetation, intensive searches for bobcat scent stations were not conducted. However, those scent stations that were located on the area were found primarily in areas of known home range overlap between two or more individuals, suggesting that scent stations were used to demarcate home range areas.

Table 6. Coefficients of static overlap (Macdonald et al. 1980, Voight and Tinline 1980) of bobcat home ranges calculated using the minimum convex polygon home range model.

| Overlap<br>on<br>Home<br>Range<br>of | Overlap By |           |            |             |             |              |              |
|--------------------------------------|------------|-----------|------------|-------------|-------------|--------------|--------------|
|                                      | Male<br>4  | Male<br>8 | Male<br>12 | Female<br>1 | Female<br>7 | Female<br>10 | Female<br>13 |
| Male 4                               | --         | 0         | 0          | 0           | 0           | 0            | 0            |
| Male 8                               | 0          | --        | 0.28       | 0.42        | 0.82        | 0            | 1.00         |
| Male 12                              | 0          | 0.22      | --         | 0           | 0.37        | 0            | 0            |
| Female 1                             | 0          | 0.33      | 0          | --          | 0.27        | 0            | 0.54         |
| Female 7                             | 0          | 0.86      | 0.50       | 0.35        | --          | 0            | 1.00         |
| Female 10                            | 0          | 0         | 0          | 0           | 0           | --           | 0            |
| Female 13                            | 0          | 0.18      | 0          | 0.13        | 0.17        | 0            | --           |

The time of association between monitored bobcats was brief, even during (presumed) mating contacts when both individuals were monitored. During the mating season, male and female bobcats met, stayed together for periods of 5 to 30 minutes, and then traveled separately for 15 minutes to 1 hour before joining again. This pattern of association extended over intervals of 2 to 4 hours.

### Activity Patterns

Bobcats moved an average of 10.0 km/24-hour period, based on straight-line distances between sequential relocations at 15-minute intervals. Rate of movement for both sexes was significantly ( $p < 0.05$ ) greater during the spring than during any other season (Fig. 2), and males moved significantly farther per diurnal period than females throughout the year (Wilcoxon matched-pairs,  $T = 31$ ,  $N = 22$ ,  $p < 0.05$ ). The average rate of movement was greatest for males during the winter and spring, when mean distance traveled per 24-hour period was 12.7 and 17.5 km, respectively (Fig. 2). The average rate of movement of males increased rapidly during midwinter and remained at a high level through the spring, probably reflecting increased travel associated with seeking mates. Females moved an average of 7.1 km during the winter, but, like males, traveled much more widely (an average of 13.2 km per 24 h period) during the spring. There was no significant ( $p > 0.05$ ) difference between rates of male and female movement during the summer or fall, when males moved an average of 8.8 km and 8.5 km and females moved an

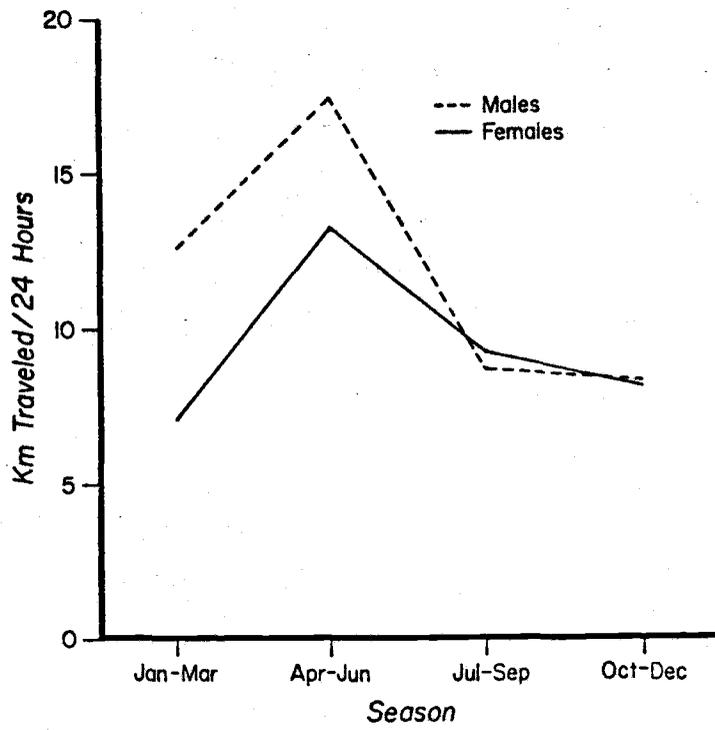


Figure 2. Seasonal mean distance traveled by male and female bobcats per 24-hour period.

average of 9.3 km and 8.2 km, respectively (Fig. 2). The average daily rate of movement by bobcats involved much circuitous travel within a relatively confined portion of the home range and was not related to the distance between relocations on successive days. The average distance between consecutive day locations was 1.72 km. Seasonally, the greatest average distance between consecutive day locations (1.93 km) occurred during the summer (when average rate of movement by bobcats during a 24-hour period was near minimum), and the least distance between consecutive day locations (1.42 km) occurred during the spring, when actual rate of movement was maximum for both sexes.

Periodicity in diurnal activity of bobcats was only weakly developed (Figs. 3 and 4). On a daily basis, bouts of activity lasting 4 to 8 hours were interspersed with periods of inactivity lasting 1 to 8 hours, and the bouts of activity and inactivity were seemingly unrelated to solar rhythms. Plots of the mean rate of diurnal movement for males (Fig. 3) and females (Fig. 4) through each of the four seasons suggests that bobcat activity was related to thermal conditions. During winter, the period of least activity by males occurred between 0800 to 1200 hours, which corresponded to the coldest portions of the day. Activity increased from 1200 to 2400 hours and peaked between 2000 and 2400 hours and then declined rapidly. In spring, diurnal movement of males between 2400 and 1200 hours was higher than in other seasons of the year. The peak of activity occurred between 0800 and 1200 hours and the least activity

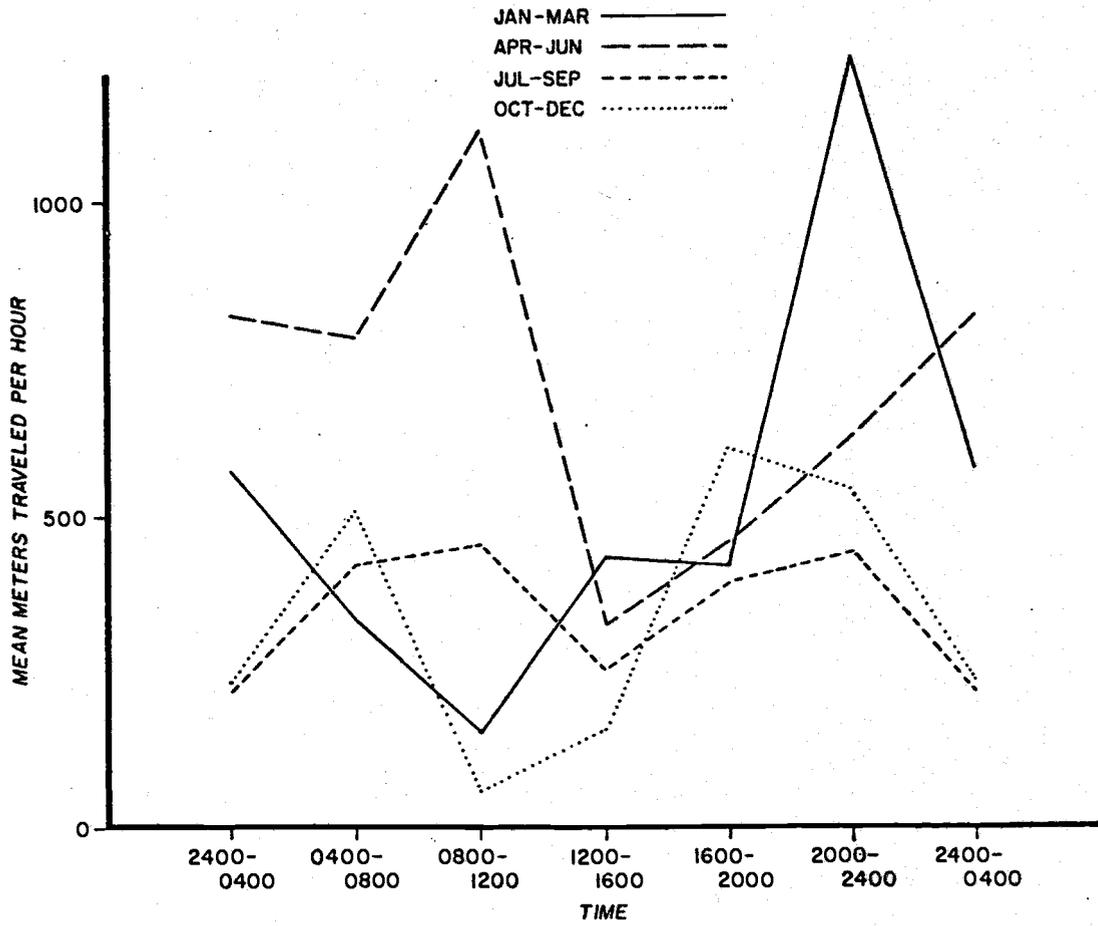


Figure 3. Seasonal periodicity in mean distances traveled by male bobcats.

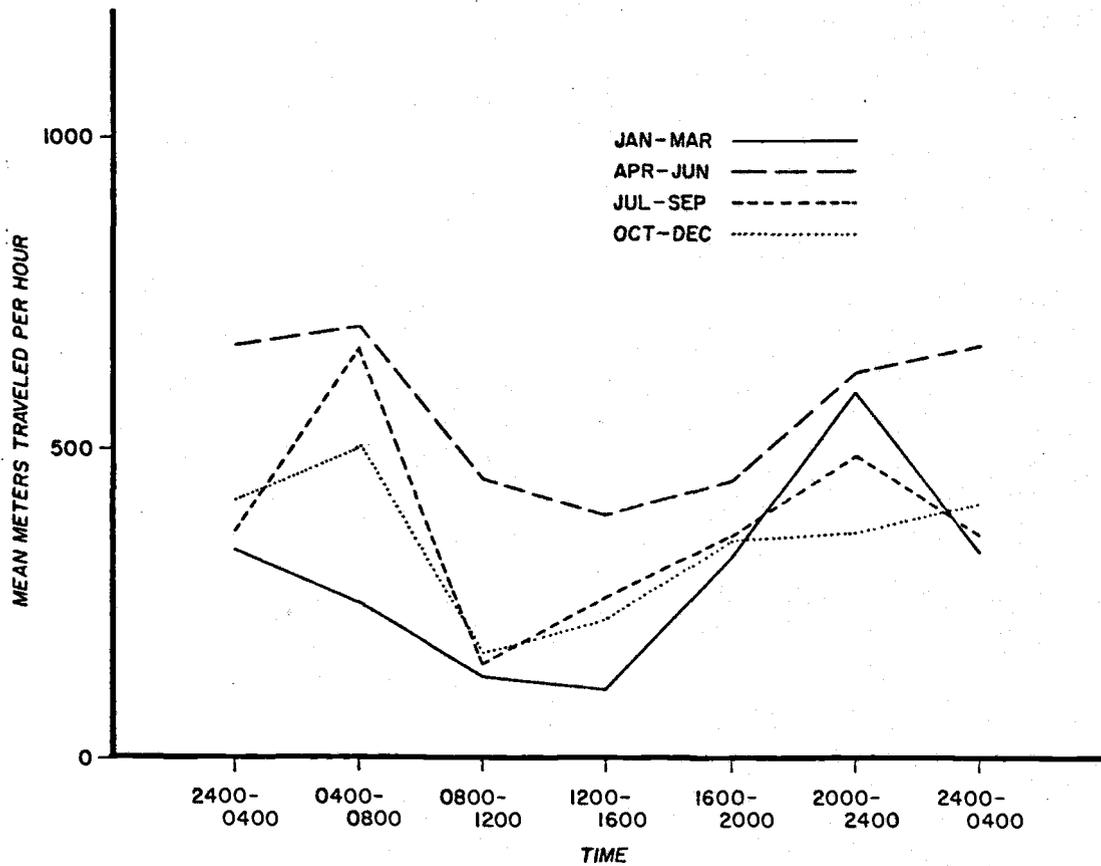


Figure 4. Seasonal periodicity in mean distances traveled by female bobcats.

occurred between 1200 and 1600 hours, during the warmest portion of the day. Activity increased slowly until darkness fell, and remained at a high level through the night. Summer activity was similar, although bimodal, with periods of inactivity just prior to midnight and just after midday. Most of the activity was initiated during cooling trends of early morning and late afternoon. During the fall, activity of male bobcats was transitional between summer and winter activity patterns. Activity remained bimodal as during the summer, but the periods of greatest activity occurred between 0400 and 0800 hours in the morning and 1600 and 2000 hours in the evening (i.e., each peak was four hours earlier than during the summer). The highest rate of activity occurred during the hours just before midnight, as in winter (Fig. 3). Activity of female bobcats was similar to that of males, but at lower average rates of travel and with less pronounced peaks in activity (Fig. 4). Female bobcats showed a greater tendency toward bimodal patterns of activity, with peak periods of activity typically occurring between 0400 and 0800 hours in the morning and between 2000 and 2400 hours at night. As with males, activity during the spring was higher than during all other seasons.

#### Habitat Selection

Relative abundance of habitats within bobcat home ranges did not differ from availability of habitats in the study area, indicating that bobcats did not exhibit macrohabitat selection.

Within home ranges (microhabitat selection) none of the habitats identified was consistently selected for or against on an annual basis (Table 7). However, on a seasonal basis, bobcats selected sawtimber stands in the fall and sparse vegetation forage in the winter ( $p < 0.05$ ). Selection for sawtimber stands during the fall may have reflected interception of snow by trees, resulting in shallower snow depths than in more exposed sites. Snow depth and crusting during the winter may have influenced bobcats to selectively use sparse vegetation sites during this period. Bobcat prey species, particularly snowshoe hares and grouse, use sparse vegetation areas extensively during the winter, and use by bobcats may have resulted from hunting activity. Bobcats avoided dense vegetation in the fall and closed sapling/pole/sawtimber stands in the winter (Table 8).

Some seasonal differences in habitat selection were also identified between sexes of bobcats. Female bobcats used sawtimber during the fall and open sapling/pole stands during the winter to a greater degree than expected. These stands offered not only decreased snow accumulation but also thermal protection and visual screening. Female bobcats avoided dense shrub stands during the fall, and males selected sawtimber stands during the winter.

Examination of habitat selection in relation to activity periods revealed that sawtimber stands were preferred during the fall (Table 8). By contrast, bobcats used sawtimber stands significantly ( $p < 0.05$ ) more than expected during periods of

Table 7. Number and proportion of sequential bobcat locations seasonally by habitat in Oregon's Cascade Mountain Range.

| Habitat                           | Proportional Availability | Jan - Mar        |                    | Apr - Jun        |            | Jul - Sep        |            | Oct - Dec        |                    | Annual           |            |
|-----------------------------------|---------------------------|------------------|--------------------|------------------|------------|------------------|------------|------------------|--------------------|------------------|------------|
|                                   |                           | No. <sup>a</sup> | Proportion         | No. <sup>a</sup> | Proportion | No. <sup>a</sup> | Proportion | No. <sup>a</sup> | Proportion         | No. <sup>a</sup> | Proportion |
| Sawtimber                         | 0.456                     | 225              | 0.511              | 359              | 0.422      | 340              | 0.402      | 329              | 0.586 <sup>b</sup> | 1,253            | 0.485      |
| Closed Sapling/Pole/<br>Sawtimber | 0.193                     | 33               | 0.075 <sup>c</sup> | 190              | 0.223      | 166              | 0.196      | 121              | 0.216              | 510              | 0.189      |
| Open Sapling/Pole                 | 0.104                     | 72               | 0.164              | 86               | 0.101      | 122              | 0.144      | 46               | 0.082              | 328              | 0.121      |
| Dense Shrub                       | 0.216                     | 89               | 0.202              | 172              | 0.202      | 194              | 0.230      | 58               | 0.103 <sup>c</sup> | 513              | 0.190      |
| Sparse Vegetation                 | 0.030                     | 21               | 0.048 <sup>b</sup> | 44               | 0.052      | 23               | 0.027      | 7                | 0.012              | 95               | 0.035      |
| <b>TOTALS</b>                     |                           | <b>440</b>       |                    | <b>851</b>       |            | <b>845</b>       |            | <b>561</b>       |                    | <b>2,697</b>     |            |

<sup>a</sup> Number of locations.

<sup>b</sup> Use greater than expected; 2-tailed test at  $p < 0.10$  (Neu et al. 1974).

<sup>c</sup> Use less than expected; 2-tailed test at  $p < 0.10$  (Neu et al. 1974).

Table 8. Number and proportion of sequential bobcat locations seasonally by activity class and habitat in Oregon's Cascade Mountain Range.

| Activity Class/<br>Habitat        | Habitat<br>Proportional<br>Availability | Jan - Mar        |                    | Apr - Jun        |            | Jul - Sep        |                    | Oct - Dec        |                    | Annual           |                    |
|-----------------------------------|---|------------------|--------------------|------------------|------------|------------------|--------------------|------------------|--------------------|------------------|--------------------|
|                                   |   | No. <sup>a</sup> | Proportion         | No. <sup>a</sup> | Proportion | No. <sup>a</sup> | Proportion         | No. <sup>a</sup> | Proportion         | No. <sup>a</sup> | Proportion         |
| <b>ACTIVE</b>                     |   |                  |                    |                  |            |                  |                    |                  |                    |                  |                    |
| Sawtimber                         | 0.456                                   | 138              | 0.471              | 267              | 0.394      | 249              | 0.435              | 224              | 0.563 <sup>b</sup> | 878              | 0.452              |
| Closed Sapling/Pole/<br>Sawtimber | 0.193                                   | 29               | 0.099              | 142              | 0.209      | 100              | 0.175              | 78               | 0.196              | 349              | 0.180              |
| Open Sapling/Pole                 | 0.104                                   | 37               | 0.126              | 57               | 0.084      | 74               | 0.129              | 39               | 0.098              | 207              | 0.107              |
| Dense Shrub                       | 0.216                                   | 68               | 0.232              | 168              | 0.248      | 137              | 0.240              | 50               | 0.126              | 423              | 0.218              |
| Sparse Vegetation                 | 0.030                                   | 21               | 0.072              | 44               | 0.065      | 12               | 0.021              | 7                | 0.018              | 84               | 0.043              |
| TOTAL                             |   | 293              |                    | 678              |            | 572              |                    | 398              |                    | 1,941            |                    |
| <b>INACTIVE</b>                   |   |                  |                    |                  |            |                  |                    |                  |                    |                  |                    |
| Sawtimber                         | 0.456                                   | 87               | 0.592 <sup>b</sup> | 92               | 0.532      | 91               | 0.333 <sup>c</sup> | 105              | 0.644 <sup>b</sup> | 375              | 0.496              |
| Closed Sapling/Pole/<br>Sawtimber | 0.193                                   | 4                | 0.027              | 48               | 0.277      | 66               | 0.242              | 43               | 0.264              | 161              | 0.213              |
| Open Sapling/Pole                 | 0.104                                   | 35               | 0.238              | 29               | 0.168      | 48               | 0.176              | 7                | 0.043              | 119              | 0.157              |
| Dense Shrub                       | 0.216                                   | 21               | 0.143              | 4                | 0.023      | 57               | 0.209              | 8                | 0.049              | 80               | 0.119 <sup>c</sup> |
| Sparse Vegetation                 | 0.030                                   | 0                | 0                  | 0                | 0          | 11               | 0.040              | 0                | 0                  | 11               | 0.015              |
| TOTAL                             |   | 147              |                    | 173              |            | 273              |                    | 163              |                    | 758              |                    |

<sup>a</sup> Number of locations.

<sup>b</sup> Use greater than expected; 2-tailed test at  $p < 0.10$  (Neu et al. 1974).

<sup>c</sup> Use less than expected; 2-tailed test at  $p < 0.10$  (Neu et al. 1974).

inactivity in the fall and winter; sawtimber stands were used significantly ( $p < 0.05$ ) less than expected during the summer. Sparse vegetation stands were avoided during periods of inactivity by bobcats in the fall, winter, and spring, probably because such stands offered little visual screening (Table 8).

No pattern of habitat selection was evident when active daytime locations were separated from active night locations. During periods of daytime inactivity, sawtimber stands were selected to a significant degree, while dense forage was avoided. Bobcats selected the warmer, south-southeast facing aspects to a significant degree year-around ( $p < 0.05$ ), and avoided the cooler north-northwest facing aspects. All other aspects and all slope classes were used in proportion to their availability.

### Food Habits

Four hundred ninety-four bobcat scats were collected during this study, and numbers of scats analyzed quarterly ranged from 90 to 187 (Table 9). Snowshoe hares (Lepus americanus), black-tailed deer (Odocoileus hemionus), and mountain beaver (Aplodontia rufa) were the food items most commonly identified from bobcat scats. Hares dominated the diet throughout the year but they were taken most frequently during the fall and winter periods, when alternate prey species were probably least available. Pikas (Ochotona princeps) were present on the study area and were most frequently taken by bobcats during summer months. Second only behind hares in the diet of bobcats were

Table 9. Prey items identified from 494 bobcat scats from Oregon's Cascade Range. Values are number of occurrences; percent frequency of occurrence follows.

| Prey Item                         | Jan - Mar<br>(N=112) |         | Apr - Jun<br>(N=187) |         | Jul - Sep<br>(N=105) |         | Oct - Dec<br>(N=90) |         | Annual<br>(N=494) |         |
|-----------------------------------|----------------------|---------|----------------------|---------|----------------------|---------|---------------------|---------|-------------------|---------|
|                                   | No.                  | Percent | No.                  | Percent | No.                  | Percent | No.                 | Percent | No.               | Percent |
| <u>Odocoileus hemionus</u>        | 35                   | 31      | 30                   | 16      | 20                   | 19      | 24                  | 27      | 109               | 22      |
| <u>Cervus elaphus</u>             | 5                    | 4       | 4                    | 2       | 2                    | 2       | 4                   | 4       | 15                | 3       |
| <u>Spilogale gracilis</u>         | 0                    | 0       | 1                    | 1       | 0                    | 0       | 1                   | 1       | 2                 | -       |
| <u>Canis latrans</u>              | 0                    | 0       | 2                    | 1       | 0                    | 0       | 0                   | 0       | 2                 | -       |
| <u>Lepus americanus</u>           | 43                   | 38      | 48                   | 26      | 29                   | 28      | 30                  | 33      | 150               | 30      |
| <u>Ochotona princeps</u>          | 2                    | 2       | 4                    | 2       | 8                    | 8       | 1                   | 1       | 15                | 3       |
| <u>Aplodontia rufa</u>            | 9                    | 8       | 30                   | 16      | 18                   | 17      | 0                   | 0       | 57                | 12      |
| <u>Thomomys mazama</u>            | 1                    | 1       | 10                   | 5       | 10                   | 10      | 2                   | 2       | 23                | 5       |
| <u>Castor canadensis</u>          | 1                    | 1       | 0                    | 0       | 0                    | 0       | 0                   | 0       | 1                 | -       |
| <u>Glaucomys sabrinus</u>         | 5                    | 4       | 1                    | 1       | 1                    | 1       | 10                  | 11      | 17                | 3       |
| <u>Tamiasciurus douglasii</u>     | 8                    | 7       | 6                    | 3       | 1                    | 1       | 3                   | 3       | 18                | 4       |
| <u>Tamias townsendii</u>          | 2                    | 2       | 11                   | 6       | 5                    | 5       | 7                   | 8       | 25                | 5       |
| <u>Tamias amoenus</u>             | 2                    | 2       | 3                    | 2       | 1                    | 1       | 0                   | 0       | 6                 | 1       |
| <u>Spermophilus beecheyi</u>      | 0                    | 0       | 3                    | 2       | 1                    | 1       | 2                   | 2       | 6                 | 1       |
| <u>Spermophilus lateralis</u>     | 0                    | 0       | 2                    | 1       | 1                    | 1       | 1                   | 1       | 4                 | 1       |
| Unknown Sciurid                   | 1                    | 1       | 1                    | 1       | 2                    | 2       | 2                   | 2       | 6                 | 1       |
| <u>Neotoma cinerea</u>            | 3                    | 3       | 5                    | 3       | 1                    | 1       | 2                   | 2       | 11                | 2       |
| <u>Peromyscus maniculatus</u>     | 2                    | 2       | 13                   | 7       | 4                    | 4       | 3                   | 3       | 22                | 4       |
| <u>Clethrionomys californicus</u> | 2                    | 2       | 6                    | 3       | 2                    | 2       | 1                   | 1       | 11                | 2       |
| <u>Arborimus albipes</u>          | 0                    | 0       | 2                    | 1       | 0                    | 0       | 0                   | 0       | 2                 | -       |
| <u>Zapus trinotatus</u>           | 0                    | 0       | 5                    | 3       | 5                    | 5       | 0                   | 0       | 10                | 2       |
| <u>Ondatra zibethica</u>          | 0                    | 0       | 2                    | 1       | 1                    | 1       | 1                   | 1       | 4                 | 1       |
| <u>Microtus oregoni</u>           | 0                    | 0       | 13                   | 7       | 1                    | 1       | 1                   | 1       | 15                | 3       |
| <u>Microtus richardsoni</u>       | 0                    | 0       | 4                    | 2       | 1                    | 1       | 2                   | 2       | 7                 | 1       |
| <u>Microtus longicaudus</u>       | 1                    | 1       | 4                    | 2       | 1                    | 1       | 0                   | 0       | 6                 | 1       |
| Unknown cricetid                  | 2                    | 2       | 16                   | 9       | 6                    | 6       | 2                   | 2       | 26                | 5       |

Table 9. Continued.

| Prey Item                      | Jan - Mar<br>(N=112) |         | Apr - Jun<br>(N=187) |         | Jul - Sep<br>(N=105) |         | Oct - Dec<br>(N=90) |         | Annual<br>(N=494) |         |
|--------------------------------|----------------------|---------|----------------------|---------|----------------------|---------|---------------------|---------|-------------------|---------|
|                                | No.                  | Percent | No.                  | Percent | No.                  | Percent | No.                 | Percent | No.               | Percent |
| <b>MAMMALS (CONTINUED)</b>     |                      |         |                      |         |                      |         |                     |         |                   |         |
| <u>Scapenus orarius</u>        | 0                    | 0       | 13                   | 7       | 0                    | 0       | 0                   | 0       | 13                | 3       |
| <u>Scapenus townsendii</u>     | 0                    | 0       | 2                    | 1       | 0                    | 0       | 0                   | 0       | 2                 | -       |
| <u>Neurotrichus gibbsii</u>    | 0                    | 0       | 4                    | 2       | 0                    | 0       | 0                   | 0       | 4                 | 1       |
| <u>Sorex trowbridgii</u>       | 0                    | 0       | 6                    | 3       | 0                    | 0       | 0                   | 0       | 6                 | 1       |
| <u>Sorex vagrens</u>           | 1                    | 1       | 4                    | 2       | 0                    | 0       | 0                   | 0       | 5                 | 1       |
| <u>Sorex monticolus</u>        | 0                    | 0       | 1                    | 1       | 0                    | 0       | 0                   | 0       | 1                 | -       |
| <u>Sorex sp.</u>               | 0                    | 0       | 1                    | 1       | 0                    | 0       | 0                   | 0       | 1                 | -       |
| Unknown Mammal                 | 6                    | 5       | 16                   | 9       | 7                    | 7       | 8                   | 9       | 37                | 7       |
| <b>BIRDS</b>                   |                      |         |                      |         |                      |         |                     |         |                   |         |
| <u>Bonasa umbellus</u>         | 1                    | 1       | 3                    | 2       | 3                    | 3       | 4                   | 4       | 11                | 2       |
| <u>Junco hyemalis</u>          | 0                    | 0       | 0                    | 0       | 0                    | 0       | 1                   | 1       | 1                 | -       |
| Unknown Passerine              | 7                    | 6       | 9                    | 5       | 10                   | 10      | 4                   | 4       | 30                | 6       |
| <u>Eggshell</u>                | 0                    | 0       | 4                    | 2       | 1                    | 1       | 0                   | 0       | 5                 | 1       |
| <b>REPTILES</b>                |                      |         |                      |         |                      |         |                     |         |                   |         |
| <u>Scaloporus occidentalis</u> | 0                    | 0       | 8                    | 4       | 0                    | 0       | 0                   | 0       | 8                 | 2       |
| <u>Eumeces skiltonianus</u>    | 0                    | 0       | 1                    | 1       | 0                    | 0       | 0                   | 0       | 1                 | -       |
| <u>Diadophis punctatus</u>     | 0                    | 0       | 1                    | 1       | 0                    | 0       | 0                   | 0       | 1                 | -       |
| <u>Thamnophis sp.</u>          | 0                    | 0       | 1                    | 1       | 0                    | 0       | 0                   | 0       | 1                 | -       |
| Unknown Snake                  | 0                    | 0       | 6                    | 3       | 0                    | 0       | 0                   | 0       | 6                 | 1       |
| <b>INSECTS</b>                 | 0                    | 0       | 4                    | 2       | 0                    | 0       | 1                   | 1       | 5                 | 1       |
| <b>FRUIT</b>                   | 3                    | 3       | 1                    | 1       | 25                   | 24      | 4                   | 4       | 33                | 7       |

black-tailed deer, which occurred in 22% of all scats examined (Table 9). Deer remains occurred in over one-quarter of all scats from the fall and winter months, and were the single most frequently identified prey item during December and January, when they occurred in 46% of all bobcat scats examined. While some portion of deer remains in bobcat scats represented scavenging, the regularity of deer in the diet of bobcats indicated that bobcats may have killed deer as prey. Black-tailed deer were the second most abundant prey species in the bobcat diet during February, March, April, and May, when alternate prey were least available. Remains of fawns were identified from a single bobcat scat collected in May, from 6 scats (8%) in June, 8 (18%) from July, and 1 (2%) from August. Fawns accounted for 11, 55, 6, and 17% of all deer remains identified from bobcat scats collected in May, June, July, and August, respectively. In July, black-tailed deer remains (fawns and adults) were the most frequently identified food item.

Remains of calf elk (Cervus elaphus) were identified in four bobcat scats from June and July. Other instances of elk in the diet of bobcats probably represent scavenging. In one instance, a radio transmitter-equipped bobcat encountered the carcass of an adult elk and was killed at the site by a coyote.

Mountain beaver were the third-ranking item in bobcat diets and almost all were taken during spring and summer months. Cricetid rodents of 9 species (Table 9) occurred in nearly one-quarter of the scats examined. Frequency of occurrence of

members of this group varied from 9% in winter to 37% in spring; on an annual basis, they appeared in 23% of all bobcat scats examined. Most commonly encountered were deer mice, (Peromyscus maniculatus) (4%), creeping voles, (Microtus oregoni) (3%), western red-backed voles, (Clethrionomys californicus) (2%), and woodrats, (Neotoma cinerea) (2%) (Table 9). Six species of sciurid rodents (Table 9) comprised 17% of the bobcat diet. Townsend's chipmunks (Tamias townsendii), Douglas' squirrels (Tamiasciurus douglasii), and northern flying squirrels (Glaucomys sabrinus) were most commonly consumed. Squirrels were eaten by bobcats most frequently in the fall (28%) and least frequently in the summer (11%).

Insectivores were found in bobcat scats during the spring months only. While insectivores occurred in only 6% of the bobcat diet on an annual basis, this group comprised 17% of spring diets. In particular, insectivores were found in 23% of June scats. The coast mole (Scapanus orarius) was eaten most frequently (Table 9).

Remains of birds occurred in 47 (10%) scats; most were unidentified passerines but remains of 11 ruffed grouse (Bonasa umbellus) and 1 slate-colored junco (Junco hyemalis) were found. Eggshell fragments were found in 5 scats. Reptile remains occurred in 9% of spring scats, but at no other period of the year (Table 9).

Masticated green grass was found in 55 (11%) of the scats, and some scats consisted solely of grass. We believe that the grass was ingested as a purgative for an accumulation of tapeworms within the intestinal tract; on 2 occasions, freshly passed scats that consisted solely of masticated grass and entwined tapeworms were found. Blackberries (Rubus sp.), huckleberries (Vaccinium sp.), Cascade hollygrape (Berberis nervosa), and manzanita (Arctostaphylos sp.) were identified in 33 (7%) scats. In each instance, fruit was associated with other, animal prey and may represent food of other animals ingested by bobcats. Human refuse including plastic sandwich bags, cotton cloth, and paper was found in 5 scats.

Diet overlap indices (Horn 1966) indicated that fall and winter diets were most similar (Table 10). Snowshoe hares, black-tailed deer, and a variety of sciurid and cricetid rodents, in that order, comprised the bulk of the fall and winter diet. Bobcat diets changed markedly in the spring; winter diets and spring diets were the most dissimilar of any seasonal comparison (Table 10). Spring diets included insectivores and greatly increased numbers of mountain beaver, western pocket gophers (Thomomys mazama), microtines, cricetines, birds, and reptiles. The number of kinds of animal prey identified in the bobcat diet increased from 17 during the winter to 35 during the spring; coincident with the increase in number of kinds of animals preyed on by bobcats was a decline in frequency of occurrence of snowshoe hares and black-tailed deer. Mean size of prey found in

Table 10. Degree of seasonal bobcat diet overlap (Horn 1966).

| Season | Winter | Spring | Summer | Fall  |
|--------|--------|--------|--------|-------|
| Spring | 0.759  | --     | --     | --    |
| Summer | 0.779  | 0.803  | --     | --    |
| Fall   | 0.942  | 0.770  | 0.779  | --    |
| Annual | 0.906  | 0.935  | 0.906  | 0.919 |

bobcat scats during the spring averaged 426 g, about half the average size of prey taken by bobcats in the winter (827 g). Bobcat diets during the summer were diverse, with snowshoe hares, black-tailed deer (largely fawns), mountain beaver, western pocket gophers, and passerine birds all occurring in more than 10% of scats examined (Table 9). The second-greatest change in bobcat diet between seasons occurred between summer and fall (Table 10). Percentages of snowshoe hares, black-tailed deer, and sciurids all increased markedly, while numbers of mountain beaver, mice, and birds declined markedly. The number of kinds of prey items in the diet (21 in summer, 19 in fall) remained constant, as did mean prey size (529 g in summer and 539 g in fall).

## DISCUSSION

### Population Characteristics

Characteristics of harvested bobcats from the four-county study area differ little from data reported previously for all of western Oregon (Toweill 1980, Kistner and Wyse 1981, Kistner 1982, Trainer 1985a, Trainer 1985b) or western Washington (Knick et al. 1985). The preponderance of males found in this sample is exceptional, although a slight but consistent preponderance of males has been reported in all previous harvest samples from western Oregon and western Washington. Nationally, sex ratios of harvested bobcats have fluctuated widely, although most samples

have been dominated by males (see McCord and Cardoza 1982 for review). The dominance of males in the 2 to 3-year-olds in the 1983-84 harvest may have resulted from activities associated with dispersal and home range establishment of juvenile males, as has been suggested for lynxes (Stewart 1973). Many hypotheses have been advanced concerning selection of males in the harvest, including misidentification of sex of harvested bobcats and differential vulnerability of males related to either greater average home range size, increased travel during the mating season, or harvest method. Most of these hypotheses were rejected by McCord and Cardoza (1982), who concluded, from re-analysis of data collected by Brittell, that any differences in sex ratio of harvested bobcats most likely resulted from method of harvest, with hunting taking a greater percentage of males than trapping. Their hypothesis cannot be tested against data reported here, since method of take was not recorded. The apparent increase in vulnerability of both sexes (but particularly males) as the season progressed through January tends to support a hypothesis by Parker and Smith (1983) that bobcats become more vulnerable to harvest with the onset of mating season. This hypothesis is further supported by testimony of trappers, who use sex-pheromone-based lures at trap sites.

Underrepresentation of kitten in the harvest, found in this study, has also been reported elsewhere (McCord and Cardoza 1982, Parker and Smith 1983, Knick et al. 1985). Comparable data from

Oregon (Toweill 1980, Kistner and Wyse 1981, Kistner 1982, Trainer 1985a, Trainer 1985b) and Washington (Knick et al. 1985) indicate that the kitten cohort is less well represented in harvest samples from the heavily vegetated western portions of both states than from the eastern portions. Representation of other age groups is apparently comparable to their relative abundance in the population. Bobcats 2.5 years and older have comprised slightly over half of the harvest sample in all harvest samples from western Oregon and western Washington (Toweill 1980, Kistner and Wyse 1981, Kistner 1982, Trainer 1985a, Trainer 1985b, Knick et al. 1985). Lack of proportional representation of kittens in the harvest sample violates the assumption of equal catchability of individuals in the bobcat population, an assumption critical to development of life tables (Caughley 1977).

The breeding rate for western Oregon bobcats 1.5 years and older reported here (65 percent) is below that reported by Toweill (1980) for eastern Oregon bobcat populations (74 percent). Similarly, the mean litter size reported here for western Oregon bobcats 3.5 years and older ( $2.29 \pm 0.67$ ,  $n = 51$ ) is significantly below that reported by Toweill (1980) for eastern Oregon bobcats 1.5 years and older (3.04,  $n = 27$ ). Mean litter sizes of western Washington bobcats were significantly smaller than those from eastern Washington (Knick et al. 1985). These findings are consistent with Bailey's (1981) hypothesis that reproductive fitness of bobcat populations in stable

environments may be maximized by reductions in litter size and increases in maternal investment in comparison to bobcat populations in less stable environments. He hypothesized that reductions in litter size and delayed dispersal of kittens could be expected, since kitten survival would be less influenced by weather and more by survival skills taught by the adult female. Mean survival rates calculated for bobcats using a standard life table approach and harvest data from the four-county study area indicated that annual survival averaged about 0.68, or conversely, that average annual losses averaged about 30 percent of the population. While this rate is similar to the annual survival rate of 0.59 calculated for an exploited bobcat population in Oklahoma by Rolley (1985) using a life table approach, it is suspect because of failure of certain assumptions required for life table calculations. Mean survival rates (95 percent confidence intervals in parentheses) for bobcats monitored during this study ranged from a minimum of 0.36 (0.06-0.68) to a maximum of 0.53 (0.23-0.81) quarterly. These rates were similar to those reported for exploited bobcat populations studied in Missouri (0.57; Hamilton 1982), Oklahoma (0.56 to 0.66; Rolley 1985), and Minnesota (0.61; Fuller et al. 1985). (A lower survival rate, 0.19 (0.04-0.81) was also reported by Fuller et al. (1985) for one of their study areas, but was believed a non-representative value because of extensive poaching on that area.) While these data indicate that harvest of bobcats undoubtedly was the major factor influencing bobcat

survival, predators also had a serious impact on bobcat populations. Three of the 5 bobcats known to have died during this study were killed by predators. In other studies, the proportion of bobcat mortalities due to natural causes has ranged from none (Rolley 1985) to 31% (3 of 11 mortalities; Hamilton 1982).

Bobcat density on the study area (0.03 - 0.04 bobcats/km<sup>2</sup>) was as low as has been reported anywhere (Table 11), although comparable to that reported for forested habitats in Minnesota (Berg 1979) and New York (Fox 1980) and for desert habitats in Idaho (Bailey 1972), California (Zezulak and Schwab 1979) and Utah (Karpowitz 1981). Bobcat density on the study area was considerably greater (0.09 bobcats/km<sup>2</sup>) when calculated on the basis of the fully-occupied western portion of the study area, but was still below the density of 0.12 to 0.43 estimated for Oregon's Coast Range by deCalesta and Witmer (1983). A much larger prey base available to bobcats in Oregon's Coast Range, less subject to winter snow accumulation and having much larger populations of mountain beaver and other rodents, may account for much of the difference in bobcat populations. Based on the range of bobcat densities reported in the literature, we believe that either habitats in Oregon's Cascade Range were generally marginal for bobcats or that populations were depressed during the course of this study.

Table 11. Relative densities of bobcats (bobcats/km<sup>2</sup>) reported for North America.

| State          | Bobcats km <sup>2</sup> | Reference                 |
|----------------|-------------------------|---------------------------|
| California     | 1.25                    | Gould 1980                |
| California     | 1.27 - 1.53             | Lembeck 1978              |
| Texas          | 0.58 - 2.74             | Brownlee 1977             |
| Alabama        | 0.77 - 1.16             | Miller and Speake 1979    |
| South Carolina | 0.58                    | Provost et al. 1973       |
| Oregon         | 0.12 - 0.43             | deCalesta and Witmer 1983 |
| Arizona        | 0.24 - 0.28             | Jones and Smith 1979      |
| Nevada         | 0.20                    | Golden 1982               |
| South Carolina | 0.13 - 0.19             | Kight 1962                |
| Massachusetts  | 0.10 - 0.13             | McCord 1977               |
| California     | 0.10 - 0.19             | Zezulak and Schwab 1980   |
| Virginia       | 0.09 - 0.18             | Progulske 1952            |
| Oklahoma       | 0.09                    | Rolley 1985               |
| Missouri       | 0.06 - 0.10             | Hamilton 1982             |
| New York       | 0.06                    | Fox 1980                  |
| Utah           | 0.06                    | Karpowitz 1981            |
| Idaho          | 0.05                    | Bailey 1972               |
| California     | 0.05                    | Zezulak and Schwab 1979   |
| Minnesota      | 0.04 - 0.05             | Berg 1979                 |
| Oregon         | 0.03 - 0.04             | This study                |

### Social Organization and Movements

Home ranges of bobcats in this study were larger than most bobcat home ranges reported elsewhere (Table 12), although they were comparable to those reported from forested habitats in Massachusetts (McCord 1977) and Minnesota (Berg 1979). Despite the fact that the harmonic mean method is probably best suited to area-use comparisons, almost all comparable home range data available for bobcats were calculated using the minimum convex polygon method or the modified minimum area. The large size of bobcat home ranges reported here is a further indication that these habitats may be somewhat marginal for bobcat survival.

Social structure of bobcats in the western Cascades was similar to the pattern described by Bailey (1972, 1974), featuring home ranges established on a land tenure system maintained on the basis of prior rights. However, several key differences between western Oregon bobcat populations and the desert population studied by Bailey were apparent. In western Oregon bobcat home ranges were much more strongly influenced by topography than the desert population studied by Bailey. Established home ranges of bobcats of the same sex apparently overlapped more extensively, and few transients existed in the western Oregon population.

Topography of the area influenced bobcat home range size. Winter weather severity and associated lack of prey at high elevations during the winter dictated that higher-elevation portions of established home ranges could be used only

Table 12. Mean home range areas (km<sup>2</sup>) estimated for male and female bobcats.

| Region, State          | Method            | Mean Home<br>Range<br>Area (km <sup>2</sup> ) | No. of<br>Bobcats | Source                     |
|------------------------|-------------------|---|-------------------|----------------------------|
| <b>Northern States</b> |                   |   |                   |                            |
| Oregon                 | Min. Convex Poly. | 25.2  | 4F                | This study                 |
|                        |                   | 24.9  | 3M                |                            |
| Idaho                  | Min. Convex Poly. | 19.3  | 8F                | Bailey 1974                |
|                        |                   | 42.1  | 4M                |                            |
| Montana                | Min. Convex Poly. | 17.8  | 1F                | Knowles 1981               |
|                        |                   | 44.6  | 2M                |                            |
| Minnesota              | Min. Area         | 38  | 6F                | Berg 1979                  |
|                        |                   | 62  | 16M               |                            |
| Minnesota              | Min. Convex Poly. | 49  | 3F                | Fuller et al.<br>1985      |
|                        |                   | 46  | 4M                |                            |
|                        |                   | 32  | 8F                |                            |
|                        |                   | 61  | 18M               |                            |
| Maine                  | Min. Convex Poly. | 27.5  | 1F                | Major 1983                 |
|                        |                   | 138.6   | 6M                |                            |
| <b>Southern States</b> |                   |   |                   |                            |
| California             | Min. Convex Poly. | 2.1   | 3F                | Lembeck 1978               |
|                        |                   | 3.0   | 9M                |                            |
| California             | Min. Convex Poly. | 43  | 4F                | Zezulak 1981               |
|                        |                   | 73  | 3M                |                            |
| California             | Min. Convex Poly. | 17.5  | 1F                | Zezulak and<br>Schwab 1979 |
|                        |                   | 28  | 6M                |                            |
| Nevada                 | Min. Convex Poly. | 7.7   | 5F                | Golden 1982                |
|                        |                   | 22.8  | 10M               |                            |
|                        |                   | 26.6  | 1F                |                            |
|                        |                   | 21.6  | 3M                |                            |
| Utah                   | Min. Convex Poly. | 16.4  | 3F                | Karpowitz<br>1981          |
|                        |                   | 22.5  | 3M                |                            |

Table 12. (Continued)

| Region, State     | Method            | Mean Home<br>Range<br>Area (km <sup>2</sup> ) | No. of<br>Bobcats | Source                       |
|-------------------|-------------------|---|-------------------|------------------------------|
| Missouri          | Min. Convex Poly. | 16.1<br>60.4                                  | 8F<br>9M          | Hamilton 1982                |
| Louisiana         | Mod. Min. Area    | 1.0<br>4.9                                    | 3F<br>3M          | Hall and<br>Newsom 1976      |
| Alabama           | Min. Convex Poly. | 1.5<br>3.0                                    | 6F<br>6M          | Miller 1980                  |
| Tennessee         | Min. Convex Poly. | 16.3<br>26.7                                  | 3F<br>2M          | Kitchings and<br>Story 1979  |
| South<br>Carolina | Min. Convex Poly. | 2.5<br>3.9                                    | 1F<br>3M          | Marshall and<br>Jenkins 1966 |
| South<br>Carolina | Mod. Min. Area    | 10.4<br>20.7                                  | 3F<br>3M          | Buie et al.<br>1979          |

seasonally, resulting in contraction of home ranges to lower elevations during the winter. Loss of snow cover in the spring allowed bobcats to range more widely, and exploratory spring travel by bobcats may have contributed significantly to the amount of home range overlap between animals of the same sex. Bailey (1981) hypothesized that scent-marking would be used little in areas having high amounts of rainfall, as occurred in the Cascade Range, and predicted that overlap of home ranges among animals of the same sex would result. Topographical constraints of long, high ridges may have led to the observed clustering of home ranges along drainages at lower elevations. The observed male:female:female arrangement of home ranges along drainages on southeast facing slopes would minimize home range overlap during the period of home range contraction and during movements up drainages to higher elevations as weather moderated in the spring and summer.

The arrangement of home ranges found in this study probably also developed, in part, as a result of harvest pressure exerted on the population. Bobcats occupying areas where ease of access allowed entry for harvest would have been more vulnerable to trappers than those occupying less-accessible areas. Over time, harvest of the most vulnerable bobcats would have created clusters of home ranges in some portions of available habitat. The apparent stability of these areas would be maintained through time because (1) transient bobcats occupying the more accessible areas were regularly removed, and (2) a sufficient number of

bobcats resident in cluster areas were removed to provide suitable territories for most transients to occupy. Transients were rare in this situation because a large amount of vacant habitat was available for establishment of home ranges, and vacancies in the most favorable habitat were regularly created as a result of harvest.

Male bobcats moved more widely than females throughout the year, as has been reported for bobcats elsewhere (Hall and Newsom 1976). However, the actual rate of movement of both sexes was not related to distance between locations on consecutive days, as has been suggested by Marshall and Jenkins (1966), Bailey (1974), Hall and Newsome (1976), and Berg (1979). The average rate of daily movement as revealed through intensive monitoring during this study (10.0 km/day) was somewhat greater than reported daily rates of movement of 8.8, 5.6, and 4.9 km/day in forest habitats in Minnesota, Michigan, and Massachusetts, respectively, based on tracking of bobcats in snow (Rollings 1945, Erickson 1955, McCord 1974), and considerably greater than has been reported as a result of telemetry studies in other habitats (Marshall and Jenkins 1966, Hall and Newsom 1976).

Intensive monitoring of bobcats suggested that rather than being truly crepuscular, as has been suggested (Marshall and Jenkins 1966, Zezulak and Schwab 1980, deCalesta and Witmer 1983), bobcats should more accurately be described as arrhythmic, as demonstrated under laboratory conditions by Kavanau (1971).

Crepuscular activity patterns, where they have been described, probably have resulted from thermal regulation in hot environments.

### Habitat Selection

Habitat selection of bobcats was not pronounced in western Oregon coniferous forest habitats. Analysis of macrohabitat selection indicated that bobcats were not attracted to particular, unique features of available terrain. Others have reported that rock outcroppings (Bailey 1972, McCord 1974) or coniferous bogs or swamps (Rollings 1945, Berg 1979) were the most important terrain features in bobcat habitats. These findings are most similar to those of Hall and Newsom (1976) and Miller and Speake (1978), who found that bobcats showed little selectivity for particular habitats as long as thick vegetative screening was available. They do not show selection for particular types of habitat such as exhibited by bobcats in Oklahoma (Rolley and Warde 1985). Bobcats apparently are influenced by visual screening in their use of habitats. Bobcats avoided areas of sparse vegetation during periods of inactivity but did use them while active. These data lead to a conclusion that timber management practices that provide a diversity of vegetative types and that lead to increased populations of potential prey species by opening closed forest canopies probably directly benefit bobcat populations.

Within home ranges, selection for particular kinds of habitat appeared influenced most greatly by ease of travel and perhaps prey availability. McCord (1974) reached a similar conclusion regarding habitat utilization in forest habitats in Massachusetts. In contrast, bobcats in western Oregon habitats tended to avoid roads and most often were found occupying steep terrain. This behavior may have been a result of resource partitioning between bobcats and coyotes (which regularly traveled roads in these habitats, and which were absent from bobcat habitat in Massachusetts).

#### Food Habits

The relative importance of Lagomorphs in bobcat diets has been reported almost universally in food habits studies conducted throughout the United States (McCord and Cardoza 1982). Rabbits or hares dominated prey remains in eastern Oregon (Towell 1982), the Cascade Range (Nussbaum and Maser 1975) and in several portions of the Coast Range (Schwartz and Mitchell 1945, Nussbaum and Maser 1975). Mountain beaver dominated bobcat diets in some portions of the Coast Range (Sweeney 1978, Witmer and deCalesta in press).

The frequency of occurrence of black-tailed deer in the diet of bobcats in the Cascade Range was unexpected because of the size differential of the two species (6.0 kg vs. 68 kg). The ability of bobcats to kill adults as well as fawn deer has been documented (see McCord and Cardoza 1982). Many authors have

attributed remains of deer found in bobcat food habit studies to scavenging (Hamilton and Hunter 1939, Rollings 1945, Pollack 1951, Erickson 1955, Progulske 1955, Gashwiler et al. 1961). The high incidence of deer in the bobcat diet, particularly when alternate prey availability was low (Marston 1942, Westfall 1956, McCord 1974, Beasom and Moore 1977, Fritts and Sealander 1978, this study), indicated that bobcats may have relied on deer in some situations, perhaps as predators upon deer. In this study, bobcat predation on deer occurred primarily during the fawning period and again during the winter, when alternate prey was least available. The high incidence of deer in the bobcat diet, coupled with the major changes in diet between winter and spring (overlap = 0.76) and summer and fall (overlap = 0.78), indicate that prey availability during fall and winter may have been a limiting factor on bobcat populations.

#### MANAGEMENT IMPLICATIONS

This study was conducted to provide information on the ecology of bobcats in Oregon's Cascade Mountain Range and to better manage the species. Bobcat harvests in these habitats, as elsewhere throughout North America, have increased dramatically since 1971 when the annual harvest from these four counties amounted to an estimated 168 bobcats and the average price paid per pelt was about \$21 (Fig. 5). Harvest in 1980, just prior to initiation of this investigation, reached an all-time high of an estimated

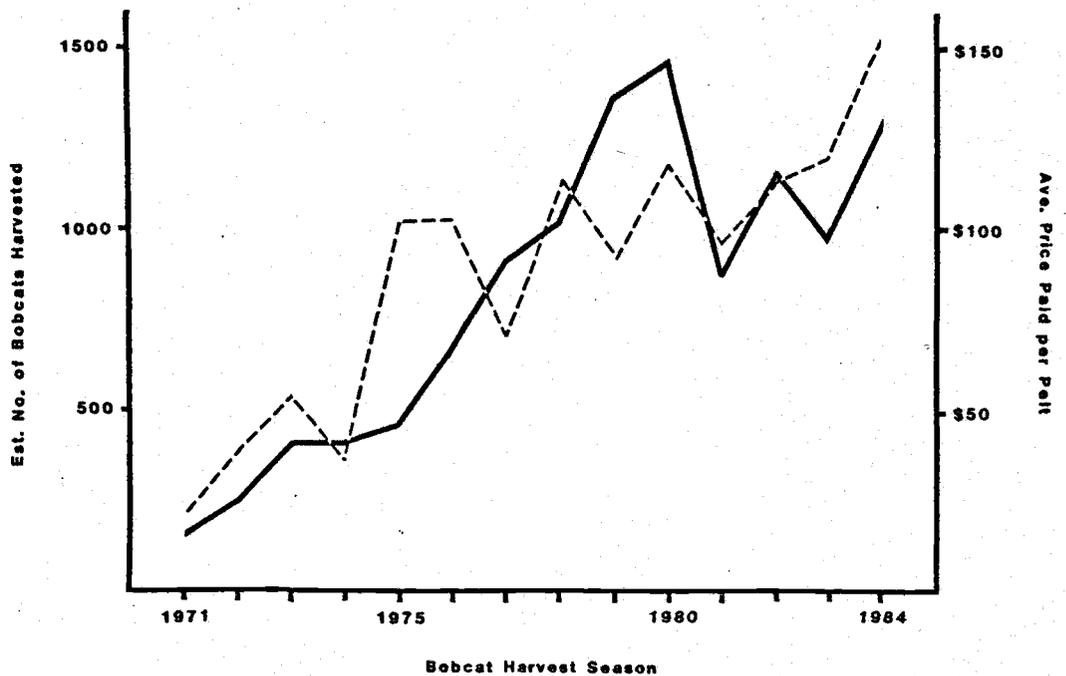


Figure 5. Number of bobcats harvested per year from Douglas, Linn, Lane, and Marion Counties, Oregon (solid line), and average price paid per bobcat pelt (dashed line), 1971 through 1984.

1,475 bobcats, with the average price paid per pelt about \$119. Since that time, annual bobcat harvests have declined. In the 1984-85 season, pelt prices averaged 22% more than in 1980 but 15% fewer bobcats were harvested.

Densities of bobcats during this study were low, as estimates were the lowest reported for any population studied in North America. Large areas of apparently suitable habitat were not occupied during this period. Resident bobcats were found in small clusters of individuals, and in those areas, bobcat densities of about 0.09 bobcats/km<sup>2</sup>, similar to densities reported elsewhere in North America, occurred. Two hypotheses account for the observed low densities of bobcats in these habitats. The first is that the observed bobcat density resulted from marginal habitat, and accurately reflected the ability of the habitat to support a bobcat population. The second hypothesis is that the observed low density of bobcats resulted directly from harvest of bobcats and that populations could increase if harvest were reduced. Data for each of these hypotheses will be examined in turn.

Evidence that bobcat habitat in Oregon's Cascade Range was marginal for bobcats includes the relatively high incidence of natural mortality in the monitored sample, the high rate of daily movement, and scarcity of prey items available to bobcats in the late winter and early spring. The high rate of daily movement may reflect high levels of energy expenditure for hunting

activity, and the high incidence of deer in the bobcat diet may indicate that smaller prey was not available in sufficient quantity to support bobcats through this period of food shortage.

Evidence that harvest may have affected bobcat numbers comes from several sources. The percentage of bobcat kittens in the harvest increased from 19% in 1982-83 to 26% in 1984-85, as pelt prices likewise increased. This increase may reflect greater harvest effort on decreasing numbers, even given that kittens are typically underrepresented in the harvest. No change in population structure in any other cohort was noted during this study, but none should be expected. As discussed by Caughley (1977), if trap capture data are relatively bias-free, over-harvest would affect all cohorts equally and no change in proportional representation of cohorts would necessarily occur. Bobcat harvests throughout western Oregon increased each year from 1974 through 1980, but have fluctuated at levels below the 1979-80 and 1980-81 harvests since those years despite substantial increases in the average price paid per pelt. Additional evidence that harvest may have reduced bobcat populations includes the high rate of loss of marked animals during this study and after it was terminated. Although the sample was very small, the mortality rate observed was large. Because home range areas of bobcats monitored in this study were of comparable size to those in other areas where bobcats existed in greater numbers, and because of the observed clustering of resident animals in steep terrain away from roads, one could

argue that harvest pressure, not habitat selection, restricted bobcats to remote areas. Trappers familiar with this study area suggest that bobcat numbers were far greater during the mid-1970's than during the period of this study.

No definitive conclusion relative to causes of low bobcat densities in Oregon's Cascade Range can be reached from this data. However, both hypotheses could be tested by implementing a limited closure or reduction in harvest season in a portion of the Cascades. Suitably paired with an area in which no closure or reduction occurred as a control, this approach should provide, within 2 years, data with which to assess the degree of bobcat population change, if any, under reduced harvest pressure.

## CHAPTER TWO

## ECOLOGY OF COYOTES IN THE CASCADE MOUNTAINS OF WESTERN OREGON

## Part 1

## COYOTE HABITAT USE IN A HIGH-ELEVATION CONIFEROUS FOREST

Coyotes (Canis latrans) have demonstrated wide plasticity in adapting to many and varied biomes (Nowak 1978). However, information on habitat use is limited. Although references to habitat use occur widely throughout the literature, quantitative measures of habitat preference are restricted to an investigation that involved snow tracking of coyotes in a forested portion of Michigan (Ozoga and Harger 1966) and studies of radio-collared coyotes in the plains of Oklahoma (Litvaitis and Shaw 1980) and Alberta (Roy and Dorrance 1985), farmlands in Nebraska (Andelt and Andelt 1981) and mixed forests in Maine (Major 1983). This paper reports habitat use, movements, and home ranges of coyotes in a high altitude, coniferous forest in Oregon's Cascade Mountain Range.

STUDY AREA AND METHODS

This study was conducted in the Willamette National Forest, approximately 55 km east of Eugene in Oregon's Cascade Mountain Range (43°, 55' N and 122°, 30' W), at elevations ranging from 55 to 1,500 m. Topography was abruptly dissected by the North Fork of the Middle Fork Willamette River and Christy Creek into a complex series of ridges surrounding a high plateau at an

elevation of about 900 m. Climate was typical of Western Cascade maritime areas with mild, wet winters and warm, dry summers; days with precipitation averaged about 160 per year (Lahey 1979).

Vegetation was typical of the western hemlock (Tsuga heterophylla) vegetation zone of Franklin and Dryness (1973).

Timber harvest and reforestation have lead to dominance of Douglas-fir (Pseudotsuga menziesii) over most of the area. The impact of these practices was extensive, so that the area was very unlike pristine forest. No permanent human habitations occurred within 10 km of any portion of the study area.

Availability of vegetation types on a 279 km<sup>2</sup> core study area was determined using multi-spectral scanner (MSS) reflectance data obtained via LANDSAT satellite during high sun angle periods. Data were analyzed by the Earth Remote Sensing Laboratory of the University of Washington in conjunction with the Oregon Department of Fish and Wildlife. Six major vegetation habitats were recognized:

Large sawtimber: Tree stands with trunks > 50 cm dbh. This class included 131 km<sup>2</sup> (47%) of the area.

Closed sapling/pole/sawtimber: Douglas-fir or mixed conifer stands with trunks averaging 2 to 50 cm dbh and having crown cover  $\geq$  60%. This class included 55 km<sup>2</sup> (20%) of the area.

Open sapling/pole: Tree stands with trunks averaging 2 to 50 cm dbh and crown cover < 60%. This class included 25 km<sup>2</sup> (9%) of the area.

Dense shrub: Shrub stands with crown cover  $\geq$  40% and tree stands having trunks averaging  $<$  2 cm dbh with trees  $\geq$  1.5 m tall. This class included 61 km<sup>2</sup> (22%) of the area.

Sparse vegetation: A mixed class ranging from grass/forb stands to shrub stands with  $<$  40% crown cover and heights  $<$  1.5 m or tree stands with heights  $<$  1.5 m. This class included 6 km<sup>2</sup> (2%) of the area.

Nonhabitats: A mixed class, including water, rock, bare soil, or snow. This class included 1 km<sup>2</sup> ( $<$ 1%) of the area.

Past timber harvests have resulted in thorough intermingling of these stands throughout the study area, creating a "fine-grained" environment.

Coyotes were live trapped using Victor and Blake & Lamb 1.75 coil spring traps placed near bait or scent attractors. Traps were variously modified with padding on the trap jaws, extension chains, and drags for field use. Trapping was conducted through all seasons of the year except late spring and early summer to avoid stress to female coyotes during late pregnancy or soon after parturition. Captured coyotes were restrained through use of a spring-loaded, Ketch-All noose (Ketch-All Equipment Company, San Diego, CA). Each coyote was anesthetized with ketamine hydrochloride, which was injected intramuscularly at approximately 25 mg/kg body weight. Sedated

animals were equipped with radio-transmitter collars, weighed, measured, and examined for determination of sex and evidence of trap injury and general physical condition.

Coyotes with transmitter collars were monitored using hand-held, four-element, Yagi antennas and radio receivers built by AVM Instrument Co. and Telonics Inc. Field tests indicated accuracy in determination of true bearing of transmitters of approximately  $\pm 3^\circ$  under ideal conditions. Locations of coyotes were determined by triangulation following a series of directional bearings by 1 or more observers. Often 10 to 15 successive bearings were recorded, each allowing the observer to more closely approach the animal and approximate its location. To minimize error induced by animal movement during the location process, each animal's position was determined by using only 2 or 3 directional bearings recorded within a span of no more than a few minutes from a distance of 500 m or less whenever possible. To further reduce potential for error, each animal position was determined to within a grid unit of 1 ha<sup>2</sup> using Universal Transverse Mercator system markings on 1:24,000 scale orthophoto-quadrangle maps. These grid units provided the standard level of resolution for all animal location data and vegetative mapping. Monitoring of radio-equipped coyotes featured both "scanning" and "focal animal" approaches (Lehner 1979). "Scanning" consisted of locating each individual animal 3 to 7 days per week. These data were used in all home range calculations and to evaluate macro-habitat selection.

"Focal-animal" monitoring consisted of locating an individual animal sequentially once every 15-min period in bouts of 6 to 12 h conducted around the clock. Focal-animal monitoring of each coyote encompassed at least one 24-h diurnal period every season. These data were used to determine micro-habitat selection and activity patterns during seasonal and diurnal periods.

Habitat selection by coyotes was examined on two levels. Macro-habitat selection (or second-order selection as defined by Johnson 1980) referred to the mix of habitats selected in coyote home ranges (minimum convex polygon method) compared to availability on the core study area. Micro-habitat selection (or third-order selection as defined by Johnson 1980) referred to actual use of habitats as compared to availability within home ranges. In addition to the 6 vegetation classes, 6 categories of slope (none, 1 to 10%, 11 to 20%, 21 to 30%, 31 to 40%, and > 40%) and 9 categories of aspect (none, 1° to 45°, 46° to 90°, 91° to 135°, 136° to 180°, 181° to 225°, 226° to 270°, 271° to 315°, and 316° to 360°) were identified and coyote use of each evaluated. Selection or avoidance of habitats was determined following the approach of Neu et al (1974) after chi-square analysis led to rejection of the null hypothesis that seasonal patterns of habitat use followed an "expected" pattern. Necessary assumptions for this approach, namely that animals had opportunity to select any available habitat and that observations were collected in an unbiased manner, were believed justified.

Habitats were small and thoroughly intermingled, creating a "fine-grained" environment. This approach is conservative owing to use of Bonferroni normal statistics, and has been shown to perform well when numbers of habitats and animals are small and numbers of locations large (Alldredge and Rätti 1986).

All data were summarized seasonally, with seasons designated as follows: winter--January 1 through March 31, spring--April 1 through June 30, summer--July 1 through September 30, and fall--October 1 through December 31.

Home ranges of coyotes were estimated using the harmonic mean estimator (Dixon and Chapman 1980) at the 95% utilization distribution and the minimum convex polygon estimator (Southwood 1966). Calculations utilized "Program Home Range" (Samuel et al. 1983). Other utilization distributions and methods were calculated for comparison (see Appendix Table 29). No home range estimates were calculated for coyotes relocated fewer than 25 times over a period of 180 days. Based on the average amount of area added to minimum convex polygon home ranges as the number of locations increased (see Appendix Fig. 10), at least 10 relocations were required for calculation of seasonal home range values.

Differences in timing and extent of coyote activity were tested using the nonparametric Wilcoxon matched-pairs, signed-ranks test (Siegel 1956).

## RESULTS AND DISCUSSION

Three male and 3 female coyotes were equipped with radio collars and relocated 475 times during this study. Numbers of daily relocations of individuals ranged from 5 to 157 over monitoring periods of 7 to 483 days (Table 13). In addition, 285.5 h of focal-animal monitoring yielded 1,186 locations of coyotes at 15-minute intervals. The animals monitored included 3 adults and 3 juveniles.

### Home Range and Movements

Coyote home ranges were large in comparison to those reported elsewhere (for reviews, see Beckoff 1982, and Laundre and Keller 1984) as ranges of male coyotes were at the upper end of reported values; those for females were near the mid-range. Using the harmonic mean estimator (Dixon and Chapman 1980) of coyote home range at the 95% confidence interval as an index to the amount of area used by coyotes, male home ranges averaged 138.3 km<sup>2</sup> while those of females averaged 30.9 km<sup>2</sup>. Home range estimates by the minimum convex polygon estimator averaged about 30% smaller (Table 13).

The harmonic mean estimator (Dixon and Chapman 1980) was used to compute the amount of area used seasonally by coyotes. Because I was concerned with seasonal adaptations of coyotes to habitats, I divided coyote use along the solar seasons, which influenced vegetative growth and coyote prey abundance. The amount of area used fluctuated by season and differed among males

Table 13. Summary data for coyotes monitored, 1983-1984.

| Coyote Number  | Sex | Age | Days Monitored | Number of Locations |            | Home Range Size (km <sup>2</sup> ) <sup>a</sup> |                    |
|----------------|-----|-----|----------------|---------------------|------------|---|--------------------|
|                |     |     |                | Daily               | Successive | Min. Polygon                                    | Harmonic Mean      |
| 1              | M   | Ad  | 483            | 94                  | 110        | 151.6 <sup>c</sup>                              | 142.6 <sup>c</sup> |
| 2              | M   | Ad  | 393            | 157                 | 420        | 78.8  | 248.8              |
| 4 <sup>b</sup> | F   | Juv | 7              | 5                   | 0          | — <sup>d</sup>                                  | — <sup>d</sup>     |
| 5              | F   | Ad  | 457            | 138                 | 289        | 30.3 <sup>c</sup>                               | 39.2 <sup>c</sup>  |
| 6              | F   | Juv | 315            | 53                  | 236        | 15.5 <sup>c</sup>                               | 22.5 <sup>c</sup>  |
| 7              | M   | Juv | 291            | <u>27</u>           | <u>131</u> | 61.7 <sup>e</sup>                               | 23.5 <sup>e</sup>  |
| TOTAL          |     |     |                | 475                 | 1,186      |   |                    |

<sup>a</sup>Based on daily locations.

<sup>b</sup>Coyote 3 not monitored.

<sup>c</sup>One location excluded for home range calculation.

<sup>d</sup>Not calculated.

<sup>e</sup>Three locations excluded for home range calculation.

and females (Table 14). There was little correlation between the size of seasonal areas used by coyotes as calculated by harmonic mean and minimum convex polygon home range estimators (Table 14). Seasonal use areas of males were largest during the winter, when they averaged ten times the size of summer ranges. Male coyotes monitored may have been transients (Andelt 1985), as they appeared to exhibit little fidelity to particular areas but rather used a relatively small area for a short time and then moved to another area. This does not necessarily imply that no defense of territories occurred; an adult male was found dead of wounds sustained in a fight with another coyote on the study area. Much of the winter activity of males included extensive travel on roads plowed free of snow. During summer months, movements of male coyotes were very localized near patches of fruit, particularly blackberries (Rubus sp.) and huckleberries (Vaccinium sp.).

Two females had home range areas smaller than those of males and showed a much different pattern of seasonal fluctuation in area used (Table 2). Although the small home range estimate of females in the fall was influenced by the fact that 1 of the 2 females monitored during this time was a juvenile just beginning to disperse from her den area, the relatively small winter and spring home range estimates and the large summer home range probably reflect the impact of pup-rearing activities on female movement. Females used progressively more area in the summer months than males as litters began accompanying the females on

Table 14. Seasonal variation in home range sizes (km<sup>2</sup>) of male and female coyotes monitored between January 1983 and June 1984 in Oregon's Cascade Range. Number of coyotes included in each calculation in parentheses.

| Sexes  | Methods of Home Range Estimation <sup>a</sup> | Seasons  |          |          |          |
|--------|---|----------|----------|----------|----------|
|        |   | Winter   | Spring   | Summer   | Fall     |
| Male   | Harmonic mean <sup>b</sup>                    | 32.0 (3) | 23.7 (2) | 3.2 (3)  | 17.7 (2) |
|        | Convex polygon                                | 31.2 (3) | 35.8 (2) | 19.2 (3) | 54.8 (2) |
| Female | Harmonic mean <sup>b</sup>                    | 8.1 (1)  | 7.6 (2)  | 13.2 (2) | 3.2 (2)  |
|        | Convex polygon                                | 16.7 (1) | 10.4 (2) | 15.3 (2) | 13.3 (2) |

<sup>a</sup> Based on  $\geq 10$  locations/season.

<sup>b</sup> Following Dixon and Chapman (1980) at 95% confidence interval.

foraging trips. Laundre and Keller (1984) reported a decline in average rates of female movement during the gestation period followed by an increase in female movement during the pup-rearing period.

Dispersal of juvenile coyotes from den areas was variable in time. Exploratory movements of male 7 began in November; by January, he had moved approximately 7 km to the west of his (presumed) natal den. In January, female 6 left the study area; she was later discovered 21 km northwest of her natal area. Female 4, captured on March 23, was emaciated at time of capture; and she died of starvation on March 30 (see Appendix Table 30). Dispersal of young coyotes has been reported to occur from October through the following August (Nellis and Keith 1976; Bowden 1982).

The extent of coyote movements, like the patterns of home range and habitat use, varied seasonally. Mean distance between relocations on consecutive days and the mean distance traveled per 24-h period of sequential monitoring were least during the winter (Table 15). Beckoff and Wells (1981) reported that coyotes rested more and hunted less frequently during winter months when forced to rely heavily on ungulate carrion for food. In this study, coyotes were active throughout most of the day during winter, although there was a marked decline in coyote activity in the predawn hours (Fig. 6). The average rate of movement increased dramatically from 12.8 km/24 h in winter to 22.1 km/24 h in the spring. Most of the increased movement was

crepuscular activity (Fig. 6). These movements may have been associated with short-term, exploratory excursions into high-elevation areas as the snowpack retreated. No such increase in average spring daily movement among coyotes in low elevation habitats was recorded by Springer (1982); Laundre and Keller (1984) reported a decline in movements of female coyotes during gestation. Coyote movement patterns during the summer were relatively constant through the 24-h period, although a slight peak of activity occurred immediately after dusk (Fig. 6). Coyote movement patterns showed a switch to primarily daytime activity during fall (Fig. 6); average rates of movement declined; but the distance between locations on successive days increased slightly (Table 15). These fall movements may have been associated with changes in availability and locations of potential prey. Berries, a staple of food during the summer, had decayed and were inedible, migratory species had left the study area, and deer had moved to lower elevations in the study area. The seasonal shifts in the timing of coyote activity found in this study are unlike the typically crepuscular or nocturnal activity reported elsewhere (Gipson and Sealander 1972; Andelt and Gipson 1979; Andelt 1985).

#### Habitat Preference

No evidence of macro-habitat selection by coyotes, that is, selection for a particular arrangement or group of habitats within home ranges different from what was generally available,

Table 15. Average rates of movement (km) of coyotes by season in Oregon's Cascade Mountain Range.

| Mean Movement                   | Season |        |        |      | Annual |
|---------------------------------|--------|--------|--------|------|--------|
|                                 | Winter | Spring | Summer | Fall |        |
| Between consecutive<br>locatons | 1.8    | 2.1    | 2.5    | 3.4  | 2.3    |
| Per 24-h period                 | 12.8   | 22.1   | 16.0   | 13.3 | 16.2   |

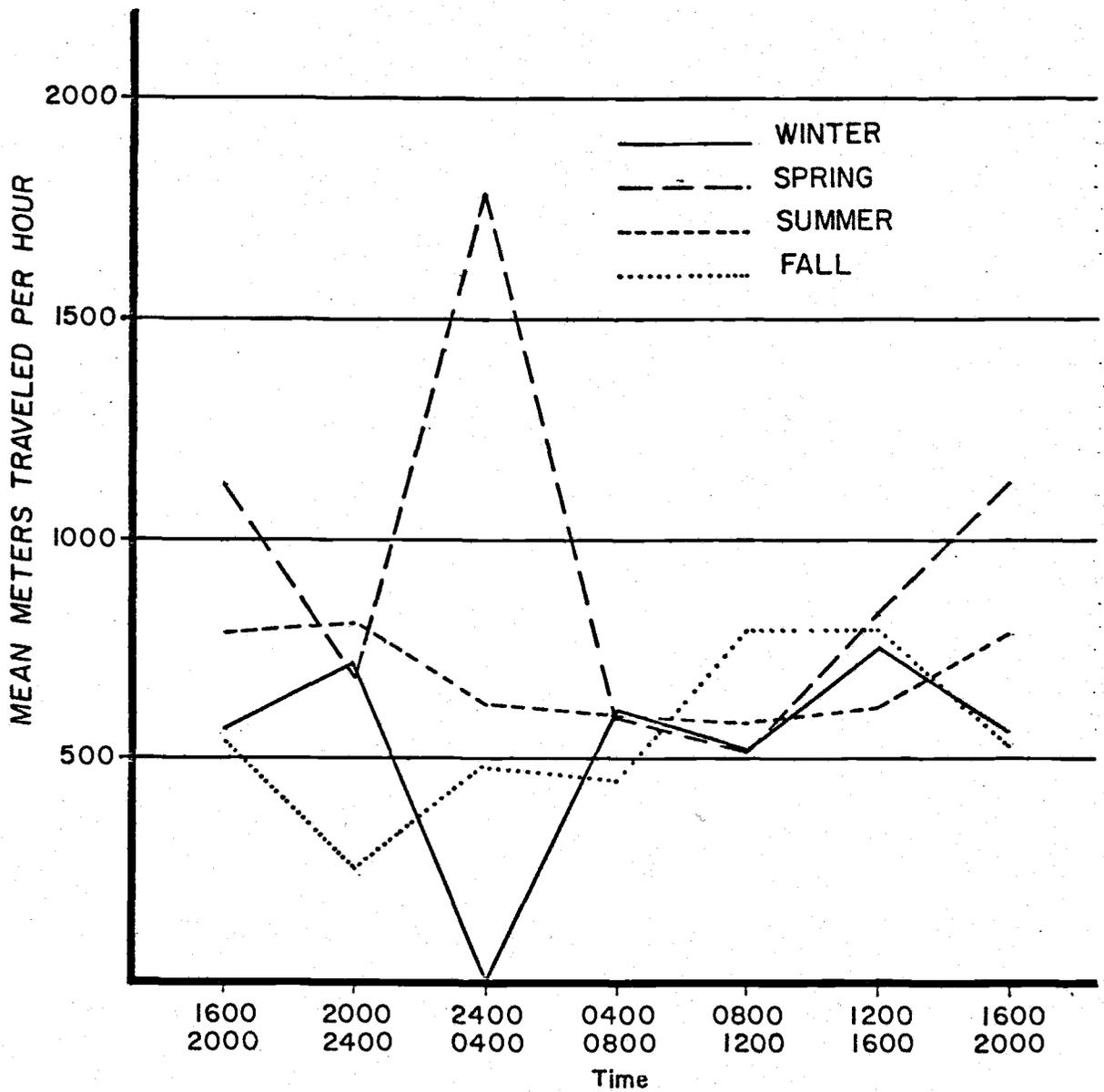


Figure 6. Seasonal periodicity in mean rate and time of movements by coyotes.

was found. However, coyotes showed extensive evidence of micro-habitat selection, i.e., selection of particular habitats within home ranges. Sawtimber was used more than expected and open sapling/pole and sparse vegetation stands were avoided on an annual basis (Table 16).

Sawtimber was the most abundant vegetation class on the study area, and it was used significantly ( $p < 0.05$ ) more than expected based on availability (Table 16). Most of the use occurred during the spring and fall months when coyotes were active (Table 17). Sawtimber was used proportional to availability during coyote activity in the winter; it was, however, avoided completely during periods of winter inactivity. Daytime use of sawtimber stands significantly ( $p < 0.05$ ) exceeded expectations based on frequency of occurrence. Coyote selection for timber stands, where available, has been documented for many types of habitats (Ozoga and Harger 1966, Litvaitis and Shaw 1980, Andelt and Andelt 1981, and Roy and Dorrance 1985). In Maine, coyotes selected for softwood and hardwood habitats during winter and pursued and killed more prey in softwoods than in other habitat types (Major 1983). Others (Andelt and Andelt 1981, Roy and Dorrance 1985, Witmer and deCalesta in press) have also noted, as in this study, that coyote association with woodlands was greater during daylight than night hours.

Closed sapling/pole/sawtimber stands were preferred by coyotes during winter but were avoided during spring and summer

Table 16. Number and proportion of sequential coyote locations, by season and habitat in Oregon's Cascade Mountain Range.

| Habitat                           | Proportional Availability | Jan - Mar        |                   | Apr - Jun        |                   | Jul - Sep        |                   | Oct - Dec        |                   | Annual           |                   |
|-----------------------------------|---------------------------|------------------|-------------------|------------------|-------------------|------------------|-------------------|------------------|-------------------|------------------|-------------------|
|                                   |                           | No. <sup>a</sup> | Proportion        |
| Sawtimber                         | 0.456                     | 75               | .362 <sup>c</sup> | 162              | .672 <sup>b</sup> | 251              | .456              | 124              | .521              | 612              | .517 <sup>b</sup> |
| Closed Sapling/Pole/<br>Sawtimber | 0.193                     | 88               | .425 <sup>b</sup> | 25               | .104 <sup>c</sup> | 59               | .118 <sup>c</sup> | 42               | .176              | 214              | .181              |
| Open Sapling/Pole                 | 0.104                     | 24               | .116              | 10               | .042 <sup>c</sup> | 52               | .104              | 12               | .050 <sup>c</sup> | 98               | .083 <sup>c</sup> |
| Dense Shrub                       | 0.216                     | 20               | .097 <sup>c</sup> | 43               | .178              | 132              | .265 <sup>b</sup> | 57               | .240              | 252              | .213              |
| Sparse Vegetation                 | 0.030                     | 0                | 0                 | 1                | .004 <sup>c</sup> | 4                | .008 <sup>c</sup> | 3                | .013              | 8                | .007 <sup>c</sup> |
| <b>TOTALS</b>                     |                           | <b>207</b>       |                   | <b>241</b>       |                   | <b>498</b>       |                   | <b>238</b>       |                   | <b>1,184</b>     |                   |

<sup>a</sup> Number of locations.

<sup>b</sup> Greater use than expected; 2-tailed test at  $p > 0.90$ .

<sup>c</sup> Less use than expected; 2-tailed test at  $p > 0.90$ .

(Table 16), and this habitat was used almost exclusively during periods of winter inactivity (Table 17) when they provided protection from wind, rain, and snow. Ozoga and Harger (1966) reported that heavily stocked conifer stands were preferred as daytime coyote resting areas in Michigan. No selection or avoidance of these stands by day or night was indicated in this study.

Open sapling/pole stands were avoided, particularly during spring and fall (Table 16). Use of these habitats occurred during periods of coyote activity in winter and summer. Therefore, this habitat may have been used exclusively while foraging; no use of open sapling/pole stands by coyotes was recorded during periods of inactivity during the winter, spring, or fall (Table 17).

Dense shrub stands were preferred by coyotes during summer months but avoided during the winter (Table 16) when snow was deep. During the summer, significant ( $p < 0.05$ ) selection of this habitat occurred during periods of coyote activity (Table 17). These stands typically included dense patches of blackberries and huckleberries and so provided not only fruit but also rodents and birds drawn to the available fruit. Females, typically foraging with pups during the summer months, frequented these stands to a significant ( $p < 0.05$ ) degree during summer.

Sparse vegetation areas were avoided by coyotes throughout the year (Table 16). The only use of these stands occurred during periods of coyote activity (Table 17). Significant

Table 17. Number and proportion of sequential coyote locations, by season, activity class, and habitat in Oregon's Cascade Mountain Range.

| Activity Class/<br>Habitat | Habitat<br>Proportional<br>Availability | Jan - Mar        |                   | Apr - Jun        |                   | Jul - Sep        |                   | Oct - Dec        |                   | Annual           |                   |
|----------------------------|---|------------------|-------------------|------------------|-------------------|------------------|-------------------|------------------|-------------------|------------------|-------------------|
|                            |   | No. <sup>a</sup> | Proportion        |
| <b>ACTIVE</b>              |   |                  |                   |                  |                   |                  |                   |                  |                   |                  |                   |
| Sawtimber                  | 0.456                                   | 75               | .481              | 124              | .660 <sup>b</sup> | 188              | .511              | 102              | .543 <sup>b</sup> | 489              | .543 <sup>b</sup> |
| Closed Sapling/Pole        | 0.193                                   | 41               | .263              | 21               | .112 <sup>c</sup> | 38               | .103 <sup>c</sup> | 30               | .160              | 130              | .144 <sup>c</sup> |
| Open Sapling/Pole          | 0.104                                   | 24               | .154              | 10               | .053 <sup>c</sup> | 36               | .098              | 12               | .064              | 82               | .091              |
| Dense Forage               | 0.216                                   | 18               | .103 <sup>c</sup> | 32               | .170              | 102              | .277 <sup>b</sup> | 41               | .218              | 191              | .212              |
| Sparse Forage              | 0.030                                   | 0                | 0                 | 1                | .005 <sup>c</sup> | 4                | .011 <sup>c</sup> | 3                | .016              | 8                | .009 <sup>c</sup> |
| TOTALS                     |   | 156              |                   | 188              |                   | 368              |                   | 188              |                   | 900              |                   |
| <b>INACTIVE</b>            |   |                  |                   |                  |                   |                  |                   |                  |                   |                  |                   |
| Sawtimber                  | 0.456                                   | 0                | 0                 | 38               | .717 <sup>b</sup> | 63               | .485              | 22               | .440              | 123              | .458              |
| Closed Sapling/Pole        | 0.193                                   | 47               | .922 <sup>b</sup> | 4                | .076 <sup>c</sup> | 21               | .162              | 12               | .240              | 84               | .296 <sup>b</sup> |
| Open Sapling/Pole          | 0.104                                   | 0                | 0                 | 0                | 0                 | 16               | .123              | 0                | 0                 | 16               | .058 <sup>c</sup> |
| Dense Forage               | 0.216                                   | 4                | .078 <sup>c</sup> | 11               | .208              | 30               | .231              | 16               | .320              | 61               | .215              |
| Sparse Forage              | 0.030                                   | 0                | 0                 | 0                | 0                 | 0                | 0                 | 0                | 0                 | 0                | 0                 |
| TOTALS                     |   | 51               |                   | 53               |                   | 130              |                   | 50               |                   | 264              |                   |

<sup>a</sup> Number of locations.

<sup>b</sup> Greater use than expected; 2-tailed test at  $p > 0.90$ .

<sup>c</sup> Less use than expected; 2-tailed test at  $p > 0.90$ .

( $p < 0.05$ ) avoidance of these stands occurred during both day and night hours. Avoidance of open habitats by coyotes has likewise been noted in other areas (Litvaitis and Shaw 1980, Andelt and Andelt 1981, Roy and Dorrance 1985).

Regardless of habitat, coyotes exhibited significant selection for flat ground. Sites exhibiting no slope were used significantly ( $p < 0.05$ ) more than expected based on their frequency, while slopes 21% were used significantly ( $p < 0.05$ ) less than expected. This selection probably was associated with ease of travel since, in addition to the obviously greater ease of travel on flat as opposed to steep ground, the density of vegetation in terms of stems/hectare increased on steep ground as plant species competed for canopy exposure. South-southeast and south-southwest facing slopes (aspects of  $136^\circ$  to  $225^\circ$ ) were used significantly ( $p < 0.05$ ) more than expected. Slopes facing west-southwest ( $226^\circ$  to  $270^\circ$ ) were used proportional to their abundance on the area, and all other slopes were avoided ( $p < 0.05$ ). Southern slopes dried more readily than most others and were the last covered by snow in the fall and the first to show bare ground in the spring. Associated with loss of spring snow was early season growth of forbs which, in turn, attracted potential coyote prey species.

## CONCLUSIONS

Seasonal patterns of coyote movements and habitat selection appeared to correlate with numerous other studies that show that coyotes generally select habitats based on seasonal food availability (Ozoga and Harger 1966, Litvaitis and Shaw 1980, Andelt and Andelt 1981). In this study, coyote use of particular habitats also appeared influenced by ease of travel and, for females, demands of pup rearing. Coyotes in these high-elevation, coniferous forests demonstrated a great ability to adapt to seasonal changes in weather and food availability by altering their home ranges, activity patterns, and habitat selection. This high degree of plasticity implies that coyotes will continue to flourish and expand their range in high-altitude Cascade forests.

## CHAPTER TWO

## ECOLOGY OF COYOTES IN THE CASCADE MOUNTAINS OF WESTERN OREGON

## Part 2

## COYOTE FOODS IN A CONIFEROUS FOREST IN OREGON

Coyotes (Canis latrans) are among the most widespread of North American carnivores. They have demonstrated an ability to coexist with humans and to expand their range into habitats where they were rare or nonexistent until timber wolves were extirpated (Nowak 1978). Coyotes generally are opportunistic feeders with general diets (Nellis and Keith 1976, MacCracken and Uresk 1984). Although coyote food habits have been studied widely (see Beckoff 1982 for review), few studies have been conducted in coniferous forest habitats and none in the Cascade Range of Oregon and Washington where coyotes were rare or nonexistent until timber wolves (Canis lupus) were extirpated around 1930 (Bailey 1936, Young and Goldman 1944). Because coyote range expansions may lead to changes in populations of prey as coyotes compete for limited resources, the role of coyotes in these habitats should be assessed. This study was conducted to document the annual diet of coyotes as part of a study on the ecological relationships of coyotes and bobcats (Felis rufus) in Oregon's Cascade Range.

## STUDY AREA

This study was conducted in Oregon's Cascade Mountain Range, within the Willamette National Forest approximately 55 km east of Eugene, Lane County, Oregon (43°, 55' N; 122°, 30' W).

Topography was abruptly dissected by tributary drainages of the North Fork of the Middle Fork of the Willamette River.

Elevations ranged from about 500 m to 1,500 m. Climate was typical of the Western Cascade maritime area with mild, wet winters and warm, dry summers. Precipitation occurred about 160 days per year and averaged about 150 cm annually. Annual temperature extremes ranged from -18 to 38° C. Mean annual snowfall averaged about 163 cm; the latest date with 150 cm of snow usually occurred in late March (Lahey 1979).

Vegetation was typical of the Western Hemlock (Tsuga heterophylla) Zone as described by Franklin and Dyrness (1973). Logging, reforestation projects, and forest fires have led to dominance of Douglas-fir (Pseudotsuga menziesii) over most of the area. The region was characterized by extensive stands of Douglas-fir and smaller, isolated stands of western red cedar (Thuja plicata). Grand fir (Abies grandis), Pacific silver fir (Abies amabilis), western yew (Taxus brevifolia), and western white pine (Pinus monticola) occurred commonly. Understories were dominated by creambrush oceanspray (Holodiscus discolor) on dry sites, Pacific rhododendron (Rhododendron macrophyllum) and Cascade hollygrape (Berberis nervosa) on intermediate sites, and sword fern (Polystichum munitum) and Oregon oxalis (Oxalis oregana) on wet sites (Franklin and Dyrness 1973).

## METHODS

Scats were collected from the study area almost daily from 15 October 1982 through 30 June 1984. The study area was cleared of scats prior to initiation of collection so that only fresh material was collected. Each scat was labeled and air dried prior to separation and identification of prey remains. Prey items in a portion of the scats were separated from undigested residues as collected, but bones were separated from most scats using a weak solution of NaOH to digest the associated conglomerate (Degn 1978). Samples of hair were removed from scats prior to NaOH digestion for comparison with hair keys (Mayer 1952, Stains 1958, Adorjan and Kolenosky 1969) to aid in prey species identifications. Food items in the scats were identified by comparison with skeletal materials in the vertebrate museum of the Department of Fisheries and Wildlife, Oregon State University, Corvallis.

Because of difficulties in accurately identifying coyote and bobcat scats (Murie 1954), each scat was subjected to a three-part identification procedure. At time of collection, each scat was identified to species based on physical characteristics, odor, and associated "sign"; each was independently identified to species using criteria of color, texture, and odor at time of analysis; and finally, a portion of each scat was subjected to thin-layer chromatography for identification of bile acid

residues present (Major et al. 1980, Johnson et al. 1981).

Thin-layer chromatography identifications were used to derive final identification of scats where other characteristics were not definitive.

The equation of Horn (1966) was used to compute indices of similarity between seasonal diets. This index, modified from Morista (1959), is calculated as follows:

$$C(\lambda) = 2 \sum_{i=1}^s x_i y_i / \left( \sum_{i=1}^s x_i^2 + \sum_{i=1}^s y_i^2 \right)$$

Similarity indices could range between zero (no food items in common between seasons) and 1 (identical diets between seasons). Average size of prey animals eaten by coyotes was estimated by season based on average adult weight of each prey species and its frequency of occurrence in coyote scats. The average size of animal prey calculated in this manner is a slight over-estimate because numbers of occurrence in scats (not numbers of individuals consumed) were used in calculations. To avoid masking of prey size differences by season, ungulate remains were excluded from these calculations. Weights of adult mammals were taken largely from Maser et al. (1981); weights for mammals not reported by them were estimated from specimens on deposit at Oregon State University. Mammal nomenclature follows Jones et al. (1982); plant nomenclature follows Garrison et al. (1976).

## RESULTS AND DISCUSSION

A total of 844 coyote scats was identified from collections made during this study. Numbers of coyote scats analyzed quarterly ranged from 138 to 324 (Table 18). The major categories of food items found in coyote scats by frequency of occurrence included fruits (38%), rodents (37%), large ungulates (26%), and rabbits and hares (24%).

Fruit was an important component of the coyote diet during the summer months (Fig. 7). Blackberries and raspberries (Rubus sp.), huckleberries (Vaccinium sp.), Cascade hollygrape, manzanita (Arctostaphylos sp.), chokecherries (Prunus sp.), and elderberry (Sambucus sp.) were among fruits consumed by coyotes. The strongly unimodal use of fruit by coyotes corresponded with ripening and availability of fruits in the area. For example, blackberries and raspberries began ripening in July and August; during those months, seeds of these two species occurred in 53 and 94% of the scats, respectively. Huckleberries began ripening in August and were found in 59% of September scats, 20% of October scats, and 32% of November scats. High ingestion rates of fruit by coyotes leads to increased rates of coyote scat deposition because of the large component of undigestible matter (Andelt and Andelt 1984) so that percentage frequency values over-estimate its importance in the diet. However, seasonal use of fruits has been shown important to the coyote diet in many studies (Korschgen 1957, Ozoga and Harger 1966, Small 1971,

Table 18. Prey items identified from 844 coyote scats from Oregon's Cascade Range. Values are number of occurrences; percent frequency of occurrence follows.

| Prey Item                         | Jan - Mar<br>(N=190) |         | Apr - Jun<br>(N=192) |         | Jul - Sep<br>(N=324) |         | Oct - Dec<br>(N=138) |         | Annual<br>(N=844) |         |
|-----------------------------------|----------------------|---------|----------------------|---------|----------------------|---------|----------------------|---------|-------------------|---------|
|                                   | No.                  | Percent | No.                  | Percent | No.                  | Percent | No.                  | Percent | No.               | Percent |
| <b>MAMMALS</b>                    |                      |         |                      |         |                      |         |                      |         |                   |         |
| <u>Odocoileus hemionus</u>        | 83                   | 43      | 35                   | 18      | 32                   | 10      | 52                   | 38      | 202               | 24      |
| <u>Cervus elephus</u>             | 3                    | 2       | 7                    | 4       | 2                    | 1       | 7                    | 5       | 19                | 2       |
| <u>Spilogale gracilis</u>         | 1                    | 1       | 0                    | 0       | 0                    | 0       | 0                    | 0       | 1                 | —       |
| <u>Canis latrans</u>              | 0                    | 0       | 2                    | 1       | 0                    | 0       | 0                    | 0       | 2                 | —       |
| <u>Lepus americanus</u>           | 57                   | 30      | 57                   | 30      | 46                   | 14      | 22                   | 16      | 182               | 22      |
| <u>Ochotona princeps</u>          | 1                    | 1       | 7                    | 4       | 7                    | 2       | 1                    | 1       | 16                | 2       |
| <u>Aplodontia rufa</u>            | 6                    | 3       | 22                   | 11      | 37                   | 11      | 5                    | 4       | 70                | 8       |
| <u>Thomomys mazama</u>            | 2                    | 1       | 15                   | 8       | 16                   | 5       | 2                    | 1       | 35                | 4       |
| <u>Erethizon dorsatum</u>         | 0                    | 0       | 2                    | 1       | 0                    | 0       | 1                    | 1       | 3                 | —       |
| <u>Glaucomys sabrinus</u>         | 1                    | 1       | 3                    | 2       | 2                    | 1       | 4                    | 3       | 10                | 1       |
| <u>Tamiasciurus douglasii</u>     | 3                    | 2       | 3                    | 2       | 5                    | 2       | 3                    | 2       | 14                | 2       |
| <u>Tamias townsendii</u>          | 4                    | 2       | 9                    | 5       | 7                    | 2       | 3                    | 2       | 23                | 3       |
| <u>Tamias amoenus</u>             | 0                    | 0       | 1                    | 1       | 5                    | 2       | 0                    | 0       | 6                 | 1       |
| <u>Spermophilus beecheyi</u>      | 0                    | 0       | 2                    | 1       | 5                    | 2       | 1                    | 1       | 8                 | 1       |
| <u>Spermophilus lateralis</u>     | 0                    | 0       | 1                    | 1       | 4                    | 1       | 0                    | 0       | 5                 | 1       |
| Unknown sciurid                   | 0                    | 0       | 5                    | 3       | 8                    | 2       | 2                    | 1       | 15                | 2       |
| <u>Neotoma cinerea</u>            | 0                    | 0       | 0                    | 0       | 2                    | —       | 0                    | 0       | 2                 | —       |
| <u>Peromyscus maniculatus</u>     | 4                    | 2       | 17                   | 9       | 2                    | —       | 2                    | 1       | 25                | 3       |
| <u>Clethrionomys californicus</u> | 4                    | 2       | 4                    | 2       | 6                    | 2       | 1                    | 1       | 15                | 2       |
| <u>Arborimus albipes</u>          | 0                    | 0       | 1                    | 1       | 1                    | —       | 1                    | 1       | 3                 | —       |
| <u>Arborimus intermedius</u>      | 3                    | 2       | 0                    | 0       | 0                    | 0       | 0                    | 0       | 3                 | —       |
| <u>Zapus trinotatus</u>           | 0                    | 0       | 4                    | 2       | 4                    | 1       | 1                    | 1       | 9                 | 1       |
| <u>Ondatra zibethica</u>          | 0                    | 0       | 0                    | 0       | 1                    | —       | 0                    | 0       | 1                 | —       |
| <u>Microtus oregoni</u>           | 1                    | 1       | 6                    | 3       | 6                    | 2       | 0                    | 0       | 13                | 2       |
| <u>Microtus richardsoni</u>       | 0                    | 0       | 2                    | 1       | 3                    | 1       | 0                    | 0       | 5                 | 1       |
| <u>Microtus longicaudus</u>       | 1                    | 1       | 4                    | 2       | 0                    | 0       | 1                    | 1       | 6                 | 1       |
| Unknown "mouse"                   | 2                    | 1       | 14                   | 7       | 13                   | 4       | 4                    | 3       | 33                | 4       |

Table 18. Continued.

| Prey Item                      | Jan - Mar<br>(N=190) |         | Apr - Jun<br>(N=192) |         | Jul - Sep<br>(N=324) |         | Oct - Dec<br>(N=138) |         | Annual<br>(N=844) |         |
|--------------------------------|----------------------|---------|----------------------|---------|----------------------|---------|----------------------|---------|-------------------|---------|
|                                | No.                  | Percent | No.                  | Percent | No.                  | Percent | No.                  | Percent | No.               | Percent |
| <b>MAMMALS (Continued)</b>     |                      |         |                      |         |                      |         |                      |         |                   |         |
| <i>Didelphis marsupialis</i>   | 1                    | 1       | 0                    | 0       | 0                    | 0       | 0                    | 0       | 1                 | —       |
| <i>Scapanus orarius</i>        | 0                    | 0       | 4                    | 2       | 1                    | —       | 0                    | 0       | 5                 | 1       |
| <i>Scapanus townsendii</i>     | 0                    | 0       | 2                    | 1       | 0                    | 0       | 0                    | 0       | 2                 | —       |
| <i>Neurotrichus gibbsii</i>    | 0                    | 0       | 1                    | 1       | 0                    | 0       | 0                    | 0       | 1                 | —       |
| <i>Sorex trowbridgii</i>       | 0                    | 0       | 3                    | 2       | 0                    | 0       | 0                    | 0       | 3                 | —       |
| <i>Sorex vagrans</i>           | 0                    | 0       | 1                    | 1       | 0                    | 0       | 0                    | 0       | 1                 | —       |
| Unknown Chiroptera             | 0                    | 0       | 0                    | 0       | 2                    | —       | 0                    | 0       | 2                 | —       |
| Unknown Mammal                 | 26                   | 14      | 17                   | 9       | 37                   | 11      | 26                   | 19      | 106               | 13      |
| <b>BIRDS</b>                   |                      |         |                      |         |                      |         |                      |         |                   |         |
| <i>Bonasa umbellus</i>         | 5                    | 3       | 5                    | 3       | 1                    | —       | 5                    | 4       | 16                | 2       |
| <i>Turdus migratorius</i>      | 0                    | 0       | 1                    | 1       | 0                    | 0       | 0                    | 0       | 1                 | —       |
| Unknown Passerine              | 7                    | 4       | 9                    | 5       | 16                   | 5       | 9                    | 7       | 41                | 5       |
| Eggshell                       | 2                    | 1       | 5                    | 3       | 5                    | 2       | 0                    | 0       | 12                | 1       |
| <b>REPTILES</b>                |                      |         |                      |         |                      |         |                      |         |                   |         |
| <i>Sceloporus occidentalis</i> | 1                    | 1       | 5                    | 3       | 1                    | —       | 0                    | 0       | 7                 | 1       |
| Unknown snake                  | 1                    | 1       | 6                    | 3       | 0                    | 0       | 0                    | 0       | 7                 | 1       |
| <b>INSECTS</b>                 |                      |         |                      |         |                      |         |                      |         |                   |         |
|                                | 0                    | 0       | 9                    | 5       | 13                   | 4       | 0                    | 0       | 22                | 3       |
| <b>VEGETATION</b>              |                      |         |                      |         |                      |         |                      |         |                   |         |
| Fruit                          | 15                   | 8       | 11                   | 6       | 269                  | 83      | 24                   | 17      | 319               | 38      |
| Grass                          | 24                   | 13      | 29                   | 15      | 41                   | 13      | 19                   | 14      | 113               | 13      |
| <b>REFUSE</b>                  |                      |         |                      |         |                      |         |                      |         |                   |         |
|                                | 3                    | 1       | 6                    | 3       | 0                    | 0       | 2                    | 1       | 11                | 1       |

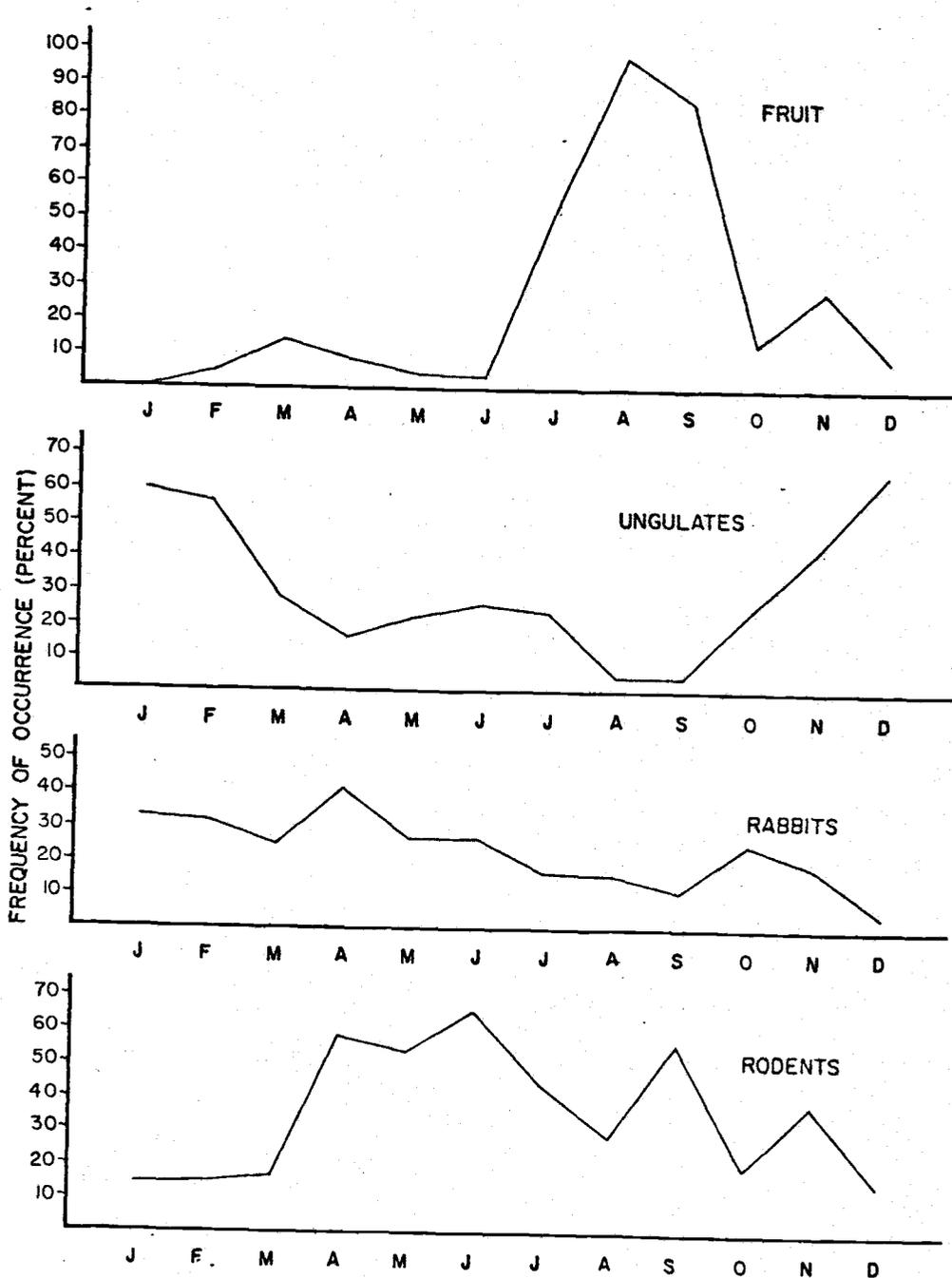


Figure 7. Frequency of occurrence of major food items identified among 844 coyote scats collected from Oregon's Cascade Mountain Range.

Gipson 1974, Salwasser 1974, Meinzer et al. 1975, Nellis and Keith 1976, Andrews and Boggess 1978, Hilton 1978, Major 1983, Harrison and Harrison 1984, Andelt 1985, Witmer and deCalesta in press), and studies of coyote activity indicate that coyotes seek out sources of fruit during all seasons (Ozoga and Harger 1966, Harrison and Harrison 1984).

A large number of rodents were identified among remains recovered from coyote scats. Use of rodents as prey increased rapidly in the spring and declined slowly through the summer and fall. Rodents were preyed upon by coyotes least during the winter when they were either hibernating or unavailable because of snow cover (Fig. 7). Mountain beaver (Aplodontia rufa) were among the most important rodents in the diet and were the third most frequently-occurring species (Table 18). Mountain beaver were preyed upon by coyotes primarily during spring and summer when lack of snow cover made them most vulnerable. These animals were the most frequently identified prey of coyotes in all seasons in Oregon's Coast Range (Witmer and deCalesta in press). Mazama pocket gophers (Thomomys mazama) and 10 species of cricetid rodents also were eaten (Table 18). Cricetid rodents occurred in 14% of all coyote scats examined and in 27% of those collected during spring months (Table 18). During the winter, summer, and fall, the occurrence of cricetid rodents was 8, 12, and 9%, respectively. At least 6 species of sciurids were eaten by coyotes (Table 18). As a group, sciurids occurred in 11% of coyote scats. Sciurids occurred in 13% of spring coyote

scats but in only 4, 4, and 9% of winter, summer, and fall scats, respectively. Rodents have been found to vary in importance to the coyote diet. Korschgen (1957), Gier (1968), and Nellis and Keith (1976) have shown that frequency of small rodents in the coyote diet was a function of both prey vulnerability and availability of alternative prey.

The most common mammal in the diet was black-tailed deer (Odocoileus hemionus) which occurred in 24% of all coyote scats examined. Deer remains were the most frequent prey item identified in November (35%), December (61%), January (60%), February (55%), March (28%), and July (24%) and second only to snowshoe hares in October (21%), April (18%), and May (18%). The occurrence of deer remains was bimodal with the major peak in the fall and winter and a minor peak in late spring and early summer. Remains of fawns accounted for 19% of all deer remains in coyote scats in the spring and 50% of those in summer months. In addition to deer, remains of Roosevelt elk (Cervus elaphus), including 3 elk calves in June, were recovered from 19 scats (Table 18). The importance of deer to the coyote diet has been clearly established in numerous studies (Ozoga and Harger 1966, Ogle 1971, Richens and Hugie 1974, Salwasser 1974, Holle 1978, Berg and Chesness 1978, Litvaitis and Shaw 1980, Major 1983, Harrison and Harrison 1984, MacCracken and Uresk 1984, Andelt 1985). Generally, timing of occurrence of fawns in coyote diets has coincided with the period of fawn births (Ogle 1971, Salwasser 1974, Berg and Chesness 1978, Holle 1978, Litvaitis and Shaw 1980, Andelt 1985), which has

led to the conclusion that coyote predation on deer fawns was direct rather than a result of scavenging. Such a conclusion was supported by research on causes of fawn mortality (Cook et al. 1971, Trainer et al. 1981). Trainer et al. (1981) monitored carcasses of fawns born dead or that died soon after birth and reported almost no scavenging of the carcasses by coyotes or other predators. Although coyotes are capable of killing adult deer (Cahalane 1947, Ozoga and Harger 1966, Cook et al. 1971, Berg and Chesness 1978, Hilton 1978, MacConnell-Yount and Smith 1978, Hamlin and Schweitzer 1979, Truett 1979, Trainer et al. 1981), most researchers have concluded that most deer fed on by coyotes were carrion (Beckoff 1982) or at least debilitated (Ozoga and Harger 1966, Andelt 1985). The importance of deer in the diet of coyotes in this area was greater than percentage frequency reported for Oregon's Coast Range by Witmer and deCalesta (in press). Differences may have been related to general lack of snow cover in the Coast Range and greater abundance of alternate prey, particularly mountain beaver. The percentage frequency of any large animal in scats is biased upward to an unknown degree by repeated feeding on carcasses and by the fact that a single large feeding may result in deer remains being deposited in more than one scat (Weaver and Hoffman 1979, Meriwether and Johnson 1980).

Snowshoe hares (Lepus americanus) occurred in 22% of coyote scats and dominated animal components of the coyote diet during April (38%), May (28%), June (20%), August (15%), and October

(23%). In addition to snowshoe hares, pikas (Ochotona princeps) occupied high elevation portions of the study area and occurred in 16 scats. Snowshoe hares and black-tailed deer were the prey most available to coyotes during the winter months on the study area when most rodents and persistent fruits were unavailable due to deep snow. Frequency of hares in the diet declined from winter through summer (Fig. 7) as reported by Harrison and Harrison (1984) and Andelt (1985). Leporids have been reported as staple of the coyote diet throughout coyote ranges (Korschgen 1957, Gier 1968, Small 1971, Ritchens and Hugie 1974, Meinzer et al. 1975, Nellis and Keith 1976, Andrews and Boggess 1978, Berg and Chesness 1978, Hilton 1978, Litvaitis and Shaw 1980, Major 1983, Harrison and Harrison 1984, MacCracken and Uresk 1984, Andelt 1985, Witmer and deCalesta in press).

Among other items identified in the coyote diet were a variety of mammals, birds, reptiles, and insects. Although insignificant in terms of annual diet, these species demonstrate the opportunistic feeding behavior of coyotes. Almost all insectivores and reptiles preyed on by coyotes were taken during spring. Birds and eggs were consumed at low frequency throughout the year. Insects (primarily beetles and grasshoppers) were consumed during spring and summer only. Remains of vespertilionid bats were recovered from two coyote scats. Masticated green grass was found in 113 coyote scats, 13% of the

total. The resistance of grass to the digestive processes of coyotes was evidenced by the fact that the grass recovered from scats was largely intact and usually still green.

Coyotes exhibited marked changes in the diet throughout the year (Table 19). Fall (October-December) and winter (January-March) diets were most similar, and these were also the seasons when the fewest varieties of prey were eaten (Table 20). The summer (July-September) diet was most dissimilar to that of all other seasons reflecting the high degree of fruit in the diet during these months (Table 19). Although comparable data for seasonal diets of coyotes have not been published, these data support the general finding of diet flexibility and adaptivity of coyotes as has been reported in most food habits studies.

Analysis of seasonal prey selection by coyotes revealed that, in general, coyote food habits in Oregon's Cascade Range may be summarized as black-tailed deer and snowshoe hares in the winter, rodents and hares in the spring, fruit and rodents in the summer, and black-tailed deer and rodents during the fall (Fig. 7). These results contrast sharply with coyote foods in Oregon's Coast Range where mountain beaver were found to dominate the diet during all seasons along with black-tailed deer in the winter (Witmer and deCalesta in press). The greatest variety of prey was taken during the spring and the least in the fall and winter (Table 20). Mean size of animal prey eaten by coyotes was greatest in the winter and fall even when large ungulates were

Table 19. Seasonal comparisons of coyote diet overlap in Oregon's Cascade Range.<sup>a</sup>

| Season | Winter      | Spring      | Summer      | Fall |
|--------|-------------|-------------|-------------|------|
| Spring | 0.75        | -           | -           | -    |
| Summer | 0.38        | 0.35        | -           | -    |
| Fall   | <u>0.93</u> | <u>0.74</u> | <u>0.54</u> | -    |
| Annual | 0.75        | 0.74        | 0.82        | 0.87 |

<sup>a</sup>Values calculated following Horn (1966); range of possible values is 0 (no overlap) to 1 (identical diets).

Table 20. Number of prey animals identified from 844 coyote scats collected from Oregon's Cascade Range, and weighted mean prey size.

|   | Summer |        |        |      |
|---|--------|--------|--------|------|
|   | Winter | Spring | Summer | Fall |
| Number of kinds of animal prey <sup>a</sup> | 22     | 35     | 29     | 20   |
| Number of occurrences <sup>b</sup>          | 105    | 227    | 214    | 68   |
| Weighted mean prey size (g) <sup>b,c</sup>  | 712    | 564    | 481    | 600  |

<sup>a</sup>From Table 1.

<sup>b</sup>Ungulates excluded.

<sup>c</sup>Mean weighted by frequency of occurrence.

excluded. Mean size of animal prey was least in the summer when coyotes were feeding largely on fruit (fruit was excluded from this analysis) and rodents.

Coyotes are a relatively new species in the Western Cascade Range of Oregon (Bailey 1936, Young and Goldman 1944). Although they apparently did not become abundant in this area until after the extirpation of wolves, coyotes in Oregon's Cascade Range clearly are not, as has been suggested by MacCracken and Uresk (1984) for South Dakota, filling a niche recently vacated by timber wolves. Our data do indicate that coyotes may compete with other carnivores that coexist in coniferous forests. Extensive use of black-tailed deer, even if used primarily as carrion, may bring coyotes into direct competition with bobcats (Toweill and Anthony in prep.) particularly during the fall and winter periods of relative food shortage. Coyote use of fruit as a major dietary component during summer months gives them a food dimension not utilized by bobcats and may confer an advantage to coyotes over the long term.

## CHAPTER THREE

RESOURCE PARTITIONING BY BOBCATS AND COYOTES IN A  
CONIFEROUS FOREST

Bobcats (Felis rufus) (McCord and Cardoza 1982) and coyotes (Canis latrans) (Beckoff 1982) range widely throughout North America. Although bobcats were distributed throughout temperate North America historically (Hall and Kelson 1959), coyotes were apparently restricted to the western half of the continent until sometime after 1800 (Nowak 1978). Coyotes have expanded their range greatly in the past century (Nowak 1978) and presently exist throughout the geographic range of bobcats. Because bobcats and coyotes are carnivores of approximately equal body size, home range size, diet, and metabolic needs (Gittleman and Harvey 1982), one must ask how bobcats and coyotes partition the available resources so that coexistence is possible. Rosenzweig (1966) hypothesized that coexistence of predators with similar metabolic requirements should be related to either specialist hunting strategies or predation by one predator on the other. Otherwise, competition should lead to extirpation of one species according to ecological theory. Anecdotal information and a review of past harvest records (Nunley 1978) suggest that bobcat populations may decline when coyote populations are high. If this is correct, interactions between these 2 species may have major implications for bobcat management.

Although competition has been studied for many species of small animals, particularly birds (see Schoener 1982 for review), few studies have investigated niche relationships of coexisting carnivores. For bobcats and coyotes, the only comparable data comes from studies in Maine (Major 1983) and Oregon (Witmer and deCalesta in press). Field data on coexisting species can provide only limited information on competition because only the actual (as opposed to virtual or precompetition) niche can be measured (Colwell and Futuyma 1971). Also, overlap in use of a given resource can be evidence either for or against competition depending on resource availability (Colwell and Futuyma 1971, Schoener 1982). Field studies can, however, provide both a better understanding of mechanisms of resource partitioning and a baseline for comparison with other research. This study was designed to measure the overlap in use of space, habitat, and food by bobcats and coyotes, record interactions that may affect availability of those resources to either species (interference), and to evaluate the mechanisms of resource partitioning in terms of bobcat and coyote management.

#### STUDY AREA AND METHODS

This study was conducted in the Willamette National Forest approximately 55 km east of Eugene, Oregon (43°, 55' N; 122°, 30' W) at elevations ranging from about 500 to 1,500 m. Topography was abruptly dissected by the North Fork of the Middle

Fork Willamette River and Christy Creek into a complex series of ridges surrounding a high plateau which lay at an elevation of about 900 m. Climate was typical of Western Cascade maritime areas with mild, wet winters and warm, dry summers. Days with precipitation averaged 160 per year (Lahey 1979). Vegetation was typical of the western hemlock (Tsuga heterophylla) vegetation zone of Franklin and Dyrness (1973). Timber harvest and reforestation activities have resulted in dominance of Douglas-fir (Pseudotsuga menziesii) over most of the area. No permanent human habitation occurred within 10 km of any portion of the study area.

Bobcats and coyotes were captured with leg-hold or live traps most frequently, although additional captures of bobcats were made using hunting dogs. Both species were anesthetised using ketamine hydrochloride, equipped with radio-transmitter collars, and released. Radio-equipped animals were monitored regularly using both "scanning" (one location/day) and "focal-animal" (one location/15 minutes in sessions of 6 to 8 h) approaches (Lehner 1979). All data were analyzed on a seasonal basis: winter (January-March), spring (April-June), summer (July-September), and fall (October-December).

Home ranges were calculated using the harmonic mean approach at a 95% confidence interval (Dixon and Chapman 1980) to obtain an estimate of the amount of area utilized. Comparisons between species were based on mean home range size by sex and season.

Minimum convex polygon home ranges (Southwood 1966) were calculated to show relative distributions of animals on the study area.

Availability of topographic and vegetation types on a 279 km<sup>2</sup> core study area and at each animal location was determined using multi-spectral scanner (MSS) reflectance data obtained via LANDSAT satellite during periods of high sun angle. Data were analyzed at the Earth Remote Sensing Laboratory of the University of Washington in conjunction with the Oregon Department of Fish and Wildlife. Topography was divided into 6 slope classes (no slope, 1 to 10°, 11 to 20°, 21 to 30°, 31 to 40°, and > 40°) and 9 aspect classes (none; NNE, 0 to 45°; ENE, 46 to 90°; ESE, 90 to 135°; SSE, 136 to 180°; SSW, 181 to 225°; WSW, 226 to 270°; WNW, 271 to 315°; and NNW, 316 to 360°). Vegetation was divided into 6 habitats based primarily on the physical structure of the stands. These habitats included:

Large sawtimber: Stands of trees with trunks averaging > 50 cm diameter at breast height (dbh). This class included 131 km<sup>2</sup> (47%) of the area.

Closed sapling/pole/sawtimber: Stands of Douglas-fir or mixed conifers with trunks averaging 2 to 50 cm dbh and having crown canopy closure > 60%. This class included 55 km<sup>2</sup> (20%) of the area.

Open sapling/pole: Stands of trees with trunks averaging 2 to 50 cm dbh and having crown canopy closure < 60%. This class included 25 km<sup>2</sup> (9%) of the area.

Dense shrub: Shrub stands with crown canopy closure  $> 40\%$ , and stands of trees having trunks averaging  $< 2$  cm dbh with trees  $> 1.5$  m in height. This class included  $61 \text{ km}^2$  (22%) of the area.

Sparse vegetation: A mixed class ranging from grass/forb stands to shrub stands having crown canopy closure  $< 40\%$  and heights  $< 1.5$  m, and stands of trees with heights averaging  $< 1.5$  m. This class included  $6 \text{ km}^2$  (2%) of the area.

Nonhabitats: A mixed class that included water, rock, bare soil, and July snowpack. This class included  $1 \text{ km}^2$  ( $< 1\%$ ) of the area.

Typical of forests managed for wood fiber production, timber harvest strategies have resulted in a thorough intermingling of each of these classes in many small blocks, creating a very "fine-grained" environment.

Bobcat and coyote diets were determined from undigested remains of food items identified in scats. A portion of each scat collected was analyzed by thin-layer chromatography for identification of bile acid residues present (Johnson et al. 1979, Major et al. 1980, Johnson et al. 1984); bile acid residues and field sign associated with each scat were used to identify bobcat and coyote scats. Prey species were identified from undigested hair, and from skeletal and other residues remaining after the associated conglomerate was dissolved in NaOH (Degn 1978).

Bobcat and coyote seasonal use of topographic features and habitats was examined by chi-square analysis using the method of Neu et al. (1974), a method shown to perform well when numbers of habitats and animals were small and numbers of relocations large (Alldredge and Ratti 1986). Necessary assumptions for chi-square analysis were (1) that animals had opportunity to select any available habitat and (2) that observations were collected in an unbiased manner. These assumptions were believed justified because blocks of habitat were small and thoroughly intermingled within each animal's home range, creating a "fine-grained" environment. Analyses were based on both macrohabitat selection (comparing classes of slope, aspect, and habitat within minimum polygon home ranges (Southwood 1966) with proportional availability of those classes on the study area) and microhabitat selection (comparing actual locations of animals obtained during focal animal monitoring with availability of classes on the study area). These are referred to as second- and third-order selection, respectively, by Johnson (1980). Indication of significant selection or avoidance of topographic classes or habitats was assumed at  $p < 0.05$ .

Indices of overlap in use of topographic features, habitats, and diet were calculated as simple overlap in resource use (Anthony and Smith 1977) and as a relative probability of

co-occurrence, using Horn's (1966) modification of Morista's (1959) index of overlap ( $C\lambda$ ):

$$C\lambda = 2 \sum_{i=1}^s x_i y_i / \left( \sum_{i=1}^s x_i^2 + \sum_{i=1}^s y_i^2 \right)$$

where  $x_i$  = frequency of  $i^{\text{th}}$  prey item in the bobcat diet, and  $y_i$  = frequency of  $i^{\text{th}}$  prey item in the coyote diet.

Coefficients of competition were calculated for bobcats and coyotes using the one-dimensional indices of overlap in spatial distribution, habitat use, and diets. Coefficients of competition were calculated as the product of individual overlaps as suggested by Levins (1968) for independent resource dimensions and arithmetic mean of individual overlaps, a more appropriate measure when resource dimensions were dependent (May 1975). As discussed by Anthony and Smith (1977), neither approach is strictly applicable with data of this nature; but the methods do provide an upper and lower bound on measures of direct competition.

Rate of hourly movement of monitored animals was determined from locations obtained during focal-animal monitoring and was estimated as the mean straight line distance between relocations at 15-minute intervals; differences between species were calculated using the Wilcoxon matched-pairs signed-ranks test (Siegel 1956).

## RESULTS

A total of 1,041 daily locations of 13 bobcats and 475 daily locations of 6 coyotes was made between October 1982 and June 1984. In addition, 630.5 and 285.5 hours of focal-animal monitoring of bobcats and coyotes, respectively, resulted in an additional 2,699 and 1,186 locations of bobcats and coyotes. These locations were used to describe spatial distributions and assess habitat use by both species. Diets of bobcats and coyotes were estimated from prey remains identified from 494 bobcat and 844 coyote scats.

### Spatial Distribution

Bobcats and coyotes occurred throughout the study area, and their home ranges overlapped extensively (Fig. 8). Bobcat and female coyote home ranges were relatively stable through the period of this study although they did fluctuate seasonally. In contrast, male coyotes exhibited little fidelity to particular areas, but rather acted as transients, using a restricted area for a short period before moving to another. The average amount of area used annually by 3 male and 4 female bobcats and by 2 female coyotes was nearly identical, 34.6, 33.8, and 30.9 km<sup>2</sup>, respectively, while that of 3 male coyotes averaged 138.3 km<sup>2</sup> (Table 21). Seasonal fluctuations in average home range size varied inversely. Bobcat ranges averaged largest in the spring and smallest in the fall and winter, while coyote home ranges were largest in the winter and smallest in the summer

(Fig. 9). Coefficients of static overlap of interspecific home ranges were not calculated because of the wide seasonal fluctuations in area use. Also, monitored animals were located in areas beyond the core study area where overlap with uncollared animals probably occurred, and at least one coyote known to occur within the core study area was not captured or monitored.

Overlap in spatial distribution of bobcats and coyotes was estimated using physiographic characteristics (slope and aspect). Neither bobcats nor coyotes exhibited macrohabitat selection for physiographic characteristics (that is, their home ranges did not feature particular slope or aspect classes different from availability on the study area). Bobcats used all slope classes in proportion to their availability, but coyotes significantly ( $p < 0.05$ ) selected areas of no slope and avoided slopes  $> 21^\circ$  (Table 22). Similarly, bobcats used flat ground and most aspects relative to abundance, selecting ( $p < 0.05$ ) only SSE slopes and avoiding ( $p < 0.05$ ) those facing NNW. In contrast, coyotes demonstrated significant ( $p < 0.05$ ) aspect selection for southern exposures (SSE and SSW slopes) and significant avoidance of all others except those facing WSW, which were used in proportion to availability (Table 22).

Seasonal changes in patterns of slope and aspect use were evident for both species (Table 23). Spatial distributions of bobcats and coyotes during winter were based on 440 and 207 locations, respectively. Bobcats used nearly all available slope and aspect classes according to availability, while coyotes

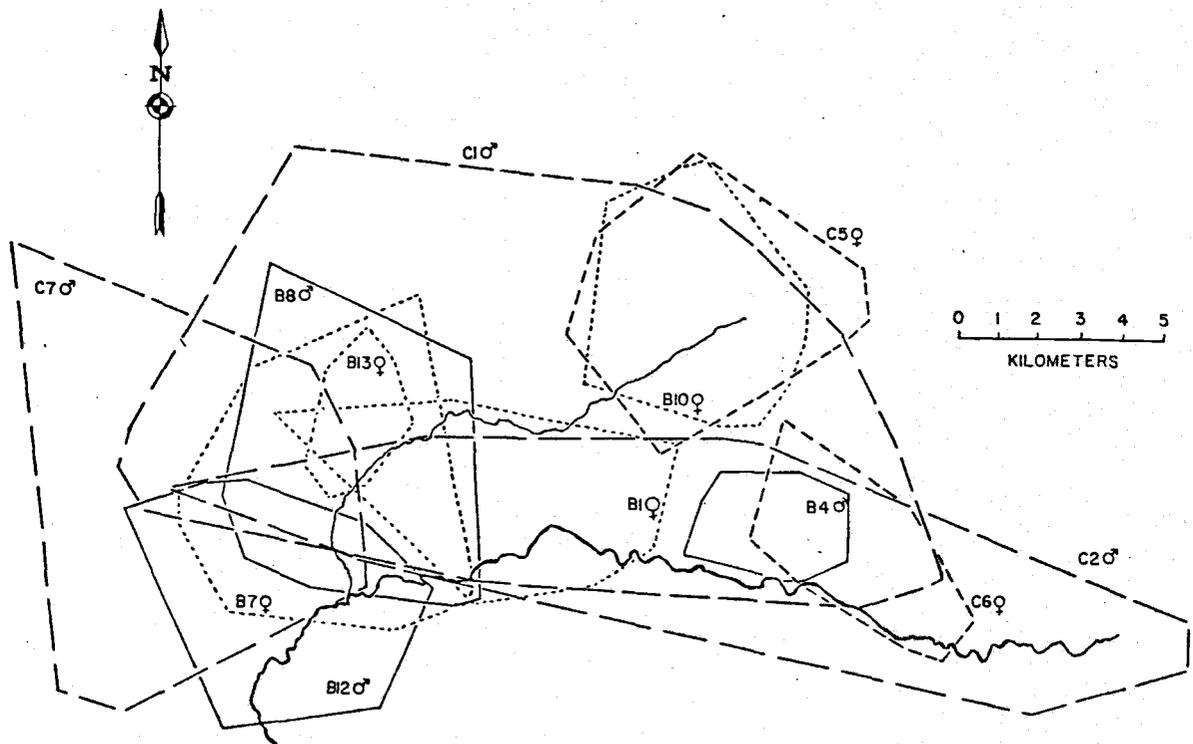


Figure 8. Home ranges of bobcats and coyotes. Home ranges of male bobcats are delineated with solid lines and those of female bobcats with dotted lines; home ranges of male coyotes are delineated with long dashes and those of female coyotes with short dashes.

Table 21. Mean and range of home range areas used by male and female bobcats and coyotes in the Cascade Range of Oregon.

| Species | Sex | No. of Animals | No. of Locations | Monitor Interval (Days) | Home Range Area (km <sup>2</sup> ) <sup>a</sup> |
|---------|-----|----------------|------------------|-------------------------|---|
| Bobcat  | M   | 3              | 110 (47-199)     | 245 ( 92-485)           | 34.6 (12.1- 58.4)                               |
|         | F   | 3              | 146 (68-193)     | 434 (306-508)           | 33.7 ( 7.2- 60.6)                               |
| Coyote  | M   | 3              | 93 (27-157)      | 389 (291-483)           | 138.3 (23.5-248.8)                              |
|         | F   | 2              | 96 (53-138)      | 386 (315-457)           | 30.9 (22.5- 39.2)                               |

<sup>a</sup>Harmonic mean estimator at 95% confidence interval (Dixon and Chapman 1980).

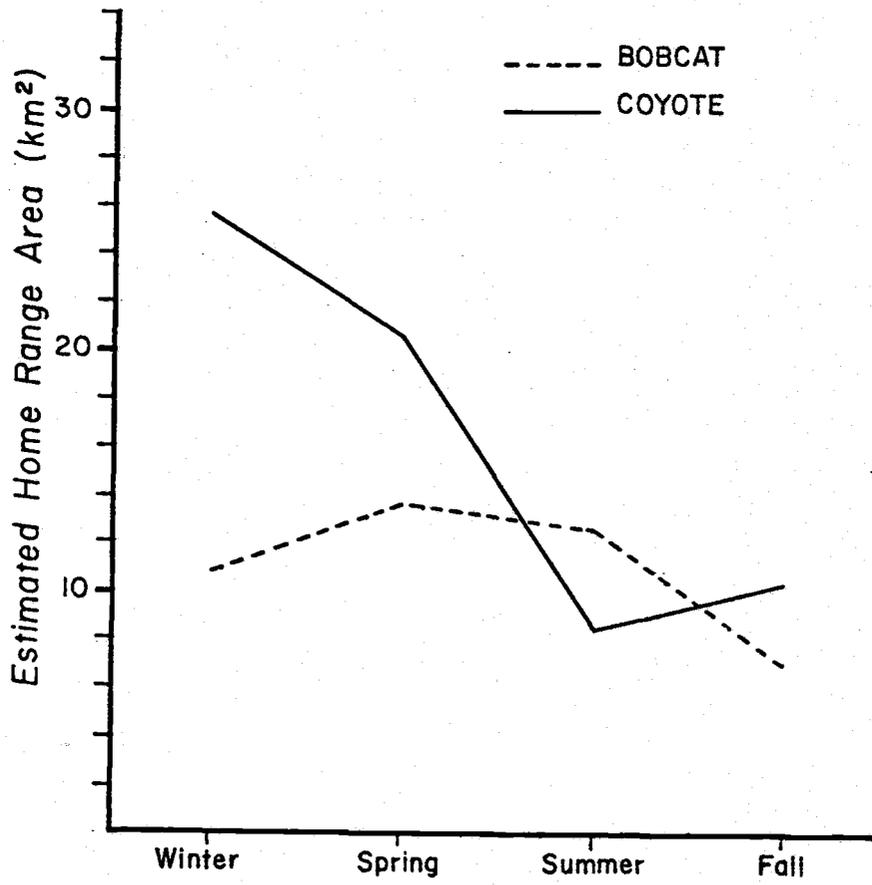


Figure 9. Seasonal home range areas used by bobcats and coyotes.

selected flat ground and southerly and westerly slopes of 1-10° significantly (Table 23). During the winter, bobcats tended to restrict their activity to small areas on steep slopes, while coyotes typically traveled widely on the flats and roadways plowed free of snow. Coyote use of steep slopes during this period typically involved movement across steep drainages.

In the spring, when snow depths were reduced, both bobcats (n = 851 locations) and coyotes (n = 241 locations) made increased use of steep terrain and all aspects (Table 23). Bobcats increased their use of southern exposures during this period, while coyotes, although still making extensive use of flat ground, also used north slopes of 11-30°.

During summer months, coyotes (n = 499 locations) used more slope and aspect classes than during any other season (Table 23). Bobcats (n = 847 locations) remained widely distributed on a variety of topographic situations, as during spring (Table 23). Both species favored southerly slopes during the summer, but selection for particular slope and aspect classes was not pronounced.

During the fall, bobcats (n = 561 locations) moved off the steepest slopes as snow began to accumulate, and both species began to move toward lower-elevation portions of the study area. Although coyote use of flat ground was minimal during the fall, coyotes (n = 238 locations) demonstrated a significant shift toward southerly aspects during this period (Table 23).

Table 22. Proportional availability and annual use of slope and aspect classes used by bobcats and coyotes in Oregon's Cascade Range.

| Slope and Aspect Class | Proportional Availability <sup>a</sup> | Proportional Use   |                    |
|------------------------|--|--------------------|--------------------|
|                        |  | Bobcat (n = 2,699) | Coyote (n = 1,186) |
| <u>Slope Class</u>     |  |                    |                    |
| None                   | .089                                   | .090               | .203 <sup>b</sup>  |
| 1°-10°                 | .271                                   | .307               | .285               |
| 11°-20°                | .357                                   | .342               | .340               |
| 21°-30°                | .213                                   | .173               | .114 <sup>c</sup>  |
| 31°-40°                | .060                                   | .073               | .054               |
| > 41°                  | .009                                   | .015               | .003 <sup>c</sup>  |
| <u>Aspect Class</u>    |  |                    |                    |
| None                   | .089                                   | .090               | .203 <sup>b</sup>  |
| NNE                    | .161                                   | .162               | .096 <sup>c</sup>  |
| ENE                    | .076                                   | .058               | .020 <sup>c</sup>  |
| ESE                    | .058                                   | .094               | .031 <sup>c</sup>  |
| SSE                    | .183                                   | .249 <sup>b</sup>  | .224 <sup>b</sup>  |
| SSW                    | .147                                   | .153               | .251 <sup>b</sup>  |
| WSW                    | .080                                   | .047               | .088               |
| WNW                    | .067                                   | .056               | .024 <sup>c</sup>  |
| NNW                    | .139                                   | .093 <sup>c</sup>  | .062 <sup>c</sup>  |

<sup>a</sup>Measured via LANDSAT satellite on 279 km<sup>2</sup> core study area.

<sup>b</sup>Use greater than expected; 2-tailed test at  $p \leq 0.10$  (Neu et al. 1974).

<sup>c</sup>Use less than expected; 2-tailed test at  $p \leq 0.10$  (Neu et al. 1974).

Table 23. Percentages of bobcats and coyotes (in parentheses) located at aspect and slope classes during focal-animal monitoring in Oregon's Cascade Range.

| Aspect                              | Slope       |             |             |           |           |
|-------------------------------------|-------------|-------------|-------------|-----------|-----------|
|                                     | 1-10°       | 11-20°      | 21-30°      | 31-40°    | 41°+      |
| <u>WINTER</u> No slope: 2.3 (35.7)  |             |             |             |           |           |
| N                                   | 1.8 ( 5.3)  | 20.2 ( 3.9) | 6.1         | 3.0 (2.4) |           |
| E                                   | 13.2 ( 1.4) | 6.4 ( 1.9)  | 0.2 ( 1.9)  | (1.4)     |           |
| S                                   | 10.2 (10.6) | 8.6 ( 7.2)  | 8.9 ( 2.4)  | 8.4 (1.0) | 4.3       |
| W                                   | 1.4 (24.6)  | 5.0         |             |           |           |
| <u>SPRING</u> No slope: 11.2 (27.0) |             |             |             |           |           |
| N                                   | 4.9 ( 2.9)  | 7.2 (19.5)  | 5.2 (13.3)  | 2.6       | 0.1 (0.4) |
| E                                   | 8.2 ( 1.7)  | 3.3 ( 2.1)  | 1.4 ( 0.4)  |           |           |
| S                                   | 18.2 ( 8.7) | 16.9 (10.0) | 5.6 ( 5.4)  | 4.3 (4.6) | 1.9       |
| W                                   | 1.4 ( 2.9)  | 3.4 ( 0.8)  | 4.0 ( 0.4)  | 0.1       |           |
| <u>SUMMER</u> No slope: 9.2 (16.2)  |             |             |             |           |           |
| N                                   | 1.1 ( 1.2)  | 7.3 ( 7.0)  | 6.5 ( 2.4)  | 4.5 (0.2) | 0.1       |
| E                                   | 9.6 ( 4.4)  | 2.7 ( 1.4)  | 0.2         |           |           |
| S                                   | 20.0 (16.8) | 12.2 (25.6) | 5.9 ( 8.4)  | 4.6 (4.6) | 0.4 (0.4) |
| W                                   | 3.5 ( 3.6)  | 8.3 ( 5.6)  | 3.2 ( 1.2)  | (0.8)     |           |
| <u>FALL</u> No Slope: 10.5 (8.8)    |             |             |             |           |           |
| N                                   | 4.6 ( 0.8)  | 17.1 ( 6.3) | 14.1 ( 1.7) | 1.6 (0.4) | (0.4)     |
| E                                   | 9.3 ( 2.5)  | 9.8 ( 0.8)  | 0.4         |           |           |
| S                                   | 8.9 (29.0)  | 11.4 (31.1) | 3.6 ( 5.9)  | 0.7 (5.9) |           |
| W                                   | 1.6 ( 2.1)  | 2.0 ( 3.8)  | 4.3 ( 0.4)  | 0.2       | 0.2       |

Indices of overlap in use of the 6 classes of slope and 9 classes of aspect were least during the winter ( $\sim 30\%$ ) and greatest during the summer ( $\sim 80\%$ ). The maximum amount of overlap during summer (Table 24) was 2 to 3 times greater than the amount of overlap in winter. Indices of overlap during spring and fall were intermediate and around 50% whether measured as simple overlap (Anthony and Smith 1977) or probability of co-occurrence (Horn 1966).

#### Habitat Use

Neither bobcats nor coyotes exhibited any macrohabitat selection; the proportion of each habitat within their respective home range areas did not differ from proportional availability on the study area. However, microhabitat selection (selection for particular habitats within home ranges) was found for both species. As with spatial distribution, bobcats showed a much lower degree of selection than coyotes. Overlap in the use of habitats by bobcats and coyotes was considerably greater than that for spatial overlap (Table 24). In fact, the mean annual index for simple overlap in use of habitats (78%) was greater than the maximum overlap in spatial distribution during any season (76%). Both indices indicated that seasonal overlaps in use of habitats ranged from about 60% to 90% (Table 24).

Selection and avoidance of habitats varied by season. The amount of overlap in use of habitats by bobcats and coyotes (Table 24) was least during the winter ( $\sim 60\%$ ) and greatest

during the summer ( $\sim 90\%$ ). In winter, most bobcats were located in sawtimber, the most abundant habitat on the study area, while coyotes used sawtimber significantly ( $p < 0.05$ ) less than its availability (Table 25). Sawtimber was the most abundant habitat on the study area and included stands of mature Douglas-fir, mixed conifers, and a few isolated old-growth stands of western redcedar (Thuja plicata), Douglas-fir, and western hemlock. Sawtimber stands provided the greatest amount of interception of snow and the greatest number of potential shelters in the form of large tangles of downed trees. Analysis of bobcat locations during periods of activity and inactivity (Table 8) revealed that sawtimber was used significantly ( $p < 0.05$ ) during periods of bobcat inactivity, perhaps because of the amount of potential shelter available. Conversely, coyotes did not use sawtimber at all during periods of inactivity in the winter (Table 17); they selected ( $p < 0.05$ ) closed sapling/pole/sawtimber stands during inactive periods, habitat avoided ( $p < 0.05$ ) by bobcats (Table 25). Both species used open sapling/pole stands proportional to availability. Dense shrub stands were used by bobcats in the winter but avoided by coyotes. Although neither species used sparse vegetation areas at all during periods of inactivity, these habitats were used by active bobcats on a regular basis, accounting for greater ( $p < 0.05$ ) than proportional use (Table 25). Bobcat habitat use during winter appeared to be related primarily to availability of shelter,

Table 24. Seasonal overlap of spatial, vegetational, and dietary resource use by bobcats and coyotes in Oregon's Cascade Range.

| Season                            | Spatial Dist. (S) | Habitat Use (V) | Distrib. Overlap (SxV) | Dietary Overlap (F) | Coefficients of Competition |               |
|-----------------------------------|-------------------|-----------------|------------------------|---------------------|-----------------------------|---------------|
|                                   |                   |                 |                        |                     | $(SxVxF)^a$                 | $(S+V+F/3)^b$ |
| <u>Simple Overlap<sup>c</sup></u> |                   |                 |                        |                     |                             |               |
| Winter                            | 0.36              | 0.65            | 0.23                   | 0.73                | 0.17                        | 0.58          |
| Spring                            | 0.62              | 0.75            | 0.46                   | 0.79                | 0.37                        | 0.72          |
| Summer                            | 0.76              | 0.86            | 0.65                   | 0.61                | 0.40                        | 0.74          |
| Fall                              | 0.50              | 0.86            | 0.43                   | 0.92                | 0.40                        | 0.76          |
| Mean                              | 0.56              | 0.78            | 0.44                   | 0.76                | 0.34                        | 0.70          |
| <u>Horn Index<sup>d</sup></u>     |                   |                 |                        |                     |                             |               |
| Winter                            | 0.27              | 0.58            | 0.16                   | 0.93                | 0.15                        | 0.59          |
| Spring                            | 0.46              | 0.61            | 0.28                   | 0.95                | 0.27                        | 0.67          |
| Summer                            | 0.83              | 0.90            | 0.75                   | 0.63                | 0.47                        | 0.79          |
| Fall                              | 0.55              | 0.67            | 0.37                   | 0.83                | 0.31                        | 0.68          |
| Mean                              | 0.52              | 0.69            | 0.39                   | 0.84                | 0.30                        | 0.68          |

<sup>a</sup>Product  $\propto$  (May 1975).

<sup>b</sup>Summation  $\propto$  (May 1975).

<sup>c</sup>Calculated in the manner of Anthony and Smith (1977).

<sup>d</sup>Calculated as described by Horn (1966).

Table 25. Availability of habitats and proportion of seasonal use by bobcats and coyotes.

| Habitat                           | Prop. Avail. <sup>a</sup> | Winter             |                    | Spring |                    | Summer |                    | Fall               |                    |
|-----------------------------------|---------------------------|--------------------|--------------------|--------|--------------------|--------|--------------------|--------------------|--------------------|
|                                   |                           | Bobcat             | Coyote             | Bobcat | Coyote             | Bobcat | Coyote             | Bobcat             | Coyote             |
| Sawtimber                         | 0.456                     | 0.511              | 0.362 <sup>c</sup> | 0.422  | 0.672 <sup>b</sup> | 0.402  | 0.456              | 0.586 <sup>b</sup> | 0.521              |
| Closed sapling/pole/<br>sawtimber | 0.193                     | 0.075 <sup>c</sup> | 0.425 <sup>b</sup> | 0.223  | 0.104 <sup>c</sup> | 0.196  | 0.118 <sup>c</sup> | 0.216              | 0.176              |
| Open sapling/pole                 | 0.104                     | 0.164              | 0.116              | 0.101  | 0.042 <sup>c</sup> | 0.144  | 0.104              | 0.082              | 0.050 <sup>c</sup> |
| Dense shrub                       | 0.216                     | 0.202              | 0.097 <sup>c</sup> | 0.202  | 0.178              | 0.230  | 0.265 <sup>b</sup> | 0.103 <sup>c</sup> | 0.240              |
| Sparse vegetation                 | 0.030                     | 0.048 <sup>b</sup> | 0                  | 0.052  | 0.004 <sup>c</sup> | 0.027  | 0.008 <sup>c</sup> | 0.012              | 0.013              |

<sup>a</sup>Measured via LANDSAT satellite on 279 km<sup>2</sup> core study area.

<sup>b</sup>Use greater than expected; 2-tailed test at  $p \leq 0.10$  (Neu et al. 1974).

<sup>c</sup>Use less than expected; 2-tailed test at  $p \leq 0.10$  (Neu et al. 1974).

while coyote use appeared related primarily to ease of travel, with selection of more open habitats and areas likely to develop a crust on accumulated snow.

In spring, overlap in habitat use increased, as neither species selectively used a habitat that was avoided by the other species. Bobcats exhibited no discernable selection for any habitat in the spring, even when locations were separated among periods of activity and inactivity (Table 8). Coyotes, however, selected sawtimber during the spring (Table 25) and used it to a greater degree than expected ( $p < 0.05$ ) during periods of both activity and inactivity (Table 17). This use, undoubtedly related to the selection for north slopes during spring, probably involved selection for cool sites as seasonal warmth increased. Use of sawtimber in spring was correlated with less than expected use of closed sapling/pole/sawtimber stands. Open sapling/pole and sparse vegetation stands, which provided little screening from the spring sun, were also avoided by coyotes, while stands of dense shrubs were used relative to their abundance (Table 25).

Overlap in use of habitats was greatest in the summer and fall, when the study area was essentially snow free (Table 24). Bobcats exhibited no selection of vegetation classes in the summer, but sawtimber was selected and dense shrub stands were avoided during fall (Table 25). Coyotes avoided closed sapling/pole/sawtimber stands in the summer as they had in the spring and selected for dense shrub stands. Coyotes spent a significant ( $p < 0.05$ ) portion of their active time traveling

through and probably hunting in shrub stands during summer while avoiding areas of sparse vegetation (Table 17). Open sapling/pole stands were avoided ( $p < 0.05$ ) during the fall, although all other habitats were used proportional to availability (Table 25).

Because of the interaction between topographic characteristics and vegetation classes and because information used in analysis was collected at the same points, indices calculated for each individually were combined into an index of distributional overlap (Table 24). This index, whether calculated on the basis of simple overlap in use of resources (Anthony and Smith 1977) or probability of co-occurrence (Horn 1966), indicated that overlap in use of habitat by bobcats and coyotes ranged from a low of about 20% in winter to a high of about 70% in summer (Table 24). Average annual overlap in habitat use was less than 50%.

#### Dietary Overlap

Diets of bobcats and coyotes were very similar throughout the year; indices of dietary overlap averaged about 80% and were much less variable than habitat indices (Table 24). Since values of 60% are generally considered indicative of similar diets (Zaret and Rand 1971), the high values for diet overlap found here strongly indicate that both species were using largely the same prey base. In marked contrast with indices of habitat overlap,

overlap in diets of bobcats and coyotes were least in the summer (when overlapping use of habitat was the greatest) and greatest in the winter (93%) and spring (95%).

Data from 112 bobcat and 190 coyote scats obtained during the winter revealed approximately equal numbers of kinds of prey taken by both species (17 by bobcats and 22 by coyotes); mean prey size during the winter was likewise similar (827 and 712 g, respectively). The mean size of prey taken during the winter was greater than during any other season (Table 26). Both bobcats and coyotes fed on black-tailed deer (Odocoileus hemionus) and, to a lesser extent, Roosevelt elk (Cervus elaphus) during the winter (Table 26). Likewise, bobcats and coyotes preyed heavily on snowshoe hares (Lepus americanus), remains of which were found in 45% of bobcat and 31% of coyote scats, respectively. Pikas (Ochotona princeps) were generally available only during periods when upper-elevation portions of the study area were free of snow. Bobcats fed more on rodents (primarily tree squirrels; see Table 9) during winter months than did coyotes (Table 26); most tree squirrels were associated with sawtimber stands avoided by coyotes during the winter (Table 25).

In the spring, 35 different kinds of prey were identified in the diets of bobcats (n = 187 scats) and of coyotes (n = 192 scats), the most recorded for any season (Table 26). Mean prey size declined from winter reflecting an increase in the number of small prey taken. Mean prey size of bobcats was 426 g, the lowest for any season, while mean prey size for coyotes in

the spring was 564 g. Both bobcats and coyotes fed extensively on snowshoe hares during spring. As snowmelt exposed southern slopes, a wide range of sciurid and cricetid rodents became available and were preyed on extensively by both bobcats and coyotes. Mountain beaver (Aplodontia rufa), in particular, were frequently eaten; remains occurred in 16% of bobcat and 11% of coyote scats. Birds and eggs were taken with about equal frequency by bobcats and coyotes (Table 26).

The least overlap (simple overlap = 61%; probability of co-occurrence = 63%) among diets of bobcats and coyotes occurred during the summer (Table 24). Prey diversity declined from spring levels, based on analysis of 105 and 324 bobcat and coyote scats, respectively. Mean size of prey increased from 426 to 529 g for bobcats while it declined still further (from 564 to 481 g) for coyotes (Table 26). Bobcat diets during summer remained very similar to spring diets, with rodents (primarily mountain beaver and the mazama pocket gopher, Thomomys mazama) and snowshoe hares comprising over half of the diet. Incidence of ungulates in the diet of bobcats remained at about 20% as in the spring. Fruit was found in many bobcat scats during this period but was believed to have ingested with animal prey eaten by bobcats. Coyote diets showed a marked contrast with bobcat diets during this period. Over 80% of all coyote scats contained fruit, including blackberries and raspberries (Rubus sp.), huckleberries (Vaccinium sp.), Cascade hollygrape (Berberis nervosa), manzanita (Arctostaphylos sp.), chokecherries

Table 26. Seasonal diet characteristics of bobcats and coyotes in Oregon's Cascade Range based on analysis of scats. Number of scats analyzed seasonally in parentheses.

|  | Winter          |                 | Spring          |                 | Summer          |                 | Fall           |                 |
|--|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|----------------|-----------------|
|  | Bobcat<br>(112) | Coyote<br>(190) | Bobcat<br>(187) | Coyote<br>(192) | Bobcat<br>(105) | Coyote<br>(324) | Bobcat<br>(90) | Coyote<br>(138) |
| <u>Number of Kinds of</u>                      |                 |                 |                 |                 |                 |                 |                |                 |
| <u>Animal Prey Identified</u>                  | 17              | 22              | 35              | 35              | 21              | 29              | 19             | 20              |
| <u>Mean Size of Animal Prey(g)<sup>a</sup></u> | 827             | 712             | 426             | 564             | 529             | 481             | 539            | 600             |
| <u>Percentage Occurrence</u>                   |                 |                 |                 |                 |                 |                 |                |                 |
| <u>of Key Prey Categories</u>                  |                 |                 |                 |                 |                 |                 |                |                 |
| Ungulates                                      | 35              | 45              | 18              | 22              | 21              | 10              | 31             | 43              |
| Rabbits and pikas                              | 45              | 31              | 28              | 33              | 36              | 16              | 34             | 17              |
| Rodents  | 36              | 16              | 75              | 60              | 61              | 39              | 41             | 22              |
| Birds  | 7               | 6               | 9               | 10              | 14              | 7               | 9              | 10              |
| Fruit  | 3               | 8               | 1               | 6               | 24              | 83              | 4              | 17              |

<sup>a</sup>Ungulates excluded.

(Prunus sp.), and elderberries (Sambucus sp.). Most of the berries were associated with dense shrub stands, which were stands selected by coyotes during this period (Table 25). Coyotes often would select productive fruit patches and stay in or near them as long as fruits were readily available; this accounted for the relatively small home ranges of coyotes during summer (Fig. 9). Rodents were abundant in these areas and made up the second most common item in the coyote diet during the summer (Table 26). By contrast, the frequency of ungulates and snowshoe hares was approximately half that of the spring diet of coyotes.

With the onset of fall, the variety of prey taken by bobcats and coyotes declined slightly from summer; 19 and 20 different kinds of prey were identified, respectively, in 90 bobcat and 138 coyote scats. Mean prey size increased slightly for both species reflecting lower availability of small rodents. Feeding on large ungulates increased (Table 26), perhaps related in part to increased availability of carrion during and soon after the October and November hunting seasons. Snowshoe hares remained a staple of the bobcat diet. Coyotes consumed snowshoe hares at about the same frequency in the fall as they had in the summer, at levels approximately half that during winter and spring. During the fall, coyotes frequented dense shrub stands, possibly gleaning any remaining persistent fruits (Table 26).

### Coefficients of Competition

Measures of mean resource overlap (Table 24) yielded similar coefficients of competition: 34 (product  $\alpha$ ) to 70% (summation  $\alpha$ ) for simple overlap (Anthony and Smith 1977) and 30 (product  $\alpha$ ) to 68% (summation  $\alpha$ ) for probability of co-occurrence (Horn 1966). Similarly, both methods indicated that the amount of resource partitioning was greatest during winter (Table 24). Partitioning of spatial distributions and habitat by bobcats and coyotes more than offset the high degree of dietary overlap during winter. The least resource partitioning between bobcats and coyotes occurred during summer and fall, seasons of relatively high prey abundance (Table 24).

### Behavioral Interactions

Behavioral mechanisms may have affected the degree of overlap in resource use between bobcats and coyotes. Although no direct interactions between bobcats and coyotes were observed during this study, several indirect observations indicated that bobcats could have been displaced from certain portions of available habitat by coyotes. During the course of this study, at least 1 bobcat was killed by a coyote and 2 other bobcats were killed by either coyotes or cougars (Felis concolor). In the 1 former instance, a yearling bobcat was killed but not eaten at the carcass of an elk. The adult male coyote that killed the bobcat had been feeding on the elk carcass periodically over a period of about 1 week.

Less direct evidence of possible interactions between coyotes and bobcats resulted from focal-animal monitoring. Bobcats exhibited generally arrhythmic activity but showed tendencies toward nocturnal activity in winter, crepuscular activity in spring, diurnal activity in summer, and crepuscular activity once more in the fall (Figs. 3 and 4). In marked contrast, coyotes exhibited largely diurnal activity in winter, crepuscular activity in spring, nocturnal activity during summer, and diurnal activity in fall (Fig. 6). These patterns of activity minimized direct contact between the 2 species during all seasons except spring, the season when loss of snow cover allowed both species to expand their travels greatly.

#### DISCUSSION

Bobcats and coyotes coexist throughout much of North America despite the fact that both are carnivores with very similar body sizes, diets, home ranges, and metabolic requirements (Rosenzweig 1966, Gittleman and Harvey 1982). Because this coexistence occurs over such a broad geographic range and array of habitats, the 2 species must partition available resources to minimize the potential for competition. If mechanisms for resource partitioning did not exist, 1 species would exclude the other according to ecological theory. Overlaps in 3 resource dimensions (spatial distribution, habitat use, and diet) were examined to study the mechanisms of resource partitioning that may be important in management of these species.

In the study, the degree of overlap in use of space by bobcats and coyotes fluctuated widely. Space apparently was not in short supply, as large expanses of apparently-suitable terrain were not occupied by either species. Also, within and among species, home ranges varied widely suggesting that constraints on home range size were related either to energetics of individual animals or availability of patchy resources. Bobcats exploited their home ranges much more intensively than coyotes as evidenced by only very limited selection for particular combinations of slope, aspect, and habitats. Coyotes were much more selective, but their movements covered a much greater amount of territory. Selection (or lack of selection) for particular slopes and aspects by these 2 species may have been related to their hunting styles. Bobcats generally hunt prey by ambush or stalking (McCord and Cardoza 1982) in which terrain plays an insignificant role. In contrast, coyotes tend to rush and seize their prey (Beckoff 1982), a prey-capture technique best adapted to flatter ground as selected by coyotes in this study. More nearly level ground is also conducive to rapid and extended travel as evidenced by coyotes monitored in this study.

Overlaps in habitat use by bobcats and coyotes were greater than those for spatial distributions and showed less fluctuation. This was due in part to the smaller number of habitats identified. Bobcats demonstrated little selective use of particular habitats during any season, which is indicative of intensive use of their home range, while coyotes selected

for or against particular habitats during all seasons (Table 24). Overlaps in habitat use in this study were considerably below those reported by Major (1983) for bobcats and coyotes in Maine (mean = 82% and range = 75 to 86%). Major (1983) did not separate use of slope and aspect by bobcats and coyotes, probably because his study area did not exhibit rugged terrain. His data were, therefore, most directly comparable with the product of spatial distribution and habitat indices calculated in this study (mean overlap = 39%, range = 16 to 75%; Table 24). In this comparison, the mean overlap found here was approximately half that reported by Major (1983) while the range of seasonal fluctuation was greater by about 5 times.

The amount of dietary overlap between bobcats and coyotes in this study was far greater (mean = 84% and range = 63 to 95%) than that reported by Major (1983) for bobcats and coyotes in Maine (mean = 67% and range = 62 to 71%) but far less than reported by Witmer and deCalesta (in press) for animals in Oregon's Coast Range (mean = 97%, range = 94 to 100%). Analysis of scats demonstrated that not only were bobcats and coyotes eating many of the same species of prey, they were selecting almost the identical range of species and prey sizes (Table 26). Proportions of prey species in the diet varied seasonally and were related in large part to habitat selection. The only significant food item consumed by 1 species and not the other was fruit which comprised a major portion of the summer

diet of coyotes. The potential for competition between bobcats and coyotes was probably highest during the winter or early spring when many potential prey species were not available. Indices of dietary overlap during the winter and spring periods were high (93% and 95%, respectively) and indicated almost total overlap in prey selection.

Analysis of overlap in use of resources must be interpreted cautiously for, as pointed out by Colwell and Futuyma (1971) and Schoener (1982), an overlap in resource use by 2 species may be evidence either for or against the existence of competition between them. Overlapping use of a resource may occur because that resource is abundant or its use is irrelevant to 1 or both species. Alternatively, even low levels of overlapping use of a critical resource in short supply may indicate direct and intense competition. Analysis of overlaps in resource use by bobcats and coyotes presented here led to the conclusion that these 2 species did partition resources. The primary mechanism of resource partitioning involved selection for different portions of the available landscape when the potential for competition for food was high, evidenced by the low indices of overlap in spatial distributions and habitats. The effectiveness of this mechanism of resource partitioning was further enhanced by shifts in activity patterns, which reduced the likelihood of bobcats and coyotes coming into direct contact. When this mechanism was insufficient to maintain separation of the 2 species, direct defense of defendable food resources resulted as exemplified by the killing of a bobcat at an elk carcass by a coyote.

Supportive evidence for this hypothesis of resource partitioning comes from several sources. In a review of temporal variability in overlap of use of resources among trophically-similar organisms, Schoener (1982) concluded that in most instances the period of least overlap coincided with the season when resources were least abundant. This occurred because potential competitors were forced to utilize those resources to which they were best adapted, thereby minimizing overlap with other species (Schoener 1982). When predators with similar metabolic requirements are forced to compete on 1 resource dimension, they will be forced to adopt specialized hunting strategies in order to continue to coexist (Rosenzweig 1966). Strategies may include specialization along other resource dimensions (i.e., selection for habitats that favor species-specific hunting strategies) which reduces competition for the resource in short supply. In this case, both food and space were least abundant during the winter when snow cover reduced the availability of prey and the amount of area available for foraging. However, resource partitioning that resulted in separation of bobcat and coyote spatial distributions and habitat use was significant and sufficient to reduce the potential for competition during this period.

Resource partitioning as described here may occur only when 1 or more resources occur in limited supply. Neither Major (1983) or Witmer and deCalesta (in press) found evidence of the potential for competition between bobcats and coyotes. Both

examined overlap in resource use, yet their conclusions were based on opposing lines of reasoning. Major (1983) concluded that neither food or habitat were in limited supply, based on less overlap in diet and greater overlap in habitat use than found in this study. Witmer and deCalesta (in press) concluded, on the basis of far greater overlap in diet than found here, that food was superabundant and therefore no potential for competition existed. Data presented here support both conclusions. The potential for competition exists only when resources are limited, and competition is avoided through resource partitioning. These results support the theoretical model developed by Rosenzweig (1966), which predicts that carnivores with similar metabolic requirements must specialize in order to coexist. Bobcats and coyotes may coexist where their diets are similar as long as habitats are sufficiently diverse to allow spatial and habitat separation during periods of food shortage. In less diverse habitats where such specialization is not an option, coexistence of the 2 species may not be possible unless, also as predicted by Rosenzweig (1966), one (the poorer predator) preys upon the other.

One implication of resource partitioning between bobcats and coyotes is that populations of coyotes may suppress bobcat populations, as suggested by Nunley (1978). Low coyote populations and absence of competition would allow bobcats to utilize an extended range; as coyote populations expanded,

resource partitioning would reduce the area available for occupancy by bobcats even though habitat diversity may preclude their elimination.

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## APPENDIX

Table 27. Effort expended in capture of bobcats and coyotes.

| Year, Month | Trapping <sup>a</sup> |                    | Hunting <sup>b</sup> | Captures |         |
|-------------|-----------------------|--------------------|----------------------|----------|---------|
|             | Leg Hold              | Live Traps         |                      | Bobcats  | Coyotes |
| <u>1982</u> |                       |                    |                      |          |         |
| October     | 141                   | 27                 | 0                    | 2        | 0       |
| November    | 256                   | 44                 | 0                    | 0        | 0       |
| December    | 811                   | 199                | 5.0                  | 1        | 0       |
| <u>1983</u> |                       |                    |                      |          |         |
| January     | 1,950                 | 209                | 70.5                 | 9        | 2       |
| February    | 2,068                 | 251                | 48.5                 | 7        | 0       |
| March       | 1,301                 | 296                | 27.0                 | 2        | 6       |
| April       | 1,017                 | 98                 | 10.0                 | 0        | 3       |
| May         | 4                     | 23                 | 17.0                 | 0        | 0       |
| June        | 0                     | 0                  | 0                    | 0        | 0       |
| July        | 287                   | 113                | 22.5                 | 0        | 1       |
| August      | 1,460                 | 191                | 19.5                 | 4        | 1       |
| September   | 1,093                 | 50                 | 0                    | 1        | 1       |
| October     | 0                     | 0                  | 33.5                 | 1        | 0       |
| November    | 0                     | 0                  | 25.0                 | 1        | 0       |
| December    | 0                     | 0                  | 25.0                 | 0        | 0       |
| <u>1984</u> |                       |                    |                      |          |         |
| January     | 0                     | 0                  | 68.0                 | 1        | 0       |
| February    | 0                     | 0                  | 14.5                 | 1        | 0       |
| March       | 0                     | 0                  | 26.0                 | 2        | 0       |
| April       | 0                     | 0                  | 0                    | 0        | 0       |
| May         | 0                     | 0                  | 0                    | 0        | 0       |
| June        | 0                     | 0                  | 0                    | 0        | 0       |
| Totals      | 10,388 <sup>c</sup>   | 1,501 <sup>d</sup> | 412.0 <sup>e</sup>   | 32       | 14      |

<sup>a</sup>Number of trap nights.

<sup>b</sup>Number of actual hunting hours.

<sup>c</sup>1 bobcat or coyote capture/281 trap nights.

<sup>d</sup>1 bobcat capture/1,501 trap nights.

<sup>e</sup>1 bobcat capture/51.5 hours of hunting.

Table 28. Sex, age, monitoring period, and fate of study animals.

| Species Number | Sex, Age | Period Monitored                   | Days Monitored | Fate                            |
|----------------|----------|------------------------------------|----------------|---------------------------------|
| <u>Bobcat</u>  |          |                                    |                |                                 |
| 1              | F, ad.   | 20 October 1982 - 30 June 1984     | 620            | Trapped 27 December 1984.       |
| 2              | F, ad.   | 22 October 1982 - 7 November 1982  | 17             | Killed by deer hunter.          |
| 3              | F, juv.  | 25 December 1982 - 9 January 1983  | 16             | Unknown.                        |
| 4              | M, ad.   | 4 January 1983 - 5 April 1983      | 92             | Killed by predator.             |
| 5              | M, ad.   | 8 January 1983 - 10 February 1983  | 34             | Killed by predator.             |
| 6              | F, ad.   | 11 January 1983 - 4 February 1983  | 25             | Unknown.                        |
| 7              | F, ad.   | 9 February 1983 - 30 June 1984     | 508            | Killed 3 January 1986 (treed).  |
| 8              | M, ad.   | 14 February 1983 - 30 June 1984    | 485            | Killed 27 January 1985 (treed). |
| 9              | F, juv.  | 26 February 1983 - 14 March 1983   | 17             | Killed by coyote.               |
| 10             | F, ad.   | 28 February 1983 - 30 June 1984    | 489            | Alive at end of study.          |
| 11             | F, ad.   | 13 August 1983                     | 0              | Unknown; escaped trap.          |
| 12             | M, ad.   | 25 August 1983 - 28 January 1984   | 157            | Trapped 28 January 1983.        |
| 13             | F, ad.   | 30 August 1983 - 30 June 1984      | 306            | Killed.                         |
| 14             | F, juv.  | 7 November 1983 - 3 March 1984     | 17             | Unknown; escaped collar.        |
| 15             | M, ad.   | 3 March 1984 - 7 March 1984        | 2              | Killed in capture.              |
| <u>Coyote</u>  |          |                                    |                |                                 |
| 1              | M, ad.   | 27 January 1983 - 24 May 1984      | 483            | Unknown.                        |
| 2              | M, ad.   | 30 January 1983 - 27 February 1984 | 393            | Unknown; escaped collar.        |
| 3              | M, ad.   | 12 March 1983                      | 0              | Found dead; killed by coyote.   |
| 4              | F, juv.  | 23 March 1983 - 30 March 1983      | 7              | Died of starvation.             |
| 5              | F, ad.   | 31 March 1983 - 30 June 1984       | 457            | Alive at end of study.          |
| 6              | F, juv.  | 11 August 1983 - 21 June 1984      | 315            | Unknown.                        |
| 7              | M, juv.  | 13 September 1983 - 30 June 1984   | 291            | Alive at end of study.          |

Table 29. Estimated home range area (km<sup>2</sup>) of bobcats and coyotes monitored during this study.

| Species | Sex,<br>Number | Number of<br>Locations <sup>a</sup> | Minimum<br>Convex<br>Polygon <sup>b</sup> | Harmonic<br>Mean <sup>c</sup> | Bivariate<br>Normal <sup>d</sup> | Weighted<br>Noncircular <sup>e</sup> |
|---------|----------------|-------------------------------------|---|-------------------------------|----------------------------------|--------------------------------------|
| Bobcat  | F, 1           | 174                                 | 29.6                                      | -f                            | 29.5                             | 23.6                                 |
|         | F, 7           | 192                                 | 39.3                                      | 60.6                          | 31.8                             | 23.5                                 |
|         | F, 10          | 176                                 | 25.2                                      | 33.4                          | 21.8                             | 17.2                                 |
|         | F, 13          | 68                                  | 6.8                                       | 7.2                           | 10.2                             | 9.4                                  |
|         | M, 4           | 84                                  | 7.8                                       | 12.1                          | 10.7                             | 8.2                                  |
|         | M, 8           | 199                                 | 37.6                                      | 58.4                          | 42.2                             | 39.0                                 |
|         | M, 12          | 47                                  | 29.4                                      | 33.4                          | 44.0                             | 36.2                                 |
|         | Coyote         | F, 5                                | 137                                       | 30.3                          | 39.2                             | 30.7                                 |
|         | F, 6           | 52                                  | 15.5                                      | 22.5                          | 25.4                             | 21.6                                 |
|         | M, 1           | 93                                  | 151.6                                     | 142.6                         | 200.3                            | 156.4                                |
|         | M, 2           | 157                                 | 78.8                                      | 248.8                         | 51.9                             | 30.1                                 |
|         | M, 7           | 24                                  | 61.7                                      | 23.5                          | 140.9                            | 108.3                                |

<sup>a</sup>Number of daily locations used for home range calculation.

<sup>b</sup>Southwood (1966).

<sup>c</sup>95% confidence interval, after Dixon and Chapman (1980).

<sup>d</sup>95% confidence interval, after Jennrich and Turner (1969).

<sup>e</sup>95% confidence interval, after Samuel et al. (1983).

<sup>f</sup>Not calculated; ellipse did not close.

Table 30. Mean daily survival rates for monitored coyotes, as calculated by the method of Trent and Rongstad (1974).

| Sex     | Survival<br>Days | Mortalities | Season       |              |              |              | Annual<br>Survival |
|---------|------------------|-------------|--------------|--------------|--------------|--------------|--------------------|
|         |                  |             | Jan - Mar    | Apr - Jun    | Jul - Sep    | Oct - Dec    |                    |
| Males   | 1,207            | 0           | 1.000        | 1.000        | 1.000        | 1.000        | 1.000              |
| Females | <u>791</u>       | <u>1</u>    | <u>0.624</u> | <u>1.000</u> | <u>1.000</u> | <u>1.000</u> | <u>0.630</u>       |
| Both    | 1,998            | 1           | 0.850        | 1.000        | 1.000        | 1.000        | 0.833              |

Table 31. Sex and age composition of 737 bobcats harvested from Douglas, Lane, Linn, and Marion Counties, Oregon during December 1983 and January 1984.

| Age (Years) | No. of Males | No. of Females |
|-------------|--------------|----------------|
| 0.5         | 89           | 78             |
| 1.5         | 73           | 60             |
| 2.5         | 106          | 69             |
| 3.5         | 53           | 45             |
| 4.5         | 25           | 35             |
| 5.5         | 22           | 20             |
| 6.5         | 11           | 9              |
| 7.5         | 9            | 6              |
| 8.5         | 3            | 2              |
| 9.5         | 3            | 4              |
| 10.5+       | 9            | 6              |
| Total       | 403          | 334            |

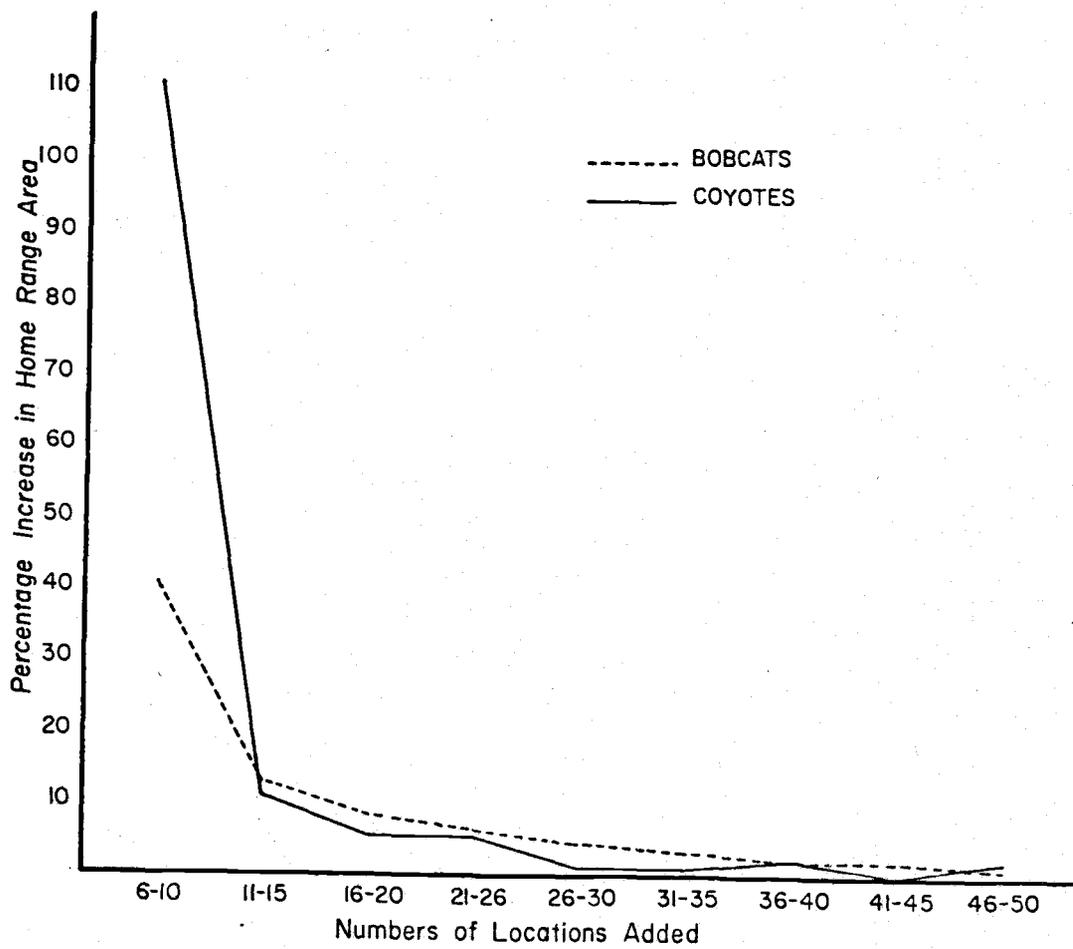


Figure 10. Generalized area/observation curves for bobcats and coyotes.