2000

Habitat ecology and vulnerability to hunting mortality of elk in the southcentral Washington Cascades

Scott M. McCorquodale
The University of Montana

Recommended Citation

McCorquodale, Scott M., "Habitat ecology and vulnerability to hunting mortality of elk in the southcentral Washington Cascades" (2000). *Graduate Student Theses, Dissertations, & Professional Papers*. 10595.
https://scholarworks.umt.edu/etd/10595

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Maureen and Mike
MANSFIELD LIBRARY

The University of **MONTANA**

Permission is granted by the author to reproduce this material in its entirety, provided that this material is used for scholarly purposes and is properly cited in published works and reports.

*** Please check "Yes" or "No" and provide signature ***

Yes, I grant permission ✓
No, I do not grant permission ____

Author's Signature Scott McCorquodale

Date 4/23/00

Any copying for commercial purposes or financial gain may be undertaken only with the author's explicit consent.

HABITAT ECOLOGY AND VULNERABILITY TO HUNTING MORTALITY OF ELK IN THE SOUTHCENTRAL WASHINGTON CASCADES

by

Scott M. McCorquodale

B. S. The University of Montana, 1982

M.S. The University of Washington, 1985

presented in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

The University of Montana

2000

Approved by:

Chairman, Board of Examiners

Dean, Graduate School

5/2/00

Date

UMI Number: 9968755

UMI®

UMI Microform 9968755

Bell & Howell Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

McCorquodale, Scott M., Ph.D. May 2000 Fish and Wildlife Biology

Habitat Ecology and Vulnerability to Hunting Mortality of Elk in the Cascade Range of Southcentral Washington (129 pp.)

Director: C. Les Marcum

I studied habitat selection and vulnerability to hunting among 81 radiocollared elk (*Cervus elaphus*) in the Cascade Range of Washington. Adult and subadult males exhibited similar habitat selection behavior at home range and patch scales during summer–autumn and winter. However, habitat use differed between males and females, especially relative to topographic features and relative to cover types during winter. Males preferred mature, semiclosed forest at both scales during summer–autumn. Females demonstrated similar cover type preferences to males at the home range scale but were nonselective in use of cover types at the patch scale.

In winter, males primarily exhibited selection for cover types at the patch scale, whereas females were primarily selective at the home range scale. Males selected conifer stands at the home range scale and females preferred oak woodland and openings at the patch scale in winter.

Estimated annual survival ($S = 0.61$, 95% *CI* = 0.50–0.70)) was similar among adult and subadult males and was lower than estimated survival among adult females ($S = 0.82$, 95% *CI* = 0.70–0.90). Most elk deaths were associated with hunting, and most elk were killed on summer–autumn home ranges. I found that the odds of an elk being killed on its summer–autumn home range were positively related to the density of roads and negatively related to topographic diversity of the home range. Elk kill sites had higher road densities, relatively more area of resource reserves (e.g., Late Successional Reserves, Watershed Reserves), and relatively less area of mature closed canopy forest than did live elk relocation sites during autumn.

I also evaluated sex–specific sighting biases in winter helicopter surveys of elk. Male elk were more than 9 time less likely to be seen than were female elk, primarily because male elk group sizes were smaller and males tended to use heavier cover. When group size and cover effects on sightability were accounted for in a logistic regression model, sex did not significantly predict sightability. Males and females were, however, distributed unevenly across the landscape, and this segregation was a potentially important source of sex–specific bias in helicopter surveys of wintering elk populations.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS (cont'd)

Page

Study Area

Methods

Results

Methods

LIST OF TABLES

CHAPTER 1

LIST OF TABLES (cont.)

CHAPTER 2

CHAPTER 3

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

ACKNOWLEDGMENTS

I thank the Bureau of Indian Affairs and the Yakama Nation for financial support, which made this research possible. I also thank Plum Creek Timber Corporation for providing a fellowship, which supported me during the year I was on campus in Missoula.

This research was the culmination of several years of hard work. I cannot, however, claim sole responsibility for the success of this endeavor. I owe thanks to a number of important people. First, I'd like to thank my late father, William McCorquodale, for instilling in me his own fascination with the natural world. I also thank the late Leslie Pengelly who encouraged me to pursue my dream of becoming a professional wildlife biologist. I owe enormous thanks to C. Les Marcum, my Ph.D. advisor and friend. Les assisted me in ways far beyond any obligation he had stemming from the usual advisor-graduate student relationship. I also thank the other members of my Ph.D. committee, Jack Ward Thomas, L. Jack Lyon, Dan Pletscher, and I. Joe Ball, for their advice and encouragement.

I returned to school in pursuit of my Ph.D. in mid-career, while working as a staff biologist for the Yakama Nation. This would not have been possible without the support of my supervisor and good friend William Bradley. I also thank the members of the Yakama Nation Tribal Council, particularly William Yallup, Sr., Lonnie Selam, Sr., and Randy Settler, for supporting this research and my personal educational goals.

A number of my colleagues assisted me in a variety of ways. I would like to thank fellow Yakama Nation biologists Gina King, Tracy Hames, and Rose Leach for their encouragement. I owe special thanks to Jeff Feen who ably supervised the field

research during the year I was on campus in Missoula. My research technician, Dave Blodgett, Jr., assisted with all aspects of the field research, and I am very appreciative of his efforts. Several Yakama Nation Wildlife Technicians helped trap elk, including Bing Olney, Darwin Sockzehigh, and Terry Heemsah. Cliff Dyer ably piloted fixed-wing aircraft used to radiotrack elk. I also thank Steve Tolle for piloting helicopters used to dart elk and Mark Clarke for piloting the helicopter used to collect data for the sightability chapter.

None of this would have been possible without the tremendous support and encouragement of my loving wife Kim. My return to school was first Kim's idea, and she made enormous sacrifices to allow me to pursue this dream, including relocating our family to Missoula for almost a year. Kim was always there to provide loving encouragement when I became discouraged or doubted my abilities. Kim has been my partner in life and love during almost 22 years of marriage, and I am deeply thankful for her love and her commitment to our relationship and our family. She is the love of my life. Accomplishments mean little without someone to share them with, and I am incredibly thankful to have Kim to share my successes with. Words cannot adequately express how much she means to me. My children, Andy, Kyle, and Katie, were also supportive and made tremendous sacrifices to allow me to return to school. It was difficult for them to move far from friends and familiar surroundings for a year, but they did it willingly, and I thank them for loving Dad enough to make those kinds of sacrifices. I also thank Kim's parents, Bruce and Nancy Ellis, for their encouragement and financial support that enabled me to return to school. Their kindness to me has been immeasurable since the day I first met them.

CHAPTER 1: SEX-SPECIFIC MOVEMENTS AND HABITAT USE BY ELK IN THE CASCADE RANGE OF WASHINGTON

Abstract: I studied sex-specific behavior of Rocky Mountain elk (*Cervus elaphus nelsoni*) in the Cascade Mountains of southcentral Washington during 1992–99 using 3,059 relocations of 81 radiocollared individuals (26 adult males, 26 subadult males, and 29 adult females). Adult males (≥ 5 yr) consistently migrated from summer–autumn home ranges earlier ($P \leq 0.0001$) than other elk, but the timing of spring migration was similar ($P = 0.16$) among all elk classes. Using compositional analysis, I found habitat use of adult and subadult male elk during winter and summer–autumn were similar ($P > 0.12$) at home range and patch scales, but use compositions for cover types and topographic features often differed ($P \leq 0.10$) between males and females. During winter, males generally used conifer stands and flat areas more, and oak woodland less, than females. Males also tended to use slightly higher elevations than females during winter. Males selected ($P \leq 0.10$) mature semiclosed forest at both scales during summer–autumn. Females demonstrated similar preferences to males at the home range scale, but used cover types nonselectively ($P = 0.12$) at the patch scale during summer–autumn. In winter, males used cover types nonselectively at the home range scale ($P = 0.25$) but selected conifer forest at the patch scale. In contrast, females selected oak woodland and openings at the home range scale but used cover types nonselectively ($P = 0.60$) at the patch scale. Males and females preferred elevations of 759–908 m at both scales during winter. All elk located their winter home ranges in relatively steep (> 40%)

terrain. Within winter home ranges, males selected gentler slopes than females. Summer–autumn relocations of all classes of elk were further ($P \leq 0.001$) from roads than expected. The effects of roads on habitat use differed among classes of elk ($P = 0.08$); adult males used summer–autumn home ranges with lower road densities and used patches further from roads than did subadult males ($P = 0.06$) and females ($P = 0.04$). During winter, female elk home ranges had lower road densities and females used areas further from roads than adult and subadult males ($P < 0.10$).

INTRODUCTION

Habitat use by Rocky Mountain elk has been well documented, but most research has focused on females because of their importance to rates of population change (Marcum 1975, Schoen 1977, Irwin 1978, Burcham et al. 1998). The factors controlling lifetime reproductive success in ungulates often differ between sexes and sometimes among age classes (Guiness et al. 1978, Gibson and Guiness 1980a, 1980b, Clutton–Brock et al. 1982). Divergent reproductive strategies can lead to differences in habitat use, diets, and spatial use by different sex and age classes (Miquelle et al. 1992, Main and Coblentz 1996, Bleich et al. 1997). Consequently, detailed knowledge of habitat use and selection behavior of adult female elk may not provide reliable about males.

Some researchers have addressed movements and habitat use of male elk (Hurley and Sargeant 1991, Lyon and Canfield 1991, Unsworth et al. 1993); however, data were collected mainly from young males and during hunting seasons. To explore differences in resource selection by different sex and age–classes of elk, I collected multiseason data from similarly sized samples of radiocollared adult female, adult male (≥ 5 yr), and subadult (≤ 4 yr) male elk in the Cascade Range of southcentral Washington during 1992–99.

I examined movement behavior at the landscape scale and habitat use at both home range and patch scales, which approximated the second and third order scales of habitat selection described by Johnson (1980). I tested the following group contrast hypotheses: (1) movements and use of habitat components at both home range and patch scales were independent of sex and age class, and (2) the apparent effects of roads on elk habitat use were independent of sex and age class. I also tested the null hypotheses that habitat components were used nonselectively at both home range and patch scales by different classes of elk.

STUDY AREA

Winter

The winter study area encompassed 57,000 ha of the Toppenish Creek watershed along the eastern slopes of the Washington Cascades (46°20', 121°00') (Fig. 1). The area consisted of a series of steep east–west canyons, the highly dissected north and south forks of Toppenish Creek, and adjacent forested plateaus. Elevations ranged from 490 to 1,400 m.

Grass–dominated openings were common on south aspects and other xeric sites. North aspects, drainage bottoms, and higher plateaus were dominated by conifers, primarily ponderosa pine (*Pinus ponderosa*), Douglas–fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*). The forest–rangeland ecotone was dominated by Oregon white oak (*Quercus garryani*) or mixed oak/pine stands.

Annual precipitation historically averaged about 64 cm in lower Toppenish Creek. Most precipitation falls during Nov–Apr, much of it as snow. Mean annual snowfall measured at nearby Yakima, Washington, 1964–94, was 61.2 cm (National Oceanic and Atmospheric Administration 1994). During 1992–99, snowfall was average or below average during each winter except 1992–93 and 1995–96, when snowfall was much above average.

Summer–autumn

The summer–autumn study area included much of the Yakima, Klickitat, and Cispus River watersheds (Fig. 1). Elk summer range encompassed about 550,000 ha, including roughly 200,000 ha of the Yakama Reservation and approximately 300,000 ha of federal land within the Gifford Pinchot and Wenatchee National Forests. Approximately 50,000 ha were managed by Boise Cascade Corporation or the State of Washington. Elevations ranged from 700 m to approximately 3,742 m at the crest of Mt. Adams, a dormant volcano. The upper watersheds were characterized by rugged terrain near the Cascade crest, whereas lower areas included a mixture of steeply walled drainages and adjacent, gently sloping plateaus.

Most of the area was forested, and ponderosa pine or mixtures of pine, Douglas fir, grand fir, western larch (*Larix occidentalis*), and western hemlock (*Tsuga heterophylla*) dominated mid elevation stands. Upper watersheds were dominated by conifers such as Douglas fir, subalpine fir (*Abies lasiocarpa*), Pacific silver fir (*Abies amabilis*), mountain hemlock (*Tsuga mertensiana*), subalpine larch (*Larix lyallii*), lodgepole pine (*Pinus contorta*), Englemann spruce (*Picea englemannii*), and western red cedar (*Thuja plicata*). Localized stands of red alder

(*Alnus rubra*), aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) were common in riparian zones and other wet sites. Nonforested habitats included numerous meadows, natural shrubfields, early seral stands, and subalpine parks.

Annual precipitation in the summer–autumn study area historically varied from 180 cm near the Cascade crest to approximately 70 cm in the lower watersheds. Deep snowpacks (>5 m) are common at higher elevations during winter and may persist until mid July. During this study, mid–elevations and south and west aspects were usually snowfree by late May. Autumn snowfalls usually began by late October near the Cascade Crest and by approximately mid to late November at lower elevations.

Land Management

The habitat mosaic used by elk included large tracts managed by the Yakama Nation and the U. S. Forest Service, and smaller tracts managed by Boise Cascade Corporation and the Washington Department of Natural Resources. The winter range was located entirely within the Yakama Reservation, and most of the winter study area was managed as critical winter habitat for ungulates. Timber harvesting and summer livestock grazing were permitted (McCorquodale et al. 1997). Toppenish Creek was extensively roaded, but only a road that accessed a series of elk traps was plowed during winter. Access to this road was controlled via a locked gate during Nov 15–Apr 1.

About 98,000 ha of the overall study area were administratively designated as true reserves (e.g., wilderness, primitive area, or alpine reserve). Additionally, 72,000 ha were managed as resource emphasis areas (e.g., tribal watershed reserves and federal late successional reserves) where limited timber harvest was permitted to enhance environmental values (McCorquodale et al. 1997). Approximately 310,000 ha of federal, tribal, and private land within the summer study area were intensively managed for commercial timber production.

METHODS

Capture and Radiotelemetry

I captured elk in small panel traps or elk–sized clover traps (Thompson et al. 1989) or darted them from a Hughes 500D helicopter during winter, 1992–99. I allocated captured elk to 1 of 3 subsamples (adult males, subadult males, or adult females) based on age and sex criteria. I selected 5 as the threshold age for adult males based on inflections of age vs. body, antler, and testes mass from the data of Flook (1970). I estimated the ages of captured elk by patterns of tooth eruption and wear (Quimby and Gaab 1957), and for males, also by the size and girth of antlers. Because I primarily used age estimates to allocate males to the correct age–class sample, precise estimates were not required. Age estimates from cementum annuli analysis (Matson's Laboratory, Milltown, Montana) were obtained for elk that died during the study, and these provided an assessment of the accuracy of estimates made at capture.

I fitted a sample of elk with radiotelemetry collars (MOD-500, Telonics, Inc., Mesa, Arizona) each winter. Transmitters had an estimated 3-yr battery life. Although I did not employ formal randomization, I attempted to deploy collars evenly across the trapping area to avoid oversampling specific social groups or matrilines.

I relocated radiocollared elk weekly during May–Nov and approximately twice monthly during Dec–Apr, following the approach of McNay et al. (1994), which emphasized a systematic interval between relocations rather than attempting to identify independent relocations *post hoc*. Relocations were obtained during daylight hours from a Cessna 182RG aircraft fitted with 2 side–looking directional antennas (RA-2A, Telonics, Inc., Mesa, Arizona), following the general procedure of Gilmer et al. (1981). Most flights were conducted during early morning hours in relatively good weather. I estimated aerial relocation coordinates with a Geographic Positioning System (GPS) receiver (Model 100, Garmin Corp., Olathe, Kansas, USA). I evaluated GPS accuracy by periodically obtaining aerial coordinates for a series of known points that were identifiable from an aircraft. I also evaluated telemetry system error (GPS + tracking error) by obtaining aerial position estimates of collars at known locations using a blind testing approach.

Home Ranges and Movements

I estimated summer–autumn and winter home ranges of elk using CALHOME software (Kie et al. 1996). I derived 90% adaptive kernel (AK) (Worton 1989) and 90% minimum convex polygon (MCP) (Michener 1979) estimates. I produced AK estimates using program defaults for optimum bandwidth and a user defined 50 × 50 grid. I estimated seasonal home ranges for all elk with ≥ 10 seasonal relocations, but most home ranges were estimated from ≥ 25 relocations during summer–autumn and ≥ 15 relocations during winter. Although home range estimates from 10–30 relocations may be negatively biased (Seaman et al. 1999), my interest in home ranges was principally to define sampling frames for habitat analyses rather than estimating home range size (Unsworth et al. 1993). I considered spatial overlap of seasonal 90% AK home ranges from different years as evidence of range fidelity (McCorquodale 1999). When fidelity was documented, I pooled interyear data for final delineations of seasonal home ranges. I tested for effects of relocation number and sex and age class membership on home range size using a 2–way analysis of variance (ANOVA). If a male instrumented as a subadult lived to ≥ age 5, I used Multiresponse Permutation Procedures (MRPP) (Mielke et al. 1981) to test the hypothesis that the same area was used before and after age 5. I pooled subadult and adult relocations and treated the male as a subadult if MRPP analysis yielded evidence that the same area was used before and after age 5. If MRPP analysis indicated that a subadult male used a different area after age 5, I used only subadult data for that male to maintain individual animals as sampling units.

I considered elk with nonoverlapping 90% AK home ranges during winter and summer–autumn as migratory. I judged seasonal migration to have begun when consecutive relocations placed an elk outside of a defined seasonal home range (90% AK) (McCorquodale 1999). I estimated migration dates as the midpoint between the last relocation within a seasonal home range and the first migration relocation (generally a span of 7–10 days). I calculated minimum migration distances as the straight–line distance between seasonal activity centers, where seasonal activity centers were defined as the mean UTM coordinates associated with seasonal 90% AK home ranges (McCorquodale 1999). I tested for the effects of sex and age class membership on migration date using a 1–way fixed–effects ANOVA.

Habitat Use

I initially created an ArcInfo® GIS database consisting of a road coverage, cover type, and management class coverages, and a 30 m resolution digital elevation model (DEM) of the study area. The cover type coverage was based on interpretation and groundtruthing of 1:12,000 color aerial photographs. I used stand structure, species composition, and ecotype attributes from the original cover type coverage to produce a simplified classification of 8 types: 1 = openings and shrubfields (tree canopy closure [CC] < 11%), 2 = oak woodland, 3 = open young forest (CC = 11–39%, dbh <30 cm), 4 = closed young forest (CC >39%, dbh <30 cm), 5 = open mature forest (CC = 11–39%, dbh ≥30 cm), 6 = semiclosed mature forest (CC = 40–69%, dbh ≥30 cm), 7 = closed mature forest (CC >69%, dbh ≥30 cm), and 8 = other (e.g., bare ground, rock, open water). The management coverage consisted of 4 classes (1 = true reserves [e.g., federal wilderness, tribal primitive area], 2 = managed forest, 3 = resource emphasis areas (e.g., federal late successional reserves), 4 = state, private, and other lands).

I used the GRID module in ArcInfo® to create a raster coverage of topographic features. I reduced aspect data from the DEM to 9 classes (a no aspect class and 8 classes of 45° width), which represented flat ground and the aspects N, NE, E, SE, S, SW, W, and NW. Similarly, I reduced slope data from the DEM to 7 classes (6 of 10% slope and a 7th class of >59% slope [1 = 0–9%, 2 = 10–19%,...,7 = >59%]. I derived 13 elevation classes consisting of a low and high elevation class and 11 intermediate classes of 150 m width (1 = <607 m, 2 = 607–757 m, 3 = 758–908 m, 4 = 909–1,059m, 5 = 1,060–1,210m, 6 = 1,211–1,361, 7 = 1,362–1,512 m,...,13 = >2,267 m). I used a raster cell size of 900 m^2 = 0.09 ha (the resolution of the original DEM data), which yielded a topographic coverage of the study area consisting of roughly 5.4×10^6 cells.

I then integrated the cover type and management class coverages into the topographic GRID. This yielded a single GRID coverage wherein each cell had a slope, aspect, elevation, management, and cover type class identity.

I also created polygon coverages from seasonal 90% AK home ranges of radiocollared elk. For patch scale analyses, I created an elk use coverage by adding a 300–m radius circular buffer to each telemetry relocation, yielding a coverage wherein each relocation was represented as a 28.3 ha circle centered on the original relocation. I used buffered telemetry points instead of the points alone because I thought these better represented habitat patches used by elk and I selected 300–m as the buffer radius because it approximated the upper 95% *CI* for telemetry system error. I created a final GRID coverage for home range scale analyses by integrating the home range coverages into the habitat feature GRID coverage previously described. Similarly, I integrated the buffered telemetry point coverage into a separate habitat feature GRID to create a final coverage for patch scale analyses.

Analytical Procedures. – I used compositional analysis (Aebischer et al. 1993a), which is based on logratio transformations of habitat component proportions (Aitchison 1986) to test hypotheses about habitat use and selection. Compositional analysis has desirable properties for analyzing habitat use data (Aebischer and Robertson 1992, Aebischer et al. 1993a), including: (1) rendering habitat composition proportions independent, (2) utilizing individual animals rather than relocations as sampling units, (3) placing inference about habitat preference in a relative, rather than absolute, context, and (4) facilitating an array of hypothesis tests using multivariate analysis of variance (MANOVA) analyses.

I created a separate habitat composition for slope, aspect, elevation, and cover type for each elk within each season and scale from the GRID coverages. For each elk sample (e.g., adult male elk home ranges during winter) I calculated a habitat composition for each habitat theme, where x_{ij} = the proportion of component i for elk j ($\Sigma x_{i1} = 1.0$, $\Sigma x_{i2} = 1.0$, $\ldots \Sigma x_{in} = 1.0$). I then transformed the habitat composition data for each elk (by each theme, season, and scale) into logratios of the form: $y_i = \ln (x_i/x_j)$ (for all i, $i \neq j$) for subsequent analyses (Aebischer et al. 1993b). I combined components for some analyses because not all components within the original classifications were used by all elk. For example, because oak woodland was largely absent from most summer–autumn home ranges, I eliminated this cover type from the summer–autumn dataset.

I tested for differences in habitat use compositions among sex and age classes using single factor MANOVA analyses of the transformed data (Aebischer and Robertson 1992, Aebischer et al. 1993b). I used Wilk's lambda (Λ) as the test statistic for testing group contrast hypotheses. I first tested for differences between adult and subadult male elk. If the results of this test suggested adult and subadult male compositions were not different ($P > 0.10$), I pooled compositions for all males and contrasted them with habitat compositions for adult females. When group differences were evident, I used t–tests to define which elements within a composition were different, following Aebischer et al. (1993b).

After establishing the number of statistically distinguishable groups for each habitat composition, I evaluated group preferences for habitat features with a use vs. availability compositional analysis (Aebischer et al. 1993a). This analysis was based on pairwise differences ($d_i = y_{Ui} - y_{Ai}$) of the logratio transformations of used and available habitat for each component within a composition (Aebsicher and Robertson 1992). I tested the hypothesis that $\Sigma d_i \equiv 0$, using the approximation: $-N \ln(\Lambda) = \chi^2_{(k-1)}$, where k = the number of classes in the composition, as a test statistic (Aebischer et al. 1993). For summer–autumn home range scale analyses, I derived available habitat compositions for the summer study area using the final GRID coverage. For winter home range scale analyses, I estimated availabilities within a 57,000 ha polygon that contained the winter home ranges of all radiocollared elk. For patch scale analyses I compared the compositions of the buffered telemetry points (use) with the compositions of seasonal home ranges (available).

When use compositions of several elk contained unused components, I combined classes within the composition. When unused components were present for only a few elk (< 5), I replaced the 0 values with a small nonzero value (0.0001) (Aebischer et al. 1993a). Because it is inappropriate to substitute for 0 values in an availability composition (i.e., an elk cannot select a component that is unavailable) (Aebischer et al. 1993a), I combined components to eliminate any 0 value in availability compositions.

I determined road densities within elk home range polygons and calculated distances between relocations and the nearest road from a road coverage (vector) using GIS. The road coverage was compiled using GIS data from 4 sources. Data from one source were not attributed by status (i.e., open vs. closed roads), so it was not possible to be confident of road status. However, most roads represented in the final road coverage were administratively open. I tested for group effects on road densities within seasonal home ranges and distances to nearest roads for seasonal relocation points using one–way ANOVAs. I also created a point coverage consisting of 5,000 random points that overlaid the summer–autumn study area. I eliminated points falling outside of the study area boundary, producing a final coverage of 3,771 random points. I used a one–way ANOVA to test for differences in distances to nearest roads for random points and summer–autumn elk relocations.

General Statistical Procedures

I conducted MANOVAs, ANOVAs, and *t*–tests using SPSS–8.0 software (SPSS, Inc. 1998). I based *Post hoc* multiple comparisons associated with ANOVAs on Least Significant Difference procedures (Carmer and Swanson 1973). I conducted MRPP tests using BLOSSOM software (Slauson et al. 1991) and used RESOURCE SELECTION FOR WINDOWS software written by F. Leban (University of Idaho, Moscow, Idaho) to test use vs. availability hypotheses with compositional analysis. I considered $P \leq 0.10$ as acceptable evidence of statistical significance for all tests (Johnson 1999).

RESULTS

Capture and Telemetry

During winters 1992–99, I instrumented 81 elk ≥ 1 yr–old (52 M:29 F). The mean absolute deviation of actual and estimated ages at capture for 11 known–age males was 1.4 yr; the error was ≤ 1 yr for 8 of 11 males. All males for which age estimates from cementum analysis were later obtained had been allocated to the correct subsample at capture. Of the 52 males I instrumented, 26 (50%) were marked as mature adults and 26 as subadults. The grand mean age of mature males radiotracked annually was 8.0 ($\bar{x}_{\text{annual}}$ = 7.6–8.4) and the grand mean age of subadult males was 3.4 ($\bar{x}_{\text{annual}}$ = 2.8–3.7).

I obtained 3,059 relocations of the 81 radiocollared elk during 1992–99. The database represented 91 male elk years and 56 female years. I radiotracked 23 of 52 (44.2%) males for > 1 yr; 11 (21.2%) were radiotracked for ≥ 3 yr. I monitored 18 of 29 (62.1%) radiocollared females for > 1 yr; 7 (24.1%) were monitored for ≥ 3 yr. Only 3 subadult males were tracked long enough to provide data after attaining the age criteria for adults. My MRPP analysis of relocation coordinates for these males suggested each used the same areas as adults as they had used as subadults (P = 0.12–0.87), so I pooled interyear data from each male and treated them as subadults. All 3 elk provided data only for a single year after reaching age 5.

I estimated the mean GPS error as 36.0 m (95% CI = 24.4–47.6 m, n = 27). Using blind testing, I estimated the mean telemetry system error (i.e., GPS + tracking error) as 196.5 m (95% CI = 138.7–269.7 m, n = 17).

Home Ranges and Movements

I estimated summer–autumn home range sizes for 22 adult males, 23 subadult males, and 26 adult females (Table 1). Home range size was similar among sex and age classes (F = 1.76, P = 0.20) and was not systematically related to numbers of relocations (F = 1.12, P = 0.40) for 90% AK estimates. Similarly, home range size was not systematically related to sex and age class (F = 0.61, P = 0.56) or relocation number ($F = 0.98$, $P = 0.53$) for 90% MCP estimates. I estimated winter home ranges for 14 adult males, 11 subadult males, and 15 adult females (Table 1); mean home range estimates were similar among sex and age classes ($F = 0.35$, $P = 0.71$) and among elk with different numbers of winter relocations ($F = 0.49$, $P = 0.92$) for 90% AK estimates. Home range size was strongly related to the number of winter relocations ($F = 9.15$, $P \leq 0.001$) for 90% MCP estimates, so sex and age class contrasts are not reported due to the high likelihood of sample size bias in winter MCP estimates.

Fidelity to seasonal home ranges was strong among most instrumented elk. Two males (1 AD, 1 SAD) and 1 female relocated their winter home ranges during the study. No elk relocated an established summer–autumn home range, although 1 subadult male that used widely separated (> 25 km), nonoverlapping areas during 2 years used one nearly exclusively the second year. One adult female and 1 subadult male were nonmigratory residents of the winter study area. Two other males (1 AD, 1 SAD) displayed atypical movements, behaving as nonmigratory residents during Nov–Aug, but moving to higher elevations and into higher elk density areas ≥ 10 km west during the rutting season each year.

Mean distances between seasonal activity centers for migratory adult males (31.4 km, $n = 22$), subadult males (29.6 km, $n = 21$), and adult females (34.3 km, $n = 16$) were similar ($F = 0.93$, $P = 0.40$); overall mean distance between activity centers was 31.6 km (*range* = 3.6–57.2 km). The date of autumn migration was affected by sex and age class ($F = 15.96$, $P < 0.0001$). The mean date of autumn migration for adult males ($\bar{x} = 25$ Oct) was earlier than the mean date for subadult males ($\bar{x} = 11$

Nov, $\bar{x}_{diff} = 17.07$, $P < 0.0001$) and adult females ($\bar{x} = 14$ Nov, $\bar{x}_{diff} = 19.56$, $P < 0.0001$). There was little evidence that the timing of spring migration was affected by sex and age class ($F = 1.92$, $P = 0.16$). The mean date of spring migration was 12 May.

Habitat Use

Group Contrasts. – Because many summer–autumn home ranges lacked specific components, I eliminated oak woodland from the cover type compositions, and combined all slope classes above 50%, all elevation classes below 909 m, and all elevation classes above 1,664 m. Adult and subadult males used habitat features similarly ($P = 0.12$–0.84) at both home range and patch scales (Table 2). Home range compositions differed slightly between males and females during summer–autumn for cover type ($P = 0.09$), but evidence for sexual differences was stronger for slope ($P = 0.03$) and elevation ($P = 0.04$) compositions (Table 2). Home ranges of males tended to have relatively more closed canopy (CC > 69%) and open canopy (CC = 11–39%) mature forest than did home ranges of females, but males made significantly ($P \leq 0.10$) greater use only of open canopy (CC = 11–39%) mature forest relative to moderate canopy mature forest (CC = 40–69%). Relative to home ranges of females, home ranges of males consistently had more area of steep (≥ 50%) and moderate slopes (40–49%) and less area of gentle slopes (≤ 19%) ($P \leq 0.10$). Home ranges of males had more ($P \leq 0.10$) area above 1,663 m relative to areas of 1,211–1,663 m and 909–1,059 m elevation. Summer–autumn home range compositions for males also had more area below 909 m relative to 909–1,059 m elevations than did compositions for females.

Patch scale use compositions during summer–autumn differed between males and females for all 4 compositions ($P = 0.001$–0.07) (Table 2). At the patch scale, males made significantly ($P \leq 0.10$) more use of closed canopy mature forest relative to moderate canopy mature forest and more use of open canopy mature forest relative to moderate canopy mature forest than females. Males used NW aspects less relative to NE, E, SE, and S aspects than did females, and males used flat areas less relative to all aspects except W and NW. Males also used W aspects significantly less relative to all aspects except N, NW, and flat areas than females used at the patch scale. At the patch scale, males made relatively more use of steep (≥ 50%) and moderately steep (40–49%) slopes and less use of gentle slopes (≤ 19%) than females ($P \leq 0.10$).

Many winter home ranges lacked specific conifer types from the original classification, so winter cover type compositions were reduced to 5 classes: openings, oak woodland, open coniferous forest (CC < 40%), closed coniferous forest (CC ≥ 40%), and all other types. Elevation compositions for winter were simplified to 3 classes: (1 = < 758 m, 2 = 758–908 m, and 3 = ≥ 909 m) to reduce the occurrence of composition elements with 0% use.

Winter habitat use compositions were similar ($P = 0.20$–0.89) for adult and subadult males at both home range and patch scales, justifying pooling the data for males (Table 3). Winter use compositions at the home range scale differed between males and females for cover type ($P = 0.04$), aspect ($P = 0.06$), and elevation ($P = 0.06$), but not for slope ($P = 0.16$) (Table 3). Male home ranges during winter contained significantly more closed canopy and open canopy conifer forest relative to openings and oak woodland than female home ranges did. Female home ranges contained more oak woodland relative to all other cover types than male home ranges. Winter home ranges of males contained more flat areas relative to N and NW aspects than female home ranges, and male home ranges had less NW aspect relative to NE and S aspects than female home ranges. Male home ranges contained more moderate elevation (758–908 m) area relative to low elevation (< 758 m) area than female home ranges during winter.

Winter use compositions differed between males and females for all 4 habitat compositions at the patch scale ($P = <0.0001–0.05$) (Table 3). Males used more closed and open canopy conifer forest relative to openings and oak woodland than females, and females used more oak woodland relative to all other cover types than males. Females used S and SE aspects more relative to NE aspects and flat areas, and males used flat areas more relative to N, SE, S, and W aspects than females. At the patch scale, males used gentle slopes (< 10%) more relative to all other slope classes except slopes ≥ 50%, and 30–39% slopes less relative to slopes < 30% than females. Males used moderate (758–908 m) and high (> 908 m) elevations more relative to low elevations (< 758 m) than females at the patch scale during winter.

Summer–autumn Habitat Selection. – During summer–autumn, male elk used cover types disproportionately to their availabilities at both home range (χ^2_6 = 48.5643, $P < 0.0001$) and patch ($\chi^2_6 = 15.3694$, $P < 0.05$) scales. At the home range scale, males preferred mature semiclosed (CC = 40–69%) forest relative to all types except mature closed forest, and mature closed forest was preferred relative to all types except mature semiclosed forest and openings (Table 4). At the patch scale, mature semiclosed forest was preferred relative to all other types except other mature forest types, and mature open forest was preferred relative to young forest types (Table 4).

During summer–autumn, female elk demonstrated selection for cover types at the home range scale ($\chi^2_6 = 49.65$, $P < 0.0001$), but cover types were used in proportion to their availabilities ($\chi^2_6 = 10.12$, $P = 0.12$) at the patch scale. Females preferred mature semiclosed forest relative to all other types at the home range scale (Table 4). Females preferred mature closed forest relative to young closed forest and openings relative to young closed forest and mature open forest.

Because my initial MANOVA analysis failed to distinguish male and female aspect compositions during summer–autumn at the home range scale, I evaluated selection for aspects using all elk. Elk selectively used aspect classes at the home range scale ($\chi^2_8 = 27.53$, $P < 0.001$). Generally, NE and E aspects were preferred relative to most other aspects and flat areas were relatively underused (Table 5). At the home range scale, males used slope classes disproportionately to their availabilities ($\chi^2_5 = 148.89$, $P < 0.0001$), as did females ($\chi^2_5 = 85.76$, $P < 0.0001$). Males demonstrated strong selection for steep slopes relative to more gentle slopes and flat areas (Table 5). Females also preferred the steepest slope classes relative to other classes, but also demonstrated preference for gentle slopes (10–20%) relative to flat areas and 20–30% slopes (Table 5). Selection for elevation classes at the home range scale was evident for both males ($\chi^2_6 = 92.63$, $P < 0.0001$) and females ($\chi^2_6 = 54.07$, $P < 0.0001$). Males generally preferred elevations of 1,211–1,663 m, with elevations of 1,362–1,512 being most preferred (Table 5). The ranking of preferred elevation classes by females was similar to males, but females tended to prefer slightly lower elevations (Table 5).

At the patch scale during summer–autumn, male elk showed selective use of aspects ($\chi^2_8 = 21.50$, $P < 0.05$), but females used aspect classes proportionate to their availability ($\chi^2_8 = 11.06$, $P = 0.20$). Males generally preferred SE and E aspects and demonstrated little preference for flat areas (Table 6). At the patch scale, selective use of slope classes was apparent for males ($\chi^2_5 = 30.18$, $P < 0.0001$) and females ($\chi^2_5 = 14.84$, $P < 0.05$). Males preferred moderate slopes (20–39%) relative to gentle slopes (< 20%) and steep (≥ 50%) slopes (Table 6). Females preferred areas of gentle slope (10–20%) relative to the steepest slope classes (≥ 40%) (Table 6). Male elk used elevation classes nonselectively ($\chi^2_2 = 1.92$, $P = 0.38$) at the patch scale, but their was some evidence that females used elevation classes selectively ($\chi^2_2 = 4.84$, $P = 0.09$). Females preferred areas below 1,362 m relative to areas above 1,512 m (Table 6).

Winter Habitat Selection. – At the home range scale during winter, males demonstrated little preference for specific cover types ($\chi^2_4 = 5.37$, $P = 0.25$), but females clearly used cover types selectively ($\chi^2_4 = 22.57$, $P < 0.001$). Females preferred oak woodland to all other types and also preferred openings relative to conifer types (Table 7). At the patch scale, females used cover types proportionate to their availabilities ($\chi^2_4 = 2.73$, $P = 0.60$), but males demonstrated selection ($\chi^2_4 = 24.70$, $P < 0.0001$). Males preferred conifer forest types and showed relatively little preference for oak woodland (Table 7).

Male elk used aspects nonrandomly ($\chi^2_7 = 27.68$, $P < 0.001$) during winter at the home range scale. Males preferred NE aspects relative to all aspect classes except flat ground, and W–NW aspects were underused relative to other aspects (Table 8). Female elk also demonstrated nonrandom use ($\chi^2_7 = 28.57$, $P < 0.001$) of aspects at the home range scale. Females showed weaker preference for individual aspect classes, preferring NE aspects to SE, S, and W–NW aspects (Table 8). Male and female elk used slopes similarly at the home range scale during winter, so selection of slopes was considered for all radiocollared elk. Selection for slope classes was evident ($\chi^2_6 = 93.79$, $P < 0.0001$); elk selected home ranges with relatively more area of steep (≥ 50%) and moderately steep slopes (40–49%), relative to areas of lesser slope, than was present in the winter habitat mosaic. Males selectively used elevation classes at the home range scale ($\chi^2_2 = 27.49$, $P < 0.0001$), preferring moderate elevations of 759–908 m relative to lower and higher areas (Table 8). Females also used elevation classes nonrandomly ($\chi^2_2 = 30.28$, $P < 0.0001$), preferring elevations of 759–908 m relative to lower and higher areas and preferring areas below 759 m relative to areas above 908 m.

At the patch scale, female elk use of aspect classes was not distinguishable from random use ($\chi^2_8 = 5.13$, $P = 0.74$), but males used aspects selectively ($\chi^2_8 = 36.87$, $P < 0.0001$). Males preferred NE aspects to all other aspects, except flat ground, and flat areas were preferred relative to S and SW aspects (Table 9). Slope classes were used nonrandomly by both male ($\chi^2_6 = 12.05$, $P = 0.06$) and female elk ($\chi^2_6 = 14.15$, $P < 0.05$) (Table 9). The evidence of selective use of slope classes by males was relatively weak; the most preferred class (20–29%) was used preferentially only relative to 10–19% slopes (Table 9). Females preferred 30–39% slopes relative to slopes of 10–19% and the steepest areas (Table 9). Male elk used elevation classes at the patch scale selectively ($\chi^2_2 = 10.27$, $P < 0.05$). Males preferred elevations of 759–908 m relative to areas below 758 m (Table 9). Female elk used elevation classes selectively ($\chi^2_2 = 6.98$, $P < 0.05$), also preferring 759–908 m elevations, but only relative to areas above 908 m (Table 9).

Roads and True Reserves. – The density of roads within summer–autumn home ranges of elk was related to group ($F = 2.64$, $P = 0.08$). Road densities were lower within the home ranges of mature males than in the home ranges of subadult males ($\bar{x}_{diff} = 0.47$ km/km^2, $P = 0.06$) or adult females ($\bar{x}_{diff} = 0.50$ km/km^2, $P = 0.04$). Road densities within the home ranges of adult female and subadult male elk were similar ($\bar{x}_{diff} = 0.04$ km/km^2, $P = 0.88$). Road densities were also related to elk sex and age class at the winter home range scale ($F = 4.06$, $P = 0.03$). Winter home ranges of female elk had lower road densities than home ranges of adult males ($\bar{x}_{diff} = 0.37$ km/km^2, $P = 0.07$) or subadult males ($\bar{x}_{diff} = 0.58$ km/km^2, $P = 0.009$). Road densities within home ranges of adult and subadult males during winter were similar ($\bar{x}_{diff} = 0.21$ km/km^2, $P = 0.32$).

During summer–autumn, the distance from elk relocations to the nearest road was related to elk sex and age class ($F = 59.73$, $P < 0.0001$). Mature males used areas farther from roads than subadult males ($\bar{x}_{diff} = 693.8$ m, $P < 0.0001$) and adult females ($\bar{x}_{diff} = 827.4$ m, $P < 0.0001$) (Table 10). Although the mean distance from roads for subadult males was greater than the mean distance for adult females, these 2 classes were not statistically distinguishable ($\bar{x}_{diff} = 133.5$ m, $P = 0.12$) (Table 10).

The distance from telemetry relocations to the nearest road was also related to elk sex and age class during winter ($F = 3.08$, $P = 0.05$). Mature males and subadult males were relocated at similar distances from roads ($\bar{x}_{diff}$ = 16.24 m, $P = 0.30$), but females were relocated further from roads than were mature males ($\bar{x}_{diff}$ = 24.99 m, $P = 0.09$) or subadult males ($\bar{x}_{diff}$ = 41.23 m, $P = 0.02$) (Table 10). The mean distance to the nearest road for a sample of random points (n = 3,771) within the summer–autumn study area was 755 m (95% CI = 713–796 m); these points were nearer to roads than summer–autumn relocations of adult male ($\bar{x}_{diff}$ = 1,061.88, $P < 0.0001$), subadult male ($\bar{x}_{diff}$ = 368.03 m, $P < 0.0001$), or adult female elk ($\bar{x}_{diff}$ = 234.50, $P = 0.001$).

The proportion of summer–autumn home ranges consisting of federal wilderness, tribal primitive area, tribal alpine reserves, and administrative withdrawals was related to elk sex and age class ($F = 3.20$, $P = 0.05$). The home ranges of adult male elk contained a higher proportion of these reserved areas ($\bar{x}$ = 0.70) than the home ranges of subadult males ($\bar{x}_{subadult}$ = 0.48, $\bar{x}_{diff}$ = 0.22, $P = 0.05$) or adult females ($\bar{x}_{female}$ = 0.46, $\bar{x}_{diff}$ = 0.24, $P = 0.02$). Reserves occurred in similar proportions in the home ranges of females and subadult males ($P = 0.81$).

DISCUSSION

Seasonal Movements

Elk in the Cascades of southcentral Washington were strongly migratory, similar to other elk populations inhabiting mountainous landscapes (White 1981, Hershey and Leege 1982, Myers and Lyndaker 1999). Migration distances were variable, but I found little evidence of systematic variation among sex and age classes of elk. Elsewhere, male elk wintered at higher elevations and in deeper snow than females (Leege and Hickey 1977, Unsworth et al. 1998), supporting the generalization that males migrate to winter range later than females and only when deep snow forces them to abandon summer ranges (Murie 1951, Adams 1982). However, concurrent telemetry data from male and female elk needed to test hypotheses about migration timing have not been published.

I found that adult males migrated from summer home ranges to winter range before other elk, contrary to previous speculation (Adams 1982). The reasons for this were not clear, but the pattern was consistent across years and individuals. I found little evidence that heavy snowfall prompted migration by adult males. In fact, during several mild winters, the timing of autumn migrations of most instrumented elk did not coincide with heavy snowfall in elk summer home ranges. Heavy snowfall did motivate elk to leave high elevation summer–autumn ranges, but in the absence of heavy snow, elk still moved to winter range by late Nov. Following rut, the fat stores of mature males are depleted (Flook 1970), possibly increasing their vulnerability to predation (Miquelle et al. 1992). Emigrating from areas of high elk density may reflect a strategy whereby rut–depleted adult males avoid detection by predators. Alternatively, perhaps rut–depleted males cannot afford the risk of delaying migration until heavy snowfall because of the energetic costs of moving long distances in deep snow or their vulnerability to predators in deep snow. Because of the lack of telemetry data on mature males elsewhere, it is unclear whether the behavior I documented is peculiar to the study population or the generalization that adult males migrate late is simplistic. When critically evaluated, other generalizations regarding the proximate causes of migration in temperate ungulates have proven to be suspect (Garrott et al. 1987, McCorquodale 1999).

My analytic strategy for studying habitat use and selection utilized 90% AK home range estimates as sampling frames, but because of mortalities, home ranges for some individuals were estimated from relatively small relocation samples (n <30). Seaman et al. (1999) suggested AK home range sizes estimated from <30 relocations are often negatively biased. However, I did not detect a relationship between home range size and relocation number in my dataset. Moreover, I found 90% AK estimates from elk with >30 and elk with <20 relocations were similar for both summer–autumn ($t_{58} = 1.07$, $P = 0.29$) and winter ($t_{33} = 0.11$, $P = 0.91$), suggesting any negative bias in estimating home ranges from elk with <30 relocations was minimal. I did not reject the null hypothesis that seasonal home range size was independent of class of elk.

I documented strong fidelity to seasonal ranges among instrumented elk. Use of seasonal ranges by female elk was highly traditional in other studies, (Hershey and Leege 1982, Irwin and Peek 1983, Edge et al. 1985), but limited data for males suggested juveniles (≤ 2.5 yr) were prone to dispersal (Hershey and Leege 1982, Hurley and Sargeant 1991). I found strong fidelity to seasonal home ranges among ≥ 3.5 yr–old males, which suggests that males establish traditional ranges similar to females. However, based on findings elsewhere, this may occur after dispersal as juveniles. This contrasts with females, which tend to inherit matrilineal fidelity to natal ranges (Clutton–Brock et al. 1982).

Habitat Use and Selection

Summer–autumn.– I found little evidence that habitat use compositions of adult and subadult males differed at either home range or patch scales, suggesting they located and used home ranges similarly relative to geomorphic and biotic features of the landscape. I instrumented only 1 yearling male and only a few 2–yr–olds, so I was unable to test for differences in habitat use between juveniles and older males. In contrast, use compositions of instrumented males and females were different. Evidence for sexual differences in the use of cover types at both scales existed, but it was relatively weak; male and female home range and patch compositions differed most relative to use of topographic features.

The propensity for summer–autumn home ranges of males to be in higher, steeper areas with somewhat more mature closed canopy forest than the home ranges of females could have alternate explanations. Males could actively select such areas from among available environmental settings, perhaps because of enhanced security (Unsworth et al. 1993) or because of preferred thermal environments (Zahn 1985). Alternatively, the patterns observed could be an artifact of differential vulnerability of males across the landscape. Because I routinely placed radiocollars on males that had already survived several hunting seasons, my sample may have been biased toward males that spent summer–autumn in high security environments. Young males that used environments similarly to females may have had a reduced probability of surviving to be captured and instrumented as older subadults or adults.

Males used cover types nonrandomly at the home range and patch scales during summer–autumn, generally preferring mature conifer forest with at least 40%

canopy closure and openings/shrubfields. Although female elk selected cover types similarly to males at the home range scale, they were not selective at the patch scale.

Recent experimental work with tame female elk failed to detect any advantages to body condition associated with use of forest cover during summer (Cook et al. 1998), but free–ranging radiocollared elk in my study clearly selected mature semiclosed and closed canopy conifer stands. This is consistent with results from other studies of free–ranging elk (Hershey and Leege 1982, Unsworth et al. 1998, Myers et al. 1999), and suggests older, closed canopy stands are preferred by elk over a broad geographic scale, at least where they are hunted. In my study, males particularly displayed selection for older forest conditions. This could reflect active selection or simply enhanced survival of males using large areas of mature closed forest (Unsworth et al. 1993). However, preference for older forest conditions by female elk suggests that all elk actually preferred landscape components supporting mature conifer stands. Despite evidence that use of cover by elk does not convey detectable energetic benefits (Cook et al. 1998), the propensity of wild elk to use mature conifer stands, suggests there may be strong, albeit undefined, benefits to use of cover on summer range.

Winter. – Adult and subadult male elk used habitat features similarly during winter, regardless of scale. However, considerable differences were apparent in habitat use by males and females. Sexual differences in use of cover types were similar at both scales; males used timbered habitats more and openings and oak woodland less than females.

During winter, males nonselectively located their home ranges relative to available cover types but selected conifer stands within home ranges. In contrast, females principally exercised selection at the home range scale, selecting areas with more oak woodland and openings than was characteristic of the winter landscape. Females used cover types nonselectively within home ranges. Collectively, elk selected steeper portions of the landscape for their winter home ranges, but within home ranges, females selected for relatively steep areas and males preferred gentler slopes.

Across the landscape, gentle slopes were characteristic of higher elevation, forested plateaus where deep snowpacks accumulated. Areas of greater relief preferred by elk were associated with lower elevation canyons and a diversity of cover types near the forest–rangeland ecotone. These areas typically supported densely forested northerly and easterly aspects and grass–dominated south aspects, providing a mix of cover and forage areas. Oak woodland was also predominantly found associated with steep lower elevation canyons. Males tended to range slightly higher than females, preferring forested draws and plateaus (Unsworth et al. 1998), whereas females apparently sought winter home range areas with less snow, typically lower, steeper country with windswept openings and extensive oak woodland.

Cook et al. (1998) evaluated condition dynamics of tame female elk kept in enclosures with varying amounts of forest cover during winter and found body condition declined more rapidly among animals in enclosures with extensive cover. Despite this experimental finding, I found male elk demonstrated considerable affinity for forest cover within their winter home ranges (see also Unsworth et al.

1998, Myers et al. 1999). Extensive use of cover by male elk suggested that males enhanced their fitness by using cover, although the adaptiveness of cover use may not have been related to thermal energetics. Other advantages to the use of cover, such as enhanced security or reduced movement costs relative to open areas with deep snow may be very important, especially if the inference of Cook et al. (1998) is applicable to free–ranging male elk.

Disturbance factors. – The negative influence of open roads on elk habitat use has been well documented (Perry and Overly 1976, Lyon 1979a, 1979b, 1998, Edge 1982, Cole et al. 1997). However, differences in aversion to roads among sex and age classes of elk have rarely been investigated (Marcum and Edge 1991). The distribution of summer–autumn relocations suggested all elk avoided roads, but there was compelling evidence that adult males were particularly unlikely to use areas near roads. This could reflect either active avoidance, or simply that males that used areas far from roads were most likely to survive to adulthood (Leptich and Zager 1991, Unsworth et al. 1993). Regardless, the results imply that managers should provide some relatively unroaded habitat to maintain high use by adult male elk where they are hunted.

Although elk were located relatively close to roads during winter, most roads were effectively closed by snowfall during Dec–Mar, limiting human activity on winter range. I suspect that in winter, elk use relative to distances from roads was simply an artifact of the likelihood of roads being in preferred habitats. Females probably appeared to avoid roads more than males because they preferred relatively steep slopes where roads were less likely to be relative to flatter areas preferred by males.

It is unlikely that elk select cover types, topographic features, and areas of relative disturbance independently. For example, selection for older forest could result from a preference for the structure of such stands or simply from selection of nonroaded environments where unlogged forest is more likely to be found. Similarly, selection for topographic settings and cover types may represent the same decision process for an elk. Compositional data are by definition proportional data that sum to 1 (Aitchison 1986, Aebischer et al. 1993a). Compositional analysis provides a statistically robust approach to identifying the relative importance of components within habitat compositions, but the data structure required yields inference about compositions independently. This sometimes makes interpretations difficult, but this difficulty is not unique to compositional analysis. However, one of the greatest strengths of compositional analysis is that it places inference about habitat component preferences in a relativistic rather than absolute context (i.e., component preferences are rated relative to other component preferences) (Aebischer et al. 1993).

The relative similarity of habitat use by different age classes of male elk that I documented is consistent with the findings of Unsworth et al. (1998) and Hurley and Sargeant (1991), although their data came primarily from young males. It is possible that differences in habitat use between mature males and younger males would be detected at different temporal scales (e.g., breeding season) or between males of much different stature (e.g., mature males and yearlings).

Divergent habitat use between males and females has previously been documented for elk (McCorquodale et al. 1986, Unsworth et al. 1998) and red deer (*C. e. elaphus*) (Watson and Staines 1978, Clutton–Brock et al. 1982). Female ungulates may maximize their fitness by selecting habitats that enhance offspring survival whereas males compromise security to maximize nutrient intake and enhance fighting success (Geist 1982, Miquelle et al. 1992). Landscape scale GIS data did not provide the resolution to rigorously test for differences in the relative availability or quality of forage in areas used by males and females. However, based on the generalization that forage biomass is higher in open habitats, females in this study appeared to select superior foraging settings in both seasons, whereas males appeared to select areas that offered higher security during summer–autumn, at least relative to human predation (Unsworth et al. 1993).

SUMMARY AND MANAGEMENT IMPLICATIONS

Sexual differences in habitat use exist for Rocky Mountain elk in the Washington Cascades. Age class–specific differences existed for males, but the evidence was not completely conclusive, because of scale dependence of the analysis. Male and female elk clearly used the landscape differently. Use of cover types was relatively similar during summer–autumn, but the sexes used different cover types during winter. Males and females differed substantially in their use of topographic features, especially during summer–autumn. Relatively disturbance–free environments with a component of mature closed-canopy forest is either preferred by male elk or appears preferred because of enhanced survival of males in these settings (Unsworth et al. 1993). Oak woodland and high relief terrain, especially in combination, appeared to have substantial value to female elk and their young during winter. Despite controversy regarding the value of winter cover to elk (Cook et al. 1998), male elk appeared to prefer uplands with considerable conifer cover, suggesting that the maintenance of such settings should continue to be a management priority for elk winter range in the Cascades.

ACKNOWLEDGMENTS

This research was supported by a grant from the U. S. Department of Interior, Bureau of Indian Affairs. G. Rankel and W. P. Bradley helped obtain funding. S. Tolle skillfully piloted helicopters used for darting elk, and C. Dyer piloted fixed–wing aircraft used in telemetry flights. I am indebted to D. Blodgett, Jr. who assisted with field work. Numerous individuals helped trap elk, including A. James, P. Olney, T. Heemsah, D. Sockzehigh, and J. Feen. R. Wiseman, H. Fraser, and M. Rowe helped with GIS analyses. I thank the staff of the Naches Ranger District, Wenatchee National Forest and Boise Cascade Corp. for providing GIS data. I thank J. P. Carroll and G. A. Sargeant for advice on compositional analysis. I appreciate the reviews of C. L. Marcum, J. W. Thomas, L. J. Lyon, D. H. Pletscher, and I. J. Ball on an earlier draft.

LITERATURE CITED

Adams, A. W. 1982. Migration. Pages 301–321 in J. W. Thomas, and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Aebischer, N. J., and P. A. Robertson. 1992. Practical aspects of compositional analysis as applied to pheasant habitat utilization. Pages 285–293 *in* I. G. Priede, and S. M. Swift, editors. Wildlife telemetry: remote monitoring and tracking of animals. Ellis Horwood Limited, Chichester, United Kingdom.

______, ______, and R. E. Kenward. 1993a. Compositional analysis of habitat use from animal radio–tracking data. Ecology 74:1313–1325.

______, V. Marcstrom, R. E. Kenward, and M. Karlbom. 1993b. Survival and habitat utilisation: a case for compositional analysis. Pages 343–353 *in* J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird populations. Birkhauser Verlag, Basel, Switzerland.

Aitchison, J. 1986. The statistical analysis of compositional data. Chapman and Hall, London, United Kingdom.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs No. 134.

Burcham, M. G., C. L. Marcum, L. J. Lyon, K. T. Weber, and W. D. Edge. 1998. Final report: Chamberlain Creek elk studies 1977–1983 and 1993–1996. School of Forestry, University of Montana, Missoula, Montana, USA.

Carmer, S. G., and M. R. Swanson. 1973. An evaluation of ten pairwise multiple comparison procedures by Monte Carlo methods. Journal of the American Statistical Association 68:66–74.

Clutton–Brock, T. H., F. E. Guiness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.

Cole, E. K., M. D. Pope, and R. G. Anthony. 1997. Effects of road management on movement and survival of Roosevelt elk. Journal of Wildlife Management 61:1115–1126.

Cook, J. G., L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. Wildlife Monographs 141.

Edge, W. D. 1982. Distribution, habitat use and movements of elk in relation to roads and human disturbances in western Montana. Thesis. University of Montana, Missoula, Montana, USA.

______, C. L. Marcum, and S. L. Olson. 1985. Effects of logging activities on home–range fidelity of elk. Journal of Wildlife Management 49:741–744.

Flook, D. R. 1970. A study of sex differential in the survival of wapiti. Report Series, No. 11, Canadian Wildlife Service, Ottawa, Ontario, Canada.

Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management 51:634–643.

Geist, V. 1982. Adaptive behavioral strategies. Pages 219–277 *in* J. W. Thomas, and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Gibson, R. M., and F. E. Guiness. 1980a. Differential reproduction among red deer (*Cervus elaphus*) stags on Rhum. Journal of Animal Ecology 49:199–208.

______, _____. 1980b. Behavioral factors affecting male reproductive success in red deer (*Cervus elaphus*). Animal Behavior 28:1163–1174.

Gilmer, D. S., L. M. Cowardin, R. L. Duval, L. M. Mechlin, C. W. Shaiffer, and V. B. Kuechle. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U. S. Fish and Wildlife Service Resource Publication 140.

Guiness, F. E., S. D. Albon, and T. H. Clutton–Brock. 1978. Factors affecting reproduction in red deer (*Cervus elaphus*) hinds on Rhum. Journal of Reproductive Fertility 54:325–334.

Hershey, T. J., and T. A. Leege. 1982. Elk movements and habitat use on a managed forest in north–central Idaho. Wildlife Bulletin 10, Idaho Dept. Fish and Game, Boise, Idaho, USA.

Hurley, M. A., and G. A. Sargeant. 1991. Effects of hunting and land management on elk habitat use, movement patterns, and mortality in western Montana. Pages 94–98 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA.

Irwin, L. L. 1978. Relationships between intensive timber culture, big game habitats, and elk habitat use patterns in northern Idaho. Dissertation, University of Idaho, Moscow, Idaho, USA.

______, and J. M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. Journal of Wildlife Management 47:664–672.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

______. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763–772.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1996. CALHOME: a program for estimating animal home ranges. Wildlife Society Bulletin 24:342–344.

Leege, T. A., and W. O. Hickey. 1977. Elk–snow–habitat relationships in the Pete King drainage, Idaho. Wildlife Bulletin 6, Idaho Fish and Game, Boise, Idaho, USA.

Leptich, D. J., and P. Zager. 1991. Road access management effects on elk mortality and population dynamics. Pages 126–131 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA

______, S. G. Hayes, and P. Zager. 1995a. Bull elk habitat use. Project W–160–R–22, Study I. Idaho Fish and Game, Boise, Idaho, USA.

Lyon, L. J. 1979a. Habitat effectiveness for elk as influenced by roads and cover. Journal of Forestry 77:658–660.

______. 1979b. Influences of logging and weather on elk distribution in western Montana. Research Paper INT–236, U. S. Forest Service, Ogden, Utah, USA.

______. 1998. Elk habitat selection at a site specific scale. Pages 50–72 *in* Final report: Chamberlain Creek elk studies 1977–1983 and 1993–1996. School of Forestry, University of Montana, Missoula, Montana, USA.

Main, M. B., and B. E. Coblentz. 1996. Sexual segregation in Rocky Mountain mule deer. Journal of Wildlife Management 60:497–507.

Marcum, C. L. 1975. Summer–fall habitat selection and use by a western Montana elk herd. Dissertation, University of Montana, Missoula, Montana, USA.

______, and W. D. Edge. 1991. Sexual differences in distribution of elk relative to roads and logged areas in western Montana. Pages 142–148 *in* A. G.

Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA.

McCorquodale, S. M., K. J. Raedeke, and R. D. Taber. 1986. Elk habitat use patterns in the shrub–steppe of Washington. Journal of Wildlife Management 50:664–669.

______, R. H. Leach, G. M. King, and K. R. Bevis. 1997. The Yakama Indian Reservation: integrating Native American values into commercial forestry. Journal of Forestry 95(11):15–18.

______. 1999. Movements, survival, and mortality of black–tailed deer in the Klickitat Basin of Washington. Journal of Wildlife Management 63: 861–871.

McNay, R. S., J. A. Morgan, and F. L. Bunnell. 1994. Characterizing independence of observations in movements of Columbian black–tailed deer. Journal of Wildlife Management 58:422–429.

Michener, G. R. 1979. Spatial relationships and social organization of adult Richardson's ground squirrels. Canadian Journal of Zoology 57:125–139.

Mielke, P. W., K. J. Berry, P. J. Brockwell, and J. S. Williams. 1981. A class of nonparametric tests based on multiresponse permutation procedures. Biometrica 68:720–724.

Miquelle, D. G., J. M. Peek, and V. Van Ballenbergh. 1992. Sexual segregation in Alaskan moose. Wildlife Monographs No. 122. 57 pp.

Murie, O. 1951. The elk of North America. Stackpole Books, Harrisburg, Pennsylvania, USA.

Myers. W. L., and B. R. Lyndaker. 1999. Elk home ranges, movements, and herd boundaries. Pages 25–42 *in* W. L. Myers, editor. An assessment of elk population trends and habitat use with special reference to agricultural damage zones in the northern Blue Mountains of Washington. Report W–96–R, Washington Dept. Fish and Wildlife, Olympia, Washington, USA.

______, _____, and B. Cosentino. 1999. Elk habitat use. Pages 73–102 *in* W. L. Myers, editor. An assessment of elk population trends and habitat use with special reference to agricultural damage zones in the northern Blue Mountains of Washington. Report W–96–R, Washington Dept. Fish and Wildlife, Olympia, Washington, USA.

National Oceanic and Atmospheric Administration. 1994. Local climatological data: annual summary with comparative data. National Oceanic and Atmospheric Administration, Washington, D. C., USA.

Perry, C., and R. Overly. 1976. Impact of roads on big game distribution in portions of the Blue Mountains of Washington. Pages 62–68 *in* S. R. Hieb, editor. Proceedings of the elk–logging–roads symposium. University of Idaho, Moscow, Idaho, USA.

Quimby, D. C., and J. E. Gaab. 1957. Mandibular dentition as an age indicator in Rocky Mountain elk. Journal of Wildlife Management 21:435–451.

Schoen, J. W. 1977. The ecological distribution and biology of wapiti, *Cervus elaphus nelsoni*, in the Cedar River watershed. Dissertation, University of Washington, Seattle, Washington, USA.

Seaman, E. D., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Slauson, W. L., B. S. Cade, and J. D. Richards. 1991. User manual for BLOSSOM statistical software. Midcontinent Ecological Science Center, Fort Collins, Colorado, USA.

SPSS, Inc. 1998. SPSS Base 8.0. SPSS, Inc., Chicago, Illinois, USA.

Thompson, M. J., R. E. Henderson, T. O. Lemke, and B. A. Sterling. 1989. Evaluation of a collapsible clover trap for elk. Wildlife Society Bulletin 17:287–290.

Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of northcentral Idaho. Journal of Wildlife Management 57:495–502.

______, ______, E. O. Garton, and B. R. Butterfield. 1998. Elk habitat selection on the Clearwater National Forest, Idaho. Journal of Wildlife Management 62:1255–1263.

Watson, A., and B. W. Staines. 1978. Differences in the quality of wintering areas used by male and female red deer (*Cervus elaphus*) in Aberdeenshire. Journal of Zoology 186:544–550.

White, G. C. 1981. Biotelemetry studies on elk. Report LA–8529–NERP, Los Alamos Scientific Laboratory, Los Alamos, New Mexico, USA.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home–range studies. Ecology 70:164–168.

Zahn, H. M. 1985. Use of thermal cover by elk (*Cervus elaphus*) on a western Washington summer range. Dissertation, University of Washington, Seattle, Washington, USA.

Table 1. Seasonal home range estimates (ha) for radiocollared elk in the Cascade Range of southcentral Washington, 1992–99.

Season Group	n	Number[c] of relocations	90% ADK[a] $\bar{x}$	90% ADK[a] *SE*	90% MCP[b] $\bar{x}$	90% MCP[b] *SE*
Summer–Autumn						
Adult males	22	30.0	8173.8	1581.5	4600.7	963.8
Subadult males	23	23.4	11212.2	1644.9	5109.0	802.2
All males	45	26.6	9726.8	1152.2	4860.5	618.6
Adult females	26	26.6	7037.6	1156.2	4013.6	682.6
Winter						
Adult males	14	21.9	2656.4	432.3	1433.9	285.8
Subadult males	11	16.6	3455.9	1139.0	1807.8	757.4
All males	25	19.5	3008.2	1598.4	1598.4	362.5
Adult females	15	14.3	4929.2	1012.9	1307.0	223.4

[a] 90% Adaptive kernel estimates.

[b] 90% Minimum convex polygon estimates.

[c] Mean number of relocations per radiocollared elk.

Table 2. MANOVA results for contrasts of summer–autumn habitat compositions of radiocollared elk in the Cascades of southcentral Washington, 1992–99.

Scale Contrast	n	Composition	Wilk's Λ	Exact F *P*–value
Home Range				
Ad vs. subad males	44	cover type	0.822	0.27
Ad vs. subad males	45	aspect	0.823	0.50
Ad vs. subad males	45	slope	0.949	0.84
Ad vs. subad males	45	elevation	0.786	0.14
Males vs. females	69	cover type	0.841	0.09
Males vs. females	70	aspect	0.833	0.17
Males vs. females	70	slope	0.825	0.03
Males vs. females	70	elevation	0.813	0.04
Patch				
Ad vs. subad males	44	cover type	0.813	0.23
Ad vs. subad males	45	aspect	0.718	0.12
Ad vs. subad males	45	slope	0.951	0.84
Ad vs. subad males	45	elevation	0.922	0.18
Males vs. females	69	cover type	0.818	0.05
Males vs. females	70	aspect	0.763	0.03
Males vs. females	70	slope	0.733	0.001
Males vs. females	70	elevation	0.923	0.07

Table 3. MANOVA results for group contrasts of winter habitat compositions of radiocollared elk in the Cascades of southcentral Washington, 1992–99.

Scale Contrast	n	Composition	Wilk's Λ	Exact F *P*–value
Home Range				
Ad vs. subad males	25	cover type	0.799	0.32
Ad vs. subad males	25	aspect	0.713	0.61
Ad vs. subad males	25	slope	0.649	0.20
Ad vs. subad males	25	elevation	0.950	0.57
Males vs. females	40	cover type	0.760	0.04
Males vs. females	40	aspect	0.641	0.06
Males vs. females	40	slope	0.767	0.16
Males vs. females	40	elevation	0.856	0.06
Patch				
Ad vs. subad males	25	cover type	0.889	0.65
Ad vs. subad males	25	aspect	0.678	0.51
Ad vs. subad males	25	slope	0.837	0.74
Ad vs. subad males	25	elevation	0.990	0.89
Males vs. females	40	cover type	0.516	<0.0001
Males vs. females	40	aspect	0.468	0.001
Males vs. females	40	slope	0.686	0.04
Males vs. females	40	elevation	0.848	0.05

Table 4. Preference rankings (0 = least preferred) for cover types during summer-autumn by radiocollared elk in the Cascades of southcentral Washington, 1992-99.

Scale Cover type	Males	Females
Home range		
Openings	4 A[a]JKLM	4 AHIJ
Young open forest	0 BFJ	3 B
Young closed forest	2 CGK	0 CGH
Mature open forest	3 DHL	1 DI
Mature semiclosed forest	6 ABCDE	6 ABCDEF
Mature closed forest	5 FGHI	5 EG
Other	1 EIM	2 FJ
Patch		
Openings	3 AKLM	
Young open forest	1 BEHK	
Young closed forest	2 CFIL	
Mature open forest	5 EFG	
Mature semiclosed forest	6 ABCD	
Mature closed forest	4 HIJ	
Other	0 DGJM	

---

[a] Cover types that share a common capital letter within a column have significantly different preference rankings ($P \leq 0.10$).

Table 5. Preference rankings (0 = least preferred) at the home range scale for topographic features during summer–autumn by radiocollared elk in the Cascades of southcentral Washington, 1992-99.

Composition	Males	Females	All elk
Aspect			
Flat			0 A*EGHIJ
N			5 BH
NE			8 ABCD
E			7 EF
SE			1 CF
S			2 D
SW			6 G
W			4 I
NW			3 J
Slope			
0–9%	0 AFJMO	0 AFJ	
10–19%	1 BGKNO	3 BGJK	
20–29%	2 CHLMN	1 CHK	
30–39%	3 DIJKL	2 DI	
40–49%	4 EFGHI	4 EFGHI	
≥50%	5 ABCDE	5 ABCDE	
Elevation			
<908m	0 AFJNPS	0 AEHKNO	
909–1059	1 BGKORS	1 BFILO	
1060–1210	3 CHLNO	3 CKLM	
1211–1361	5 DFGHI	6 ABCD	
1362–1512	6 ABCDE	5 EFG	
1513–1663	4 JKLM	4 HIJ	

Table 5. (continued)

Composition	Males	Females	All elk
Elevation			
≥1664 m	2 EIMPR	2 DGJMN	

---

[a] Components that share a common capital letter within a column have significantly different preference rankings ($P \leq 0.10$).

Table 6. Preference rankings (0 = least preferred) at the patch scale for topographic features during summer–autumn by radiocollared elk in the Cascades of southcentral Washington, 1992-99.

Composition	Males	Females
Aspect		
Flat	0 AFKMPRST	
N	2 BGNS	
NE	5 MNO	
E	7 FGHIJ	
SE	8 ABCDE	
S	6 KL	
SW	4 CHP	
W	3 DIR	
NW	1 EJLOT	
Slope		
0–9%	1 ADGI	3 E
10–19%	2 BEIJ	5 AB
20–29%	4 DEF	4 CD
30–39%	5 ABC	2 FG
40–49%	3 GH	1 ACFH
≥50%	0 CFHIJ	0 BDEGH
Elevation		
<1362 m		2 A
1362–1512		1
≥1513		0 A

---

[a] Components that share a common capital letter within a column have significantly different preference rankings ($P \leq 0.10$).

Table 7. Preference rankings (0 = least preferred) for cover types during winter by radiocollared elk in the foothills of the Cascades of southcentral Washington, 1992-99.

Scale		
Cover type	Males	Females
Home range		
Openings		3 A[a]EFG
Oak woodland		4 ABCD
Open conifer forest		1 BEH
Closed conifer forest		2 CFH
Other		0 DG
Patch		
Openings	2 ADGH	
Oak woodland	1 BEG	
Open conifer forest	3 DEF	
Closed conifer forest	4 ABC	
Other	0 CFH	

[a] Cover types that share a common capital letter within a column have significantly different preference rankings ($P \leq 0.10$).

Table 8. Preference rankings (0 = least preferred) at the home range scale for topographic features during winter by radiocollared elk on the Toppenish Creek winter range of southcentral Washington, 1992-99.

Composition	Males	Females	All elk
Aspect			
Flat	6 GH	1	
N	1 AGILNR	3	
NE	7 ABCDEF	7 ABC	
E	5 BIJK	6 D	
SE	4 CLM	5 AE	
S	3 DNO	2 BDE	
SW	2 EJP	4	
W–NW	0 FHKMOPR	0 C	
Slope			
0–9%			0 AFKOS
10–19%			1 BGLPT
20–29%			2 CHMRST
30–39%			3 DINOPR
40–49%			4 EJKLMN
50-59%			6 ABCDE
≥60%			5 FGHIJ
Elevation			
<758 m	0 A	1 AC	
759–908	2 AB	2 AB	
≥909 m	1 B	0 BC	

---

[a] Components that share a common capital letter within a column have significantly different preference rankings ($P \leq 0.10$).

Table 9. Preference rankings (0 = least preferred) at the patch scale for topographic features during winter by radiocollared elk on the Toppenish Creek winter range of southcentral Washington, 1992-99.

Composition	Males	Females
Aspect		
Flat	7 HI	
N	6 AJ	
NE	8 ABCDEFG	
E	5 BK	
SE	4 CL	
S	0 DHJKL	
SW	1 EI	
W	2 F	
NW	3 G	
Slope		
0–9%	5	2
10–19%	4 A	1 A
20–29%	6 A	3
30–39%	3	6 AB
40–49%	2	5 C
50-59%	1	4 D
≥60%	0	0 BCD
Elevation		
<758 m	0 A	1
759–908	2 A	2 A
≥909	1	0 A

---

[a] Components that share a common capital letter within a column have significantly different preference rankings ($P \leq 0.10$).

Table 10. Distances (m) from telemetry relocations of elk to the nearest road, 1992–99.

Season Group	n^a	$\bar{x}$	*SE*
Summer–autumn			
Adult males	659	1816.84 AB[b]	69.02
Subadult males	537	1123.00 A	55.65
Adult females	654	989.47 B	48.00
Winter			
Adult males	326	163.57 A	9.43
Subadult males	175	147.33 B	10.94
Adult females	215	188.55 AB	12.14

[a] Number of relocations within the group.

[b] Means within a season that share a common capital letter are significantly different ($P < 0.10$).

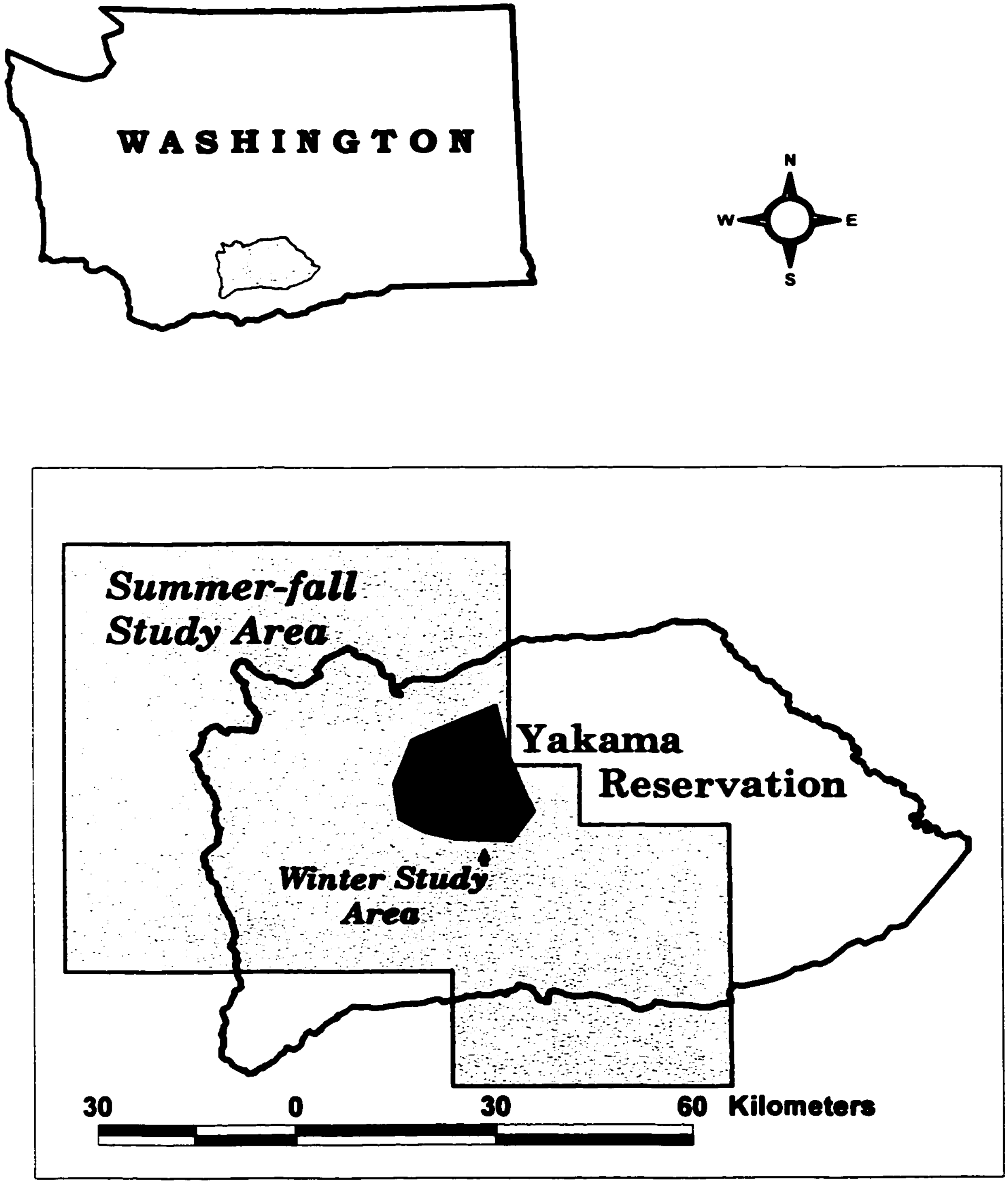

Figure 1. Location of the study area and Yakama Reservation

CHAPTER 2: SURVIVAL AND HARVEST VULNERABILITY OF ELK IN THE CASCADE RANGE OF WASHINGTON

Abstract: I studied survival and vulnerability to hunting mortality among adult male, subadult male, and adult female elk (*Cervus elaphus*) in the Cascade Range of southcentral Washington during 1992–99 using 81 radiocollared elk. Data represented 95 male elk years and 56 female years. A group–dependent model with different annual survival parameters for all males ($MLE = 0.61$, 95% $CI = 0.50$–0.70) and for females ($MLE = 0.82$, 95% $CI = 0.70$–0.90) fit the data better than a model assuming equal survival for males and females and as well as more complex models. Thirty–nine (48%) elk died during the study. All deaths among subadult (≤ 4 yr) males and all but 1 death among females were caused by hunting. However, 11 of 17 (64.7%) deaths among adult (≥ 5 yr) males were hunting related, and the proximate cause of 5 deaths (29.4%) was winter starvation. I used multivariate logistic regression modeling to identify environmental factors associated with the likelihood that elk were harvested on summer–autumn home ranges, where most hunting mortality occurred. Using data from all elk, a model predicting the likelihood of hunting mortality based on road density, median slope class, and aspect diversity within summer–autumn home ranges fit the data better than alternative models and correctly classified 75.4% of home ranges. Using male data only, risk of harvest on summer–autumn home ranges was best explained, under parsimony criteria, by a model based on aspect diversity that correctly classified 68.3% of home ranges. Road

variables associated with home ranges were not useful for predicting harvest risks among male elk because most adult males occupied areas of low road density. I also used logistic regression to identify differences between 1–km radius circles centered on live elk relocations during autumn and elk kill sites. Live elk relocations were associated with lower road densities, were farther from roads, had relatively more mature conifer cover and unroaded reserved areas, and were higher than were kill sites. A multivariate model based on road density, the proportion of resource reserves (e.g., Watershed and Late Successional Reserves), and the relative availability of mature, closed canopy forest was useful for distinguishing live elk relocations from kill sites and correctly classified 76.0% of circles.

INTRODUCTION

During recent decades, the management of elk (*Cervus elaphus*) has increasingly focused on mitigating the impacts of decreased habitat security resulting from road–building and logging (Thomas 1991). Moreover, the management of vulnerability to harvest, particularly of adult males, and the maintenance of desirable sex and age ratios in hunted populations may be the most challenging issue faced by elk managers (Mackie 1991).

The behavioral ecology of elk makes managing their vulnerability to harvest problematic. For example, reproductive success in males is predicated on a strategy of being conspicuous and aggressive, and occupying the home ranges of large numbers of females (Gibson and Guiness 1980, Clutton–Brock et al. 1982, Bowyer and Kitchen 1987). Such behavior makes adult males inherently vulnerable to detection and harvest, at least during periods when they are reproductively active. Thus, behavior that enhances reproductive success in males tends to concomitantly reduce their survival in populations where elk are hunted during or near the rut.

However, several researchers have shown that environmental factors can substantially influence the likelihood that elk are killed during hunting seasons (Leptich and Zager 1991, Unsworth et al. 1993, Weber 1997). Some of these factors can be manipulated by managers, whereas others are intrinsic geophysical features of landscapes. The effects of open road densities on elk survival are intuitive; more roads means easier access to elk habitat, higher hunter densities, and lower probabilities of elk surviving hunting seasons (Vales et al. 1991, Unsworth et al. 1993, Lyon and Burcham 1998). Other environmental factors that may affect the relative vulnerability of elk to harvest have generally not been well quantified. Data specific to habitat–mediated vulnerability of mature male elk are particularly scarce (Unsworth et al. 1993, Hurley and Sargeant 1991).

I studied the relationship between environmental features and the vulnerability of elk, particularly mature males, to hunting mortality in the southcentral Washington Cascades during 1992–99. This study area presented an excellent context for examining the relationship between environmental features and elk vulnerability to harvest. Within an ownership mosaic consisting of national forest, tribal reservation, and corporate forest, elk habitat qualitatively varied from roaded and intensively managed tracts to large unroaded areas administratively designated as federal wilderness, tribal primitive area, or resource reserve (e.g., tribal Watershed Reserves, federal Late Successional Reserves).

I tested several null hypotheses using 3 age/sex class samples of radiocollared elk: (1) mature males (≥ 5 yr), (2) subadult and young adult males (≤ 4 yr), and (3) adult females (≥ 1 yr). I selected age 5 as the criteria for mature males based on the age–specific distributions of body, antler, and testes mass reported in Flook (1970). Hypothesis tests ranged from simple comparisons of mortality risks among elk age and sex classes, to more complex inquiries about how environmental features and landscape use by elk affects the vulnerability of elk to hunting mortality. The specific hypotheses I tested were: (Ho_1) survival probabilities among elk were independent of sex and age–class, (Ho_2) the vulnerability of elk to hunting mortality was independent of environmental features characterizing their home ranges, and (Ho_3) environmental features surrounding elk hunting mortality sites were indistinguishable from features surrounding live elk relocations. Modeling survival as a function of environmental characteristics provided a useful approach for hypothesis testing in this study. Sex and age class–specific habitat use and movement parameters for elk in this study, independent of a survival context, are described elsewhere (McCorquodale *in review*).

STUDY AREA

Winter

The winter study area encompassed approximately 57,000 ha of the Toppenish Creek watershed along the eastern slopes of the Washington Cascades (46°20', 121°00') (Fig. 1). Elevations ranged from 490 to 1,259 m.

Topographically, Toppenish Creek consisted of a series of steep east–west canyons and adjacent uplands.

An interspersion of large openings, Oregon white oak (*Quercus garryani*) stands, and large areas of conifer forest characterized the dominant cover types. Conifer stands consisted mostly of ponderosa pine (*Pinus ponderosa*) on xeric sites and mixed associations of ponderosa pine, Douglas fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*) on more mesic sites.

Annual precipitation in the winter study area historically averaged about 64 cm, with most falling during Nov–Apr (National Oceanic and Atmospheric Administration 1994), mainly as snow. Mean annual snowfall measured at nearby Yakima, Washington, 1964–94, was 61.2 cm (National Oceanic and Atmospheric Administration 1994). During 1992–99, snowfall was average or below average during each winter except 1992–93 and 1995–96 when snowfall was much above average.

Summer–autumn

The summer–autumn study area consisted of approximately 550,000 ha, which encompassed portions of the Yakima, Klickitat, and Cispus River watersheds (Fig. 1). Approximately half of the summer study area was within the Yakama Reservation; the remainder consisted of federal, state, and private lands west and north of the reservation. Elevations ranged from 3,742 m at the crest of Mt. Adams, a dormant Cascade volcano, to approximately 1,200 m on the Lost Horse Plateau of

Toppenish Creek. The summer study area included rugged, precipitous terrain near the Cascade crest and gently rolling plateaus east and west of the crest.

The summer study area was heavily forested. Below 1,360 m, stands were usually dominated by ponderosa pine or mixtures of pine, Douglas fir, grand fir, western larch (*Larix occidentalis*), and western hemlock (*Tsuga heterophylla*). Higher elevation stands and wet sites were typically dominated by Douglas fir, subalpine fir (*Abies lasiocarpa*), Pacific silver fir (*Abies amabilis*), mountain hemlock (*Tsuga mertensiana*), subalpine larch (*Larix lyallii*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), or western red cedar (*Thuja plicata*). Nonforested habitats included numerous meadows, natural shrubfields, early seral stands, and subalpine parks.

Annual precipitation in the summer study area historically ranged from about 180 cm near the Cascade crest to 70 cm in areas affected by the rain shadow of the Cascade Range. Most precipitation in the summer–autumn study area occurred during Oct–May. The summer months were typically warm and relatively dry. Autumn snowfalls usually began by early Oct in the upper watersheds and by mid Nov at lower elevations.

Land Management

All portions of the study area on the Yakama Reservation were within a tribally designated Closed Area, where access was limited to enrolled members of the Yakama Nation. Federal lands within the study area were open to public use, but road closures and administratively designated roadless areas precluded vehicle access to some areas.

The habitat mosaic used by elk included large tracts managed by the Yakama Nation and the U. S. Forest Service, and smaller tracts managed by Boise Cascade Corporation and the Washington Department of Natural Resources. The winter study area was managed as critical winter range for ungulates (McCorquodale et al. 1997).

The summer study area included approximately 200,000 ha of tribal land within the Yakama Reservation, approximately 300,000 ha of federal land within the Gifford Pinchot and Wenatchee National Forests, and about 50,000 ha of state and private lands. About 34,000 ha of tribal land and 64,000 ha of federal land were administratively designated as true reserves (e.g., wilderness, primitive area, or alpine reserve). Approximately 310,000 ha of the study area was designated for intensive commercial timber harvest.

Elk Management

Elk hunting on the Yakama Reservation was limited to approximately 9,000 enrolled tribal members who could harvest antlered elk year round and antlerless elk between 1 Sept and 31 Dec. Approximately 300 km^2 of the winter study area was a tribal game refuge closed to hunting. The Yakama Treaty of 1855 secured off–reservation hunting rights for enrolled Yakamas, and tribal members legally hunted elk on public lands outside of the reservation (McCorquodale 1999a).

Nontribal hunters hunted elk adjacent to the Yakama Reservation. Modern weapon elk seasons ranged from 7–13 days and typically opened in late October.

Regulations varied over time and area; some areas were managed for spike-only hunting with limited permits for branch-antlered male harvest, whereas in other areas hunters could kill any antlered male. A limited number of permits (usually ≤ 200) authorized the killing of antlerless elk by hunters with modern weapons in all areas most years. Early seasons for archers or muzzleloaders, lasting 6–14 days, were offered in all areas and usually opened in early September for archers and early October for muzzleloaders.

METHODS

Marking and Telemetry

I captured elk by immobilizing them with rifle–fired darts shot from a Hughes 500D helicopter or by trapping them in small panel traps or elk–sized clover traps (Thompson et al. 1989) during winter, 1992–99. I estimated the ages of captured elk by patterns of tooth eruption and wear (Quimby and Gaab 1957). I derived age estimates using cementum annuli analysis for elk that died and used these estimates to assess the accuracy of estimates made at capture.

I fitted elk ≥ 1 yr–old with 5 cm–wide radiocollars, which were imprinted with a request for harvest reporting. Radiotransmitters (MOD-500, Telonics, Inc., Mesa, Arizona) operated at 148–150 MHz, had 3-yr batteries, and were equipped with motion sensors that caused signal rates to double if the transmitter remained motionless for ≥10 hr, indicating mortality.

I relocated radiocollared elk weekly during May–Nov and approximately twice monthly during Dec–Apr from a Cessna 182RG aircraft fitted with 2 side–looking directional antennas (RA-2A, Telonics, Inc., Mesa, Arizona). I estimated relocation coordinates with a Geographic Positioning System (GPS) receiver. I periodically evaluated GPS accuracy by obtaining aerial coordinates for a series of known points that were easily identifiable from an aircraft and evaluated radiotelemetry system error by locating test transmitters placed at known locations using a blind testing approach.

I delineated 90% adaptive kernel (AK) (Worton 1989) summer–autumn and winter use areas for elk using CALHOME software (Kie et al. 1996). I used program defaults for optimum bandwidth and a 50 × 50 grid. I estimated seasonal home ranges for all elk with ≥ 10 seasonal relocations, but most were estimated from ≥ 25 relocations during summer–autumn and ≥ 15 relocations during winter. Home range size estimates derived from 10–30 relocations may be negatively biased (Seaman et al. 1999). However, my interest in estimating home ranges was principally to define sampling frames for quantifying characteristics of areas used by elk (Unsworth et al. 1993). Because I was interested in the relationship between environmental features of areas used by elk and their vulnerability to harvest, I did not want to exclude data from elk that were killed before a large sample of relocations were obtained. I believed inclusion of such animals would facilitate insight into the relationship between environmental characteristics of use areas and harvest vulnerability.

Survival and Mortality

I obtained maximum likelihood estimates (MLE) of annual survival for radiocollared elk using a known fate model structure and PROGRAM MARK (G. C.

White, Colorado State University, Fort Collins, Colorado, USA). Year–dependent, age and sex class–dependent, and single–parameter models were compared using Akaike's Information Criterion (AIC) (Akaike 1973) and Likelihood Ratio χ^2 tests (Lebreton et al. 1992).

I attempted to promptly investigate all deaths of radiocollared elk to determine the cause. Site visits usually occurred ≤ 48 hr after a mortality signal was obtained and 1–10 days after the elk's death. I classified mortalities as hunting–related when carcasses with bullet holes or evidence of field–dressing were found or collars were found with corroborating evidence of a kill (e.g., gut pile or lower legs). For winter deaths where evidence of hunting mortality was absent, I qualitatively judged femur marrow characteristics to assess the likelihood that death was due to malnourishment. It was not always possible to reliably discriminate malnourishment deaths from predator kills, and I classified mortality sources as unknown when conclusive evidence of the cause of death was lacking.

Geographic Data

To facilitate testing hypotheses about elk vulnerability and environmental features, I created a geographic database from a road coverage, cover type and management class coverages, and a 30 m digital elevation model (DEM) of the study area. The cover type coverage was based on interpretation and groundtruthing of 1:12,000 color aerial photographs. I classified 6 types: openings and shrubfields (tree canopy closure [CC] < 11%), open conifer forest (CC = 11–39%), closed young forest (CC >39%, dbh <30 cm), semiclosed mature forest (CC = 40–69%, dbh ≥30 cm), closed mature forest (CC >69%, dbh ≥30 cm), and other (e.g., bare ground, rock, open water). I identified 4 management classes: true reserves [e.g., federal wilderness, tribal primitive area], managed forest, resource reserves (e.g., federal late successional reserves, tribal watershed reserves), and state and private lands.

I used the GRID module in ArcInfo® to create a raster coverage of topographic features. I reduced aspect data from the DEM to 9 classes (a no aspect class and 8 classes of 45° width) that represented flat ground and N, NE, E, SE, S, SW, W, and NW aspects. I reduced slope data from the DEM to 7 classes (6 of 10% slope and a 7th class of >59% slope. I derived 10 elevation classes consisting of low (< 607 m) and high (≥ 1,815 m) elevation classes and 8 intermediate classes of 150 m width. I used a raster cell size of $900 \text{ m}^2 = 0.09$ ha (the resolution of the original DEM data), which yielded a topographic coverage of the overall study area consisting of roughly 5.4×10^6 cells.

I also created a coverage of 90% AK summer–autumn home ranges of all radiocollared elk that met the minimum relocation criteria. I then integrated cover type, management class, and summer–autumn home range coverages into the topographic GRID. The basic data derived from the GRID coverage consisted of proportions of cover type, management, and topographic classes within summer–autumn home ranges of elk.

I also created a separate vector coverage of roads within the study area using ArcInfo® GIS data from the 4 management agencies. Data from 2 sources were not attributed by status (i.e., open vs. closed roads), so it was not possible to be confident of road status. However, most roads represented in the final road coverage were administratively open. I determined road densities within elk home ranges and calculated distances between relocations and the nearest road using GIS.

To test the null hypothesis that elk hunting mortality sites did not systematically differ from live elk relocation sites I created 2 additional coverages. I created a kill site coverage by adding a 1,000 m radius circular buffer to each known elk hunting mortality location, yielding a sample of 314.2 ha circles centered on estimated kill sites. Because most hunting deaths occurred during autumn, I created a live elk coverage using only autumn relocations. I randomly selected 100 relocations of live elk obtained between 1 Sept and 30 Nov and buffered them with 1,000 m radius buffers. I then eliminated circles that overlapped with other live elk or mortality site circles. I chose a 1,000 m radius buffer because it allowed me to define both reasonably large areas around kill sites and live relocations and avoid overlap among these sample areas.

Analytic Approach

I tested the hypothesis that the probability of surviving hunting seasons was independent of summer–autumn home range characteristics by modeling the probability that elk survived hunting seasons as a function of home range characteristics. I used multivariate logistic regression (Hosmer and Lemeshow 1989) and treated the fate of elk within summer–autumn home ranges as a dichotomous outcome variable (1 = survived, 0 = harvested) and features of elk home ranges as independent variables. I obtained maximum likelihood estimates for regression coefficients using SPSS 8.0™ (SPSS, Inc. 1998). I conducted 2 modeling iterations, 1 using data from all elk and 1 using only data from males.

The original independent variable list included the % of each home range consisting of each cover type and management class. Additionally, I calculated median slope (MEDSLP), aspect (MEDASP), and elevation (MEDELEV) classes and the circular standard deviation of aspect (SDASP) (Zar 1984, Unsworth et al. 1993) from the telemetry points defining each home range. I also calculated a Shannon–Weiner diversity index for slope ($\mathrm{DIV}_{\mathrm{slp}}$), aspect ($\mathrm{DIV}_{\mathrm{asp}}$), elevation ($\mathrm{DIV}_{\mathrm{elev}}$), and cover type ($\mathrm{DIV}_{\mathrm{cov}}$) from class proportions (p_i) within home ranges, where $H = \Sigma\, p_i \ln(p_i)$ and $\mathrm{DIV} = \mathrm{e}^{H}$ (Ricklefs 1979). I also considered road densities (km/km^2) (RDDENS) and the average distance (m) between the relocations of each elk and the nearest road (DIST) as potential independent variables.

I initially conducted univariate logistic regression to explore the relationship between each independent variable and the outcome variable. The null hypothesis tested was that independent variables did not affect the likelihood that an elk was killed within its summer–autumn home range. I assessed univariate significance from P–values associated with likelihood ratio χ^2 statistics (Hosmer and Lemeshow 1989). I subsequently examined correlation matrices to identify correlated variables prior to final selection of independent variables for multivariate analysis. Several independent variables were weakly ($r \leq 0.40$) but significantly correlated ($P \leq 0.05$), so I chose $r \leq 0.30$ as a maximum tolerance for correlation among candidate independent variables.

I used multivariate logistic regression to derive a model predicting the likelihood that elk were killed within summer–autumn home ranges. All independent variables that were marginally related ($P \leq 0.25$) to the dependent variable were initially included in the multivariate model. I subsequently eliminated independent variables stepwise if they did not significantly ($P \leq 0.05$) contribute to the model. In addition to main effects variables, I tested for the significance of variables reflecting an interaction between road variables and topographic variables (e.g., RDDENS × $\mathrm{DIV}_{\mathrm{asp}}$). I used the Log–likelihood ratio statistic to test model significance (Hosmer and Lemeshow 1989) and compared models using a *G*–statistic. I assessed model goodness–of–fit with the Hosmer–Lemeshow χ^2 statistic and classification error rates. I used a Box–Tidwell transformation (Hosmer and Lemeshow 1989) to test the hypothesis that independent variables were linear in the logit. This approach involved adding a variable of the form $(x)\ln(x)$ iteratively for each x_i to the final models. I considered nonsignificance ($P > 0.05$) of these transformed variables as evidence that variable x_i was approximately linear in the logit (Hosmer and Lemeshow 1989).

I also used logistic regression to test the hypothesis that 314.2–ha circles centered on elk kill sites and autumn relocations of live elk did not systematically differ. I treated site type (1 = live relocation, 0 = kill site) as the dependent outcome variable and considered the following as potential independent variables: % of each cover type, management class, slope class, aspect class, and elevation class within circles, distance (m) to nearest road (DIST), road density (km/km^2) (= RDDENS), and Shannon–Weiner diversity indices for slope (DIV_{slp}), aspect (DIV_{asp}), and cover type (DIV_{cov}) within kill site and live relocation circles. I also derived 2 simplified elevation variables: LOWELEV (% area < 1,060 m) and HIGHELEV (% area > 1,361 m).

The analytic strategy I used for this analysis paralleled the approach for modeling the likelihood of elk being killed within summer–autumn home ranges. I employed univariate logistic regression to identify independent variables associated with the outcome variable, eliminated independent variables that were correlated, and conducted a multivariate logistic regression analysis using the same decision rules previously outlined for the home range analyses.

RESULTS

Marking and Telemetry

During winter 1992–99, I instrumented 81 elk ≥ 1 yr (52 M:29 F). Half (n = 26) of the males marked were mature adults and half were subadults. All males for which post *mortem* age estimates from cementum analysis were obtained had been assigned to the correct age class at capture. The mean absolute deviation of actual and estimated ages at capture for 11 known–age males was 1.4 yr; the error was ≤ 1 yr for 8 of 11 males. The grand mean age of mature males radiotracked each year was 8.0 ($\bar{x}_{annual}$ = 7.6–8.4) and the grand mean age of subadult males each year was 3.4 ($\bar{x}_{annual}$ = 2.8–3.7).

The 81 radiocollared elk yielded data representing 95 male years (62 adult: 33 subadult) and 56 female years; collectively, 3,059 individual relocations were obtained during 1992–99. I estimated the mean GPS error as 36.0 m (95% *CI* = 24.4–47.6 m, $n = 27$). Using blind testing, I estimated the mean telemetry system error as 196.5 m (95% *CI* = 138.7–269.7 m, $n = 17$).

Survival and Mortality

A single parameter survival model (AIC = 121.34) (*MLE*(*S*) = 0.61, 95% *CI* = 0.50–0.70) fit the data for males as well as age–dependent (AIC = 123.43) ($\chi^2 \leq 0.0001$, $P > 0.99$), year–dependent (AIC = 126.00) ($\chi^2 = 4.01$, $P = 0.40$), and age × year–dependent models (AIC = 129.93) ($\chi^2 = 12.12$, $P = 0.20$). A single parameter model (AIC = 54.63) (*MLE*(*S*) = 0.82, 95% *CI* = 0.70–0.90) also fit the data for females as well as a year–dependent model (AIC = 63.01) ($\chi^2 = 8.61$, $P = 0.28$). A sex–dependent model (AIC = 175.93) fit the collective data for males and females better than a single parameter model (AIC = 181.65) ($\chi^2 = 7.77$, $P = 0.005$).

I recorded 39 deaths among the 81 radiocollared elk (Table 1). All deaths of subadult males ($n = 13$) and all but 1 death of adult females ($n = 9$) were hunting related. Among adult males, 11 of 17 deaths (64.7%) resulted from hunting, but 5 adult males succumbed to winter malnutrition. Two elk (1 AD M, 1 AD F) were killed by cougars (*Felis concolor*) during spring. Five of 32 (15.6 %) hunting deaths were illegal kills (Table 1).

Seventeen of 24 (70.8%) hunting deaths of male elk and 4 of 7 (57.1%) kills of females occurred within summer–autumn home ranges. Four of 24 (16.7%) kills of male elk and 1 of 7 (14.3%) kills of females occurred during migration between summer–autumn and winter home ranges; the remainder occurred on winter range.

Factors Affecting Harvest Vulnerability

Considering all elk, those that were killed had higher road densities, relatively less mature conifer cover and more open conifer cover, relatively less area of true reserves, and lower aspect diversity within summer–autumn home ranges than surviving elk (Table 2). Males that were killed had relatively more semiclosed mature cover, relatively more commercially managed forest, and lower aspect diversity within their home ranges than surviving males (Table 2).

Using data from all elk in a modeling context, both road variables, 3 cover type variables, 2 management class variables, variables reflecting cover type and topographic diversity, and median slope and aspect were at least marginally related ($P \leq 0.25$) to the likelihood that an elk was killed within its summer–autumn home range (Table 3). Using data from males only, the average distance to the nearest road, 3 cover type variables, the proportion of managed forest in the habitat mosaic, cover type diversity, and an index of aspect diversity were related to the likelihood that an elk was killed (Table 3).

Several independent variables were strongly correlated. In particular, road variables were correlated with several cover type, management class, and topographic variables. Eliminating correlated variables reduced the list of candidate independent variables. Using all data, the variables RDDENS, MSEMICLOSED (= % mature semiclosed forest), MEDSLOPE, and DIV_{asp} were considered candidate variables for multivariate analysis. Using male data only and eliminating highly correlated variables, the variables MSEMICLOSED, MANAGED (= % managed forest), and $\mathrm{DIV}_{\mathrm{asp}}$ were considered candidate variables.

Using data from all elk, a model containing RDDENS, MED SLOPE, and $\mathrm{DIV}_{\mathrm{asp}}$ explained harvest vulnerability within summer–autumn home ranges better ($P < 0.05$) than reduced models and as well ($P = 0.53$) as a model with more parameters (Table 4). Using male data only, the diversity of aspects ($\mathrm{DIV}_{\mathrm{asp}}$) within an elk's home range explained harvest vulnerability better than a constant–only model ($P = 0.07$) and as well ($P \geq 0.08$) as models with more parameters (Table 5). The linear regression components of the 2 models were:

$$\text{all elk: } Y = -3.83 - 1.15(RDDENS) - 1.35(MEDSLOPE) + 1.09(DIV_{asp}),$$

$$\text{males: } Y = -5.25 + 0.73(DIV_{asp}).$$

The model using data from all elk fit the data (Hosmer–Lemeshow $\chi^2 = 5.05$, $P = 0.65$) and correctly classified 75.4% of elk home ranges relative to the fate of elk. Most misclassifications were of elk that were predicted to have survived, based on summer–autumn home range characteristics, but were actually killed. Box–Tidwell transformed variables of the form $(x)\ln(x)$ were nonsignificant ($P \geq 0.40$) when added to the model, suggesting each variable in the final model was approximately linear in the logit. None of the variables reflecting an interaction between road and topographic feature variables were significant ($P \leq 0.10$) in models including the significant main effects variables.

The model based on male data alone also fit the data (Hosmer–Lemeshow $\chi^2 = 6.91$, $P = 0.55$) and correctly classified 68.3% of the home ranges. Again, most misclassifications were of elk predicted to survive that were actually killed. The DIV_{asp} variable in the final model was approximately linear in the logit based on the nonsignificance ($P = 0.93$) of a Box–Tidwell transformed variable added to the model. Interaction variables did not significantly ($P \leq 0.10$) contribute to the main effects models.

Approximate hunting mortality sites were determined for 26 of 32 (81.3%) elk that were killed. These elk kill sites were associated with higher road densities and were closer to roads than were a random sample of live elk relocations during autumn ($n = 72$) (Table 6). Kill sites also had less mature conifer cover, relatively more area of resource reserves (e.g., Watershed and Late Successional Reserves), and relatively more low elevation (< 1,060 m) area than live elk relocations (Table 6).

Road, cover type, management class, elevation, and variables reflecting diversity of cover types and aspects were related ($P \leq 0.22$) to the likelihood that a 314.2 ha circle centered on an elk relocation was associated with a kill site (Table 7). Aspect and slope class variables were not useful ($P > 0.25$) for discriminating live elk relocations from kill sites. Several independent variables were correlated; in particular, road variables were strongly correlated with the area of managed forest and true reserves and % open canopy conifer cover. Eliminating correlated variables, I selected RDSHA (road density [km/ha]), RESERVE (= % resource reserve [e.g., Watershed Reserve, Late Successional Reserve]), MCLOSED (= % closed canopy mature forest), and DIV_{asp} as candidate variables for multivariate logistic regression analysis. A model based on the variables RDSHA, RESERVE, and MCLOSED distinguished live elk relocations and kill sites as well ($P = 0.26$) as the full model and better than reduced models ($P \leq 0.06$) (Table 8). The linear regression portion of the logistic model was:

$$Y = 1.57 - 4.43(RDSHA) - 0.02(RESERVE) + 0.02(MCLOSED).$$

This model fit the data (Hosmer–Lemeshow $\chi^2 = 3.92$, $P = 0.86$) and correctly classified 76.0% of the 314.2 ha circles. As with the models based on home range characteristics, most misclassifications of relocation sites were of sites predicted to be from live elk that were actually kill sites. Box–Tidwell transformed variables of the form $(x)\ln(x)$ were nonsignificant ($P \geq 0.67$) when added to the model, supporting the assumption that the variables RDSHA, RESERVE, and MCLOSED were approximately linear in the logit.

DISCUSSION

Managing elk and elk hunting in Washington presents unique challenges. Washington is the smallest western state in area, yet has the second largest human population (Washington Department of Fish and Wildlife [WDFW] 1996). In southcentral Washington, in excess of 30,000 nontribal elk hunters have annually hunted elk in recent years (WDFW 1996). As a result, restrictive regulations have been increasingly needed to improve male elk survival and increase male:female ratios among adult elk (WDFW 1996).

Estimated annual survival among adult female elk in the study population (0.82) was similar to estimates for female elk in the Blue Mountains (0.79) (Myers et al. 1999), Mt. St. Helens (0.82) (Smith et al. 1994), and the Olympic Peninsula (0.85) of Washington (Smith et al. 1994). Estimated adult female survival in the southcentral Cascades was lower than estimates from northern Idaho (0.84–0.95) (Zager and Leptich 1991), northcentral Idaho (0.89) (Unsworth et al. 1993), western Montana (0.93) (Hurley and Sargeant 1991), and western Oregon (0.89-0.96) (Cole et al. 1997). During 1992–99, aerial survey results indicated the study population was steadily increasing at approximately $r = 0.08$ (McCorquodale, unpublished data).

Maximum likelihood estimates of annual survival among male elk were identical between adults and subadults (0.61). Overall, this estimated rate of male survival was lower than estimates from the Blue Mountains of eastern Washington (0.74) but much higher than estimated survival among male elk in the Mt. St. Helens (0.49), Olympic Peninsula (0.23), and Colockum areas (0.34) of Washington (Smith et al. 1994). In western Montana, estimated survival among adult males (≥ 3.0 yr) (0.60) was similar to survival estimates I obtained (Hurley and Sargeant 1991). However, subadult (≤ 2–yr) male elk in Hurley and Sargeant's (1991) study had lower estimated annual survival (0.40) than subadults in my study. In northcentral Idaho, a 5–yr weighted survival estimate for male elk (0.60) was comparable to the annual survival estimate I obtained during my 7–yr study (Unsworth and Kuck 1993).

Despite the high demand for hunting opportunity in southcentral Washington, high road densities in managed forests of the region, and liberal tribal hunting seasons, survival among male elk in this study was relatively high. This was evidenced by estimated annual survival in excess of 0.60 and the capture of a large number of older males, including individuals as old as 17-yr (unpubl. data). Escapement among male elk was likely enhanced during this study by the large area of unroaded true reserves (e.g., federal wilderness, tribal primitive area) available and the fact that a large part of the landscape was tribal reservation closed to nontribal hunting.

Similar to the results from other hunted populations (Hurley and Sargeant 1991, Leptich and Zager 1991, Unsworth et al. 1993, Smith et al. 1994), most elk mortalities in my study were associated with hunting. However, several mature males that died during late winter appeared to have succumbed to winter malnutrition. Mature males presumably consumed energy stores during the autumn rut (Geist 1982) and were apparently more susceptible to nutritional stress than were subadult males and adult females.

Consistent with other research, I found that the likelihood of elk being killed was positively related to road densities and negatively related to the mean distance between open roads and elk relocations (Unsworth and Kuck 1993, Cole et al. 1997, Gratson et al. 1997, Weber 1998). The likelihood of harvest was significantly related to other landscape variables in univariate analyses (e.g., relative area of unroaded true reserves, cover type diversity, relative area of open canopy forest), but many of these variables were strongly correlated with road variables.

Relative to the dataset from all elk, road variables were not as useful for predicting the likelihood of harvest with the data limited to males. This was surprising and seemed counterintuitive. However, radiocollared male elk, especially mature adults, displayed a strong aversion to areas near roads (McCorquodale, *in review*). Thus, among radiocollared males, few used areas supporting high road densities. This may reflect active avoidance of roads by males (Marcum and Edge 1991, McCorquodale, *in review*) or simply that males occupying areas near roads were less likely to survive to adulthood (Leptich and Zager 1991, Unsworth and Kuck 1991, Smith et al. 1994). Five radiocollared males were killed in relatively remote areas. Because the number of radiocollared males harvested was limited during the study, the impact of a few males being killed in relatively roadless areas further reduced the likelihood that road variables would prove useful in predicting harvest risks among males. However, given the propensity for males in my study to select areas distant from roads (McCorquodale, *in review*), it would be inappropriate to infer that high road densities had no harvest vulnerability implications among male elk.

Unsworth et al. (1993) found that the variance in aspect among autumn ranges of elk, an index of topographic diversity, was related to the likelihood that elk were killed in northcentral Idaho. Broken and dissected terrain predictably increased the effort needed by hunters to access elk. Consequently, diverse topography tended to reduce the density of hunter effort and led to higher escapement among male elk. Similarly, I found higher topographic diversity in summer–autumn elk ranges was associated with reduced harvest vulnerability apart from road effects. Edge and

Marcum (1991) likewise found that topographic relief tended to mitigate some of the effects of roads on elk in western Montana.

For the complete dataset, slope was negatively related ($P \leq 0.05$) to the likelihood of elk surviving within their summer–autumn home ranges. For the male–only dataset, slope was not a significant predictor of survival odds, but the relationship between slope and survival odds was still negative. It would seem logical that elk that used steep areas would be less vulnerable to hunting. Thus, I expected that slope would be positively related to survival odds. I believe this apparent anomaly resulted from the fact that the Yakama Reservation Primitive Area included a large gently sloping plateau supporting a large continuous tract of unroaded old growth forest. Numerous radiocollared elk used this area, which was centered on a large wet meadow complex, and very few of these elk were harvested.

Road densities and the relative proportion of resource reserves (e.g., watershed and late successional reserves) were negatively related and the relative proportion of mature, closed canopy forest was positively related to the odds that a 314.2 ha circle centered on an autumn relocation was from a live elk (as opposed to a kill site) in the multivariate model. Predictably, higher road densities and less mature forest cover were associated with increased vulnerability to harvest (Hillis et al. 1991). It is not clear why the proportion of resource reserves was negatively related to the likelihood that a relocation site was from a live elk. Resource reserves, especially on the Yakama Reservation were embedded within the managed forest matrix and were often well–roaded. Some areas, notably Watershed Reserves, had major system roads bisecting their length. The area of resource reserves was also significantly ($P = 0.002$) and negatively correlated ($r = -0.31$) with the area of unroaded true reserves (e.g., federal wilderness). Thus, resource reserves may have been relatively low security environments for elk. In fact, because they often had biotic characteristics of preferred habitat because of limited timber harvest but were relatively easily hunted (i.e., roaded), they may have represented high vulnerability environments to elk.

MANAGEMENT IMPLICATIONS

Habitat–based harvest risk models I derived for elk in the southcentral Cascades of Washington supplement those recently derived by Unsworth et al. (1993) and Leptich et al. (1995b) for elk in Idaho. Collectively, these models provide a means of further quantifying the link between habitat condition and harvest vulnerability.

Elk vulnerability to harvest predictably increases as hunter access to elk habitat is improved (Unsworth et al. 1993, Leptich et al. 1995b, Cole et al. 1997). High road densities clearly have negative survival implications for elk in the southcentral Cascades of Washington as has been demonstrated in many other hunted populations (Hillis et al. 1991). Road variables were not useful for predicting harvest risks among male elk, but this appeared to be because males either avoided roads more than other elk or were exceedingly vulnerable to harvest in higher road density areas (McCorquodale, *in review*). Collectively, these data and those of McCorquodale (*in review*) support the hypothesis that maintaining high use by adult males and/or managing for acceptable vulnerability risks probably requires relatively large unroaded areas within the habitat mosaic.

Vulnerability to harvest also predictably declines as topographic complexity increases because more effort is required by hunters to hunt elk in broken and dissected terrain (Unsworth et al. 1993). Managers cannot manipulate topographic complexity; it is an inherent geophysical characteristic of the landscape. However, it is apparent that where lack of topographic complexity exists, manipulation of open road densities and amount and juxtaposition of escape cover may be particularly important to manage vulnerability of elk to hunting mortality.

Based on logistic regression modeling, increasing the relative availability of mature forest cover on autumn elk ranges will also reduce harvest vulnerability. This is intuitive, but is an important finding in light of recent experimental work that supported the hypothesis that forest cover does not mediate enhanced fitness via thermal energetics (Cook et al. 1998). Even if this is true for male elk, maintaining larger tracts of mature forest on summer–autumn ranges may still be an essential prescription to managing harvest vulnerability on public lands.

ACKNOWLEDGMENTS

This research was supported by a U. S. Department of Interior, Bureau of Indian Affairs grant administered by the Yakama Nation. G. Rankel and W. P. Bradley helped obtain funding. S. Tolle skillfully piloted helicopters used for elk darting and C. Dyer piloted fixed–wing radiotracking flights. D. Blodgett, Jr. assisted with all aspects of the fieldwork. Several individuals assisted with elk trapping,

including A. James, P. Olney, T. Heemsah, D. Sockzehigh, and J. Feen. I thank R. Wiseman and H. Fraser for assistance with GIS analyses and geographic data manipulation. G. C. White kindly provided advice on the use of PROGRAM MARK.

LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petran, and F. Csáki, editors. International symposium on information theory, second edition, Akadémiai Kiadi, Budapest, Hungary.

Bowyer, R. T., and D. W. Kitchen. 1987. Sex and age–class differences in vocalizations of Roosevelt elk during rut. American Midland Naturalist 118:225–235.

Burcham, M. G., C. L. Marcum, L. J. Lyon, K. T. Weber, and W. D. Edge. 1998. Final report: Chamberlain Creek elk studies 1977–1983 and 1993–1996. School of Forestry, University of Montana, Missoula, Montana, USA.

Cole, E. K., M. D. Pope, and R. G. Anthony. 1997. Effects of road management on movement and survival of Roosevelt elk. Journal of Wildlife Management 61:1115–1126.

Clutton–Brock, T. H., F. E. Guiness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.

Edge, W. D., and C. L. Marcum. 1991. Topography ameliorates the effects of roads and human disturbance on elk. Pages 132–137 *in* A. G. Christensen, L. J.

Lyon, and T. N. Lonner, editors. Proceedings of the Elk Vulnerability Symposium. Montana State University, Bozeman, Montana, USA.

Flook, D. R. 1970. A study of sex differential in the survival of wapiti. Report Series, No. 11, Canadian Wildlife Service, Ottawa, Ontario, Canada.

Geist, V. Adaptive behavioral strategies. Pages 219–277 *in* J. W. Thomas and D. E. Toweill, editors. Elk of North America. Stackpole Books, Harrisburg, Pennsylvania, USA.

Gibson, R. M., and F. E. Guiness. 1980. Behavioral factors affecting male reproductive success in red deer (*Cervus elaphus*). Animal Behavior 28:1163–1174.

Gilmer, D. S., L. M. Cowardin, R. L. Duval, L. M. Mechlin, C. W. Shaiffer, and V. B. Kuechle. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U. S. Fish and Wildlife Service Resource Publication 140.

Gratson, M. W., C. Whitman, and P. Zager. 1997. The effects of road closures on elk mortality in northcentral Idaho. Project W–160–R–23, Study I, Job 2. Idaho Fish and Game, Boise, Idaho, USA.

Hillis, J. M., M. J. Thompson, J. E. Canfield, L. J. Lyon, C. L. Marcum, P. M. Dolan, and D. W. McCleery. 1991. Defining elk security: the Hillis paradigm. Pages 38–43 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. Wiley and Sons, Inc., New York, N. Y., USA.

Hurley, M. A., and G. A. Sargeant. 1991. Effects of hunting and land management on elk habitat use, movement patterns, and mortality in western Montana. Pages 94–98 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1996. CALHOME: a program for estimating animal home ranges. Wildlife Society Bulletin 24:342–344.

LeBreton, J., K. P. Burnham, J. Clobert, and D. R. Anderson. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Leptich, D. J., and P. Zager. 1991. Road access management effects on elk mortality and population dynamics. Pages 126–131 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA.

Leptich, D. J., S. G. Hayes, and P. Zager. 1995a. Bull elk habitat use. Project W–160–R–22, Study I. Idaho Fish and Game, Boise, Idaho, USA.

Leptich, D. J., S. G. Hayes, and P. Zager. 1995b. Elk habitat security characteristics and hunting season mortality rates. Project W–160–R–22, Study III. Idaho Fish and Game, Boise, Idaho, USA.

Lyon, L. J., and J. E. Canfield. Habitat selection by Rocky Mountain elk under hunting season stress. Pages 99–105 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the Elk Vulnerability Symposium. Montana State University, Bozeman, Montana, USA.

Lyon , L. J., and M. G. Burcham. 1998. Tracking hunters with the Global Positioning System. Pages 114–132 *in* Final report: Chamberlain Creek elk studies 1977–1983 and 1993–1996. School of Forestry, University of Montana, Missoula, Montana, USA.

Mackie, R. J. 1991. Welcome and opening remarks. Pages 1–2 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA.

Marcum, C. L., and W. D. Edge. 1991. Sexual differences in distribution of elk relative to roads and logged areas in western Montana. Pages 142–148 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA.

McCorquodale, S. M., R. H. Leach, G. M. King, and K. R. Bevis. 1997. The Yakama Indian Reservation: integrating Native American values into commercial forestry. Journal of Forestry 95(11):15–18.

McCorquodale, S. M. 1999a. Historical and contemporary policies regarding off–reservation hunting by Native Americans. Wildlife Society Bulletin 27:446–455.

McCorquodale, S. M. 1999b. Movements, survival, and mortality of black–tailed deer in the Klickitat Basin of Washington. Journal of Wildlife Management 63: 861–871.

McCorquodale, S. M. *in review.* Sex specific movements and habitat use by elk in the southcentral Cascade Range of Washington. Journal of Wildlife Management.

Myers, W. L., L. C. Bender, P. E. Fowler, and B. R. Lyndaker. 1999. Population parameters and trends. Pages 43–72 *in* W. L. Myers, editor. An assessment of elk population trends and habitat use with special reference to agricultural damage zones in the northern Blue Mountains of Washington. Washington Department of Fish and Wildlife, Olympia, Washington, USA.

National Oceanic and Atmospheric Administration. 1994. Local climatological data: annual summary with comparative data. National Oceanic and Atmospheric Administration, Washington, D. C., USA.

Quimby, D. C., and J. E. Gaab. 1957. Mandibular dentition as an age indicator in Rocky Mountain elk. Journal of Wildlife Management 21:435–451.

Ricklefs, R. E. 1979. Ecology. Chiron Press, New York, New York, USA.

Seaman, E. D., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Smith, J. L., W. A. Michaelis, K. Sloan, J. Musser, and D. J. Pierce. 1994. An analysis of elk poaching losses, and other mortality sources in Washington using biotelemetry. Washington Department of Fish and Wildlife, Olympia, Washington, USA.

Thomas, J. W. 1991. Elk vulnerability–a conference perspective. Pages 318–319 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the Elk Vulnerability Symposium. Montana State University, Bozeman, Montana, USA.

Thompson, M. J., R. E. Henderson, T. O. Lemke, and B. A. Sterling. 1989. Evaluation of a collapsible clover trap for elk. Wildlife Society Bulletin 17:287–290.

Unsworth, J. W., and L. Kuck. 1991. Bull elk vulnerability in the Clearwater drainage of northcentral Idaho. Pages 85–88 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the Elk Vulnerability Symposium. Montana State University, Bozeman, Montana, USA.

Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of northcentral Idaho. Journal of Wildlife Management 57:495–502.

Vales, D. J., V. L. Coggins, P. Matthews, and R. A. Riggs. 1991. Analyzing options for improving bull:cow ratios of Rocky Mountain elk populations in northeast Oregon. Pages 174–181 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the Elk Vulnerability Symposium. Montana State University, Bozeman, Montana, USA.

Washington Department of Fish and Wildlife. 1996. Final Environmental Impact Statement for elk management. Olympia, Washington, USA.

Weber, K. T. 1997. Identifying landscape elements in relation to elk kill sites in western Montana. Thesis. University of Montana, Missoula, Montana, USA.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home–range studies. Ecology 70:164–168.

Zager, P., and D. J. Leptich. 1991. Comparing two methods of calculating elk survival rates. Pages 106–109 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the Elk Vulnerability Symposium. Montana State University, Bozeman, Montana, USA.

Zar, J. H. 1984. Biostatistical analysis. Prentice–Hall, Inc., Englewood Cliffs, New Jersey, USA.

Table 1. Radiocollared elk mortalities, *n* (%), by source in the Cascades of southcentral Washington, 1992–99.

Age/sex class	Total mortalities	Legal kills	Illegal kills	Wounding losses	Total hunting	Winterkill	Predator kills
Adult males, *n* = 26	17	9 (52.9)	1 (5.8)	1 (5.8)	11 (64.7)	5 (29.4)	1 (5.8)
Subadult males, *n* = 26	13	8 (61.5)	2 (15.4)	3 (23.1)	13 (100.0)	0 (0.0)	0 (0.0)
Adult females, *n* = 29	9	5 (55.5)	2 (22.2)	1 (11.1)	8 (88.8)	0 (0.0)	1 (11.1)
Total , *n* = 81	39	22 (56.4)	5 (12.8)	5 (12.8)	32 (82.1)	5 (12.8)	2 (5.1)

Table 2. Variables for which means associated with summer–autumn home ranges were different ($P \leq 0.10$) between elk that survived and those that were killed.

Dataset Variable	$\bar{x}_{survivors}$	$\bar{x}_{mortalities}$	t^a	P-value
All elk	$n = 50$	$n = 21$		
RDDENS[b]	0.90	1.39	2.21	0.03
MCLOSED[c]	20.99	13.50	1.98	0.05
OPENCON[c]	25.46	36.25	2.79	0.007
WILD[c]	59.09	40.11	2.08	0.04
MANAGED[c]	20.52	36.36	2.07	0.04
DIV_{asp}[d]	7.62	7.27	1.89	0.06
Males only	$n = 28$	$n = 17$		
MSEMICLOSED[c]	21.16	25.71	1.81	0.08
MANAGED	17.98	33.07	1.67	0.10
DIV_{asp}	7.74	7.30	1.72	0.10

[a] Student's t-value for independent samples.

[b] Density of roads (km/km^2).

[c] % of the home range in cover type or management class.

Table 3. Univariate significance of independent variables affecting the likelihood that elk were killed within summer-autumn home ranges.

Dataset Variable	χ^2	P-value
All elk ($n = 71$)		
DIST	2.18	0.14
RDDENS	4.68	0.03
MCLOSED	4.12	0.04
MSEMICLOSED	1.67	0.20
OPENCON	7.16	0.008
WILD	4.20	0.04
MANAGED	4.05	0.04
MEDELEV	1.90	0.17
MEDSLOP	1.86	0.17
DIV_{ASP}	3.44	0.06
DIV_{COV}	2.10	0.15
SDASP	1.39	0.24
Males only ($n = 45$)		
DIST	1.75	0.19
MCLOSED	1.41	0.24
MSEMICLOSED	3.27	0.07
OPENCON	2.36	0.12
MANAGED	2.78	0.10

Table 3. (cont.)

Dataset

Variable	χ^2	P-value
Males only		
DIV_{asp}	3.18	0.07
DIV_{cov}	2.68	0.10
DIV_{COV}	1.69	0.19
SDASP	1.40	0.24

Table 4. Results of multivariate logistic regression analyses of independent variables vs. the probability of elk being killed within summer–autumn home ranges using data from all elk (n = 71).

		RDDENS[a]	MEDSLOPE[b]	DIV_{asp}[c]	MSEMICLOSED[d]			
Model	Constant	β (SE)	β (SE)	β (SE)	β (SE)	-2 Log Likelihood	G[e]	*P*
1	-2.967	-1.126 (0.416)	-1.356 (0.510)	1.036 (0.443)	-0.020 (0.032)	67.467	0.40	0.53
2	-3.834	-1.146 (0.412)	-1.345 (0.505)	1.087 (0.434)		67.864	7.01	0.008
3	3.284	-0.931 (0.356)	-0.930 (0.433)			74.871	4.92	0.03
4	1.359	-0.661 (0.315)				79.793		

[a] density of roads (km/km^2) within the home range.

[b] median slope calculated from the points defining the home range.

[c] Shannon-Weiner diversity index for aspect proportions within the home range.

[d] % of home range consisting of mature (dbh ≥ 30 cm) semiclosed (CC = 40-69%) forest.

[e] G = (-2 Log Likelihood [model k+1]) – (-2 Log Likelihood [model k]).

Table 5. Results of multivariate logistic regression analyses of independent variables vs. the probability of elk being killed within summer–autumn home ranges using data from males only (*n* = 45).

		DIV$_{asp}$[a]	MANAGED[b]	MSEMICLOSED[c]			
Model	Constant	β (SE)	β (SE)	β (SE)	-2 Log Likelihood	G[d]	*P*
1	-2.619	0.615 (0.464)	-0.020 (0.012)	-0.055 (0.045)	48.423	1.60	0.21
2	-5.074	0.772 (0.445)	-0.020 (0.012)		50.019	3.03	0.08
3	-5.251	0.729 (0.435)			53.050		

[a] Shannon-Weiner diversity index for aspect proportions within the summer–autumn home range.

[b] % of home range consisting of commercially managed forest.

[c] % of home range consisting of mature (dbh ≥ 30 cm) semiclosed (CC = 40-69%) forest.

[d] G = (-2 Log Likelihood [model k+1]) – (-2 Log Likelihood [model k]).

Table 6. Variables for which means associated with live autumn locations of elk and kill sites were different ($P \leq 0.10$).

Variable	$\bar{x}_{\mathrm{live}}$ ($n = 72$)	$\bar{x}_{\mathrm{mort}}$ ($n = 26$)	t[a]	P-value
RDSHA[b]	0.10	0.21	3.53	0.001
DIST[c]	1262.14	511.66	3.20	0.002
MCLOSED[d]	17.56	7.52	2.69	0.009
RESERVE[d]	5.92	21.86	2.16	0.04
LOWELEV[d]	9.33	32.37	2.59	0.01
DIV$_{\mathrm{asp}}$[e]	5.59	6.24	2.31	0.02

[a] Student's t-value for independent samples.

[b] Density of roads (km/ha).

[c] Distance (m) from site to the nearest road.

[d] % of the home range in cover type, management class, or elevation class.

[e] Shannon–Weiner diversity index for aspects.

Table 7. Univariate significance of independent variables affecting the likelihood that an autumn elk location was associated with an elk kill site.

Variable	χ^2	*P*-value
RDSHA	10.95	< 0.001
DIST	7.54	0.006
MCLOSED	5.40	0.02
OPENCON	1.75	0.19
WILD	2.07	0.15
MANAGED	1.50	0.22
RESERVE	6.55	0.01
LOWELEV	9.44	0.002
HIGHELEV	2.44	0.12
DIV_{asp}	5.53	0.02
DIV_{cov}	2.06	0.15

Table 8. Results of multivariate logistic regression analyses of 1–km radius circles centered on elk mortality sites and live elk relocations.

		RDSHA[a]		RESERVE[b]		MCLOSED[c]		DIV_{asp}[d]				
Model	Constant	β	(SE)	β	(SE)	β	(SE)	β	(SE)	-2 Log Likelihood	G[e]	*P*
1	2.909	-1.126	(0.416)	-0.150	(0.009)	0.021	(0.017)	-0.238	(0.214)	95.969	1.29	0.26
2	1.569	-4.433	(1.818)	-0.016	(0.009)	0.022	(0.017)			97.261	3.59	0.06
3	1.966	-5.028	(1.775)	-0.017	(0.009)					100.852	4.22	0.04
4	1.820	-5.513	(1.763)							105.070		

[a] density of roads (km/ha) within a 1 km radius circle.

[b] % of 1 km radius circle consisting of resource emphasis areas (e.g., watershed reserve, late successional reserve).

[c] % of 1 km radius circle consisting of mature (dbh ≥ 30 cm) closed (CC > 69%) forest.

[d] Shannon-Weiner diversity index for aspect proportions within a 1 km radius circle.

[e] G = (-2 Log Likelihood [model k+1]) – (-2 Log Likelihood [model k]).

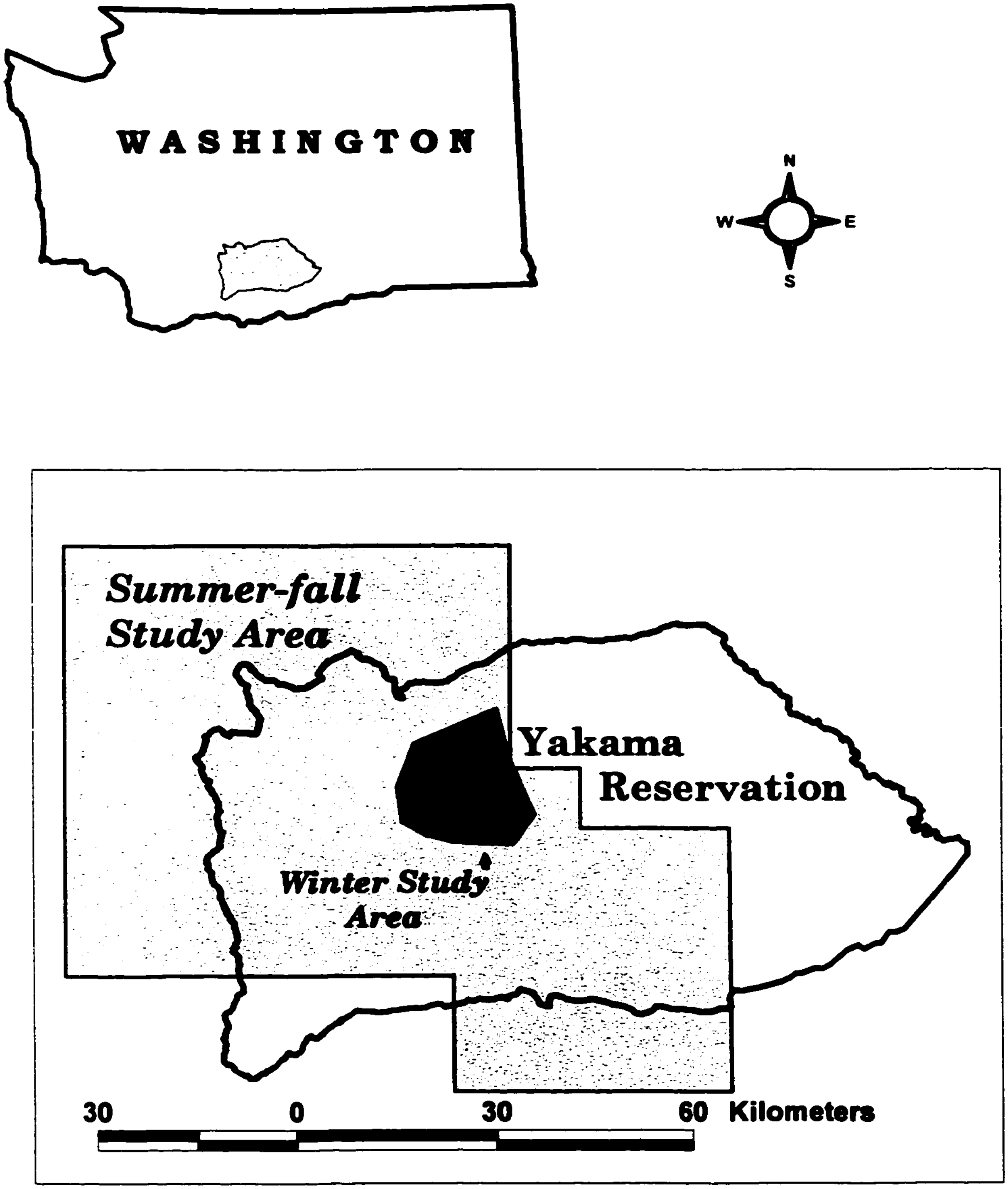

Figure 1. Location of the study area and Yakama Reservation

CHAPTER 3: EVALUATING BIAS IN HELICOPTER SURVEYS OF ELK IN SOUTHCENTRAL WASHINGTON: SEX-SPECIFIC SIGHTABILITY AND SPATIAL DISTRIBUTION

Abstract: Adult sex ratio data for elk (*Cervus elaphus*) collected from helicopters may be biased if males and females have different sighting probabilities. Sightability models can account for differential sightability if they are sex-specific or if sightability functions are the same for both sexes. I collected sightability data from a sample of radiocollared elk in Washington that included a large proportion of adult males to test 2 hypotheses about sightability: (1) male and female elk had equal sighting probabilities; (2) the functional relationship between factors affecting sightability and the probability of sighting groups was the same for both sexes. I also tested the hypothesis that the spatial distribution of male and female elk was the same during experimental surveys. Using logistic regression modeling, I found that females were >9 times more likely to be seen than males during surveys. A multivariate logistic model containing only the variables group size and overstory canopy closure explained sighting probabilities as well as models with more parameters. Sex was related ($P \leq 0.001$) to group sightability in univariate analyses, but the effect of sex was nonsignificant ($P = 0.77$) when group size and canopy closure were present in a multivariate model, indicating sex operated as a confounder but not an effect modifier. The spatial overlap of adult male and female elk in blocks of aerial sampling units was 67% during the sightability trials. The distribution of male and female elk among these blocks was significantly related to sex ($P \leq 0.05$)

and bivariate relocations from males and females were spatially distinguishable ($P < 0.0001$), indicating that males and females were spatially segregated. These results suggest that sightability models need not be sex–specific to reduce bias in sex–ratio data collected from helicopters. However, the spatial distribution of male and female elk during winter is a potential source of bias in helicopter surveys designed to yield accurate sex ratio data if survey area boundaries are defined by the distribution of high–sightability groups, which are likely to be larger groups of females.

INTRODUCTION

Differential survival of male and female elk (*Cervus elaphus*) in hunted populations has increasingly concerned wildlife managers because of its implications for elk demographics and recreational opportunity (Prothero et al. 1979, Squibb 1985, Thomas 1991, Noyes et al. 1996). As a result, several states have revised their elk harvest strategies, adopting changes such as delaying entry of males into legal cohorts and permit–only hunting for adult males (Carpenter 1991, Leckenby et al. 1991, Byrne 1993). These changes have been implemented to reduce male vulnerability to harvest, improve the balance of adult sex ratios, and increase the proportion of older males in managed populations.

The success of management strategies designed to reduce male elk vulnerability to harvest is often assessed by monitoring sex and age–class composition in populations through time, typically using helicopter–based sampling during winter. Aerial sampling has frequently been used to monitor abundance and other demographics of large mammal populations (Caughley 1977). However, aerial sampling is known to be plagued by problems such as observer bias, double counting, and limited sightability (Caughley 1974, Routledge 1981, Samuel and Pollock 1981, Pollock and Kendall 1987, Samuel et al. 1992).

Bias in helicopter surveys can result from extraneous sources of variability, such as speed and altitude effects, sampling intensity, and observer experience (DeYoung 1985, Beasom et al. 1986, Shupe and Beasom 1987), as well as differential sightability due to environmental conditions and behavior of animal groups (Steinhorst and Samuel 1989). Several investigators recently examined sightability bias in helicopter surveys of big game animals in attempts to develop correction factors for helicopter survey data (Samuel et al. 1987, Otten et al. 1993, Bodie et al. 1995, Anderson and Lindzey 1996, Cogan and Diefenbach 1998). Conceptually, these sightability models were used to quantify the effects of uncontrollable environmental and behavioral factors on the probability of sighting animals from helicopters after controlling for extraneous variation through use of strict sampling protocols (Samuel and Pollock 1981, Samuel et al. 1987, Otten et al. 1993, Anderson and Lindzey 1996).

Sex–specific sighting bias has not been assessed directly (Samuel et al. 1987, Otten et al. 1993, Cogan and Diefenbach 1998) because previous elk sightability models were developed from samples of radiocollared animals containing predominantly adult females. Subsequently, investigators assumed that male and female elk have the same probability of being sighted from a helicopter under similar levels of the independent environmental and behavioral variables affecting sightability.

I collected sightability data from a sample of radiocollared Rocky Mountain elk (*C. e. nelsoni*) that included a large proportion of adult males. This facilitated testing the hypothesis that male and female elk have equal probabilities of detection during helicopter surveys. I also tested a related hypothesis, that the relationship between variables affecting sightability and the probability of being sighted from a helicopter are fundamentally the same for adult elk of both sexes.

Sources of sex–specific sighting bias in helicopter surveys of elk may also include differences in the spatial distribution of male and female elk on winter range. Sexual segregation, which is well documented for large ungulates (Jakimchuk et al. 1987, Main and Coblentz 1990, Miquelle et al. 1992), could lead to biased adult sex–ratio data even if functional relationships between environmental variables and the probability of being sighted are the same for male and female elk. Thus, I also tested the hypothesis that the spatial distribution of adult elk in our winter study area was independent of sex. This hypothesis test evaluated whether the spatial distribution of male and female elk on winter range is a potentially substantial source of bias in survey data collected from helicopters.

Sightability parameters may vary across environments inhabited by a species (Unsworth et al. 1991, Otten et al. 1993, Cogan and Diefenbach 1998). A sightability model developed for one environment may have limited application in reducing bias in helicopter survey data collected under different conditions. Therefore, my objectives also included developing a sightability model specific to the habitat conditions occupied by the study population along the east slopes of the southcentral Washington Cascades. Modeling sightability provided a useful context for testing hypotheses about sex–specific sighting probabilities and spatial distribution in elk populations surveyed by helicopters.

STUDY AREA

I collected data for testing sightability hypotheses and developing sightability models on the 260 km^2 Toppenish Creek winter range of the Yakama Indian Reservation (Figure 1). Toppenish Creek is located on the east slopes of the Washington Cascades and supported a wintering population of approximately 3,000–4,000 elk during the study. Elevations ranged from 609 to 1340 m. Topographically, the Toppenish Creek winter range consisted of a series of steep, east–west canyons and 2 large plateaus. The area is in the rain shadow of the Cascade Range. Periodic snowfalls occur during November–March, but openings and south slopes are usually snowfree by late February. Mean annual snowfall measured at nearby Yakima, Washington, 1964–94, was 61.2 cm (National Oceanic and Atmospheric Administration 1994). Snow conditions varied during my study; early flights were conducted with relatively continuous snow except for the lowest south–facing slopes. During later flights, all south–facing slopes and most open or semiopen areas were snowfree.

South slopes generally supported a mixture of large openings and stands of Oregon white oak (*Quercus garryani*). North slopes supported extensive stands of mixed conifers, mostly ponderosa pine (*Pinus ponderosa*), Douglas–fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*). Riparian areas supported dense stands of mixed conifers and black cottonwood (*Populus trichocarpa*). Extensive ponderosa pine stands interspersed with Oregon white oak and openings on xeric sites characterized the plateau areas of the lower Toppenish Creek drainage.

METHODS

Trapping and Marking

I trapped elk in small, self–tripping panel traps during winter. Traps were constructed such that multiple animal captures were unlikely. This was desirable because of the relatively high proportion of adult males in the population and the risk of injury from agonistic behavior in traps when adult males were caught with other elk. I baited elk into traps with alfalfa hay between late November and late February, 1994–99 and immobilized them with xylazine hydrochloride (100 mg/ml). I reversed immobilizations with yohimbine hydrochloride (10 mg/ml). I estimated ages of immobilized elk by patterns of tooth eruption and wear (Quimby and Gaab 1957).

From among the adults captured each year, I selected a sample of elk of both sexes and fitted them with 5 cm–wide radiocollars. Radiocollars (MOD–500 transmitters, Telonics, Inc, Mesa, Arizona) operated at 148–150 Mhz and were white, except blue/white radiocollars were placed on males and red/white radiocollars on females during winter 1998–99. Although I did not employ formal randomization in selecting elk for radiocollaring, I attempted to deploy radios evenly among the traps.

On the few occasions when a trap held more than 1 elk, I randomly selected a single elk for radiocollaring.

Sightability data collection

I collected data for testing study hypotheses and deriving sightability models during Feb–April 1999. Thirty–six radiocollared elk (23 M: 13 F) were available for sampling. Fifteen of the 23 (65%) radiocollared males were mature adults ($\geq$ 5 yr); the remaining radiocollared males were branch–antlered subadults (3–4 yr).

I divided the study area into 23 sample subunits ranging in size from 1.3 to 7.8 km^2 for aerial sampling. I delineated subunits such that boundaries (e.g., roads, ridgetops, drainage bottoms) were easily identifiable from an aircraft. Prior to each set of helicopter flights, all radiocollared elk were relocated by an experienced 2–person crew in a Cessna 182RG equipped with side–looking, 2–element antennas (RA-2A, Telonics, Inc., Mesa, Arizona). For each fixed–wing elk relocation, a GPS coordinate and the sample unit were recorded. Data on the distribution of radiocollared elk among subunits were conveyed to a 3–person helicopter crew immediately after the conclusion of the fixed–wing flight, but the helicopter crew was not informed of the exact location of radiocollared elk within subunits.

The helicopter crew consisted of a pilot and two primary observers, neither of whom were involved in the fixed–wing relocation flight. Both primary observers were experienced in sighting elk from helicopters. One observer recorded data and sat next to the pilot, whereas the other observer sat directly behind the pilot. The helicopter, a Bell 206 Jet–Ranger II, was equipped with 2 side–looking directional antennas (RA-2A, Telonics, Inc., Mesa, Arizona) mounted on the skids. The helicopter crew visually searched subunits for radiocollared elk using transects separated by approximately 150–250 m, depending on the degree of vegetative cover (i.e., transect spacing was wider in open habitat). Transects were flown parallel to the prevailing slope of the terrain and progressed upslope. The helicopter was flown at a standard altitude (45–65 m above the ground, depending on terrain) and speed (80–110 km per hr) and the same pilot and primary observers were used for each flight.

All elk groups sighted within 250 m of the transect were scrutinized for the presence of radiocollared individuals. If a radiocollared elk was seen, the telemetry system aboard the helicopter was activated and the radiocollared elk identified. The telemetry system was then turned off again. For each group sighted that contained a radiocollared elk, I recorded the following data: group size (GRPSIZE), sex of the radiocollared elk (SEX), activity of the first elk sighted in a group (ACTIVITY = bedded or active), % canopy closure (CANOPY), cover type (COVTYPE), slope (SLOPE), and % snow cover (SNOW). SLOPE was recorded as an ordinal variable (= flat, moderate, steep) and COVTYPE was recorded as a nominal variable (= open, conifer, oak, conifer/oak). CANOPY and SNOW were visually estimated (by consensus of the primary observers) for an area that encompassed all elk in the group plus a 10 m radius perimeter. I recorded all data for the location where groups that included radiocollared elk were first sighted.

When the visual survey of a given subunit was completed by the helicopter crew, the telemetry system was reactivated and all radiocollared elk known to be in the subunit, but which had not been seen, were relocated. I recorded the same environmental and group data for elk located by telemetry as I had recorded for elk observed during the visual portion of the survey. When a group contained more than 1 radiocollared elk, I treated the group as a single observation to maintain independence of observations, whether the group had been visually located or located with telemetry.

Because of fuel capacity, each helicopter survey was limited to 2 hr plus ferry time to and from a refueling location. No more than 2 flights per day were conducted to prevent observer fatigue. Helicopter flights were conducted at all times of day, but late afternoon flights were most common because they allowed time for fixed–wing presurvey flights and also coincided with periods of elk activity. Typically, 2–3 subunits were surveyed per 2 hr flight.

Data Analysis

I explored relationships between environmental and group variables and the probability of sighting elk using logistic regression (Hosmer and Lemeshow 1989) and χ^2 contingency analyses (Zar 1984). In these analyses, I treated elk groups seen and elk groups missed as a dichotomous dependent variable ($Y = 1, 0$). The environmental and group variables associated with each elk group seen or missed were treated as the independent variables. I obtained maximum likelihood estimates for logistic regression coefficients, when they existed, using either SPSS–8.0™

(SPSS, Inc. 1998) or Log–Xact for Windows™ software (Mehta and Patel 1996). When maximum likelihood estimates did not exist because of highly imbalanced data, such as elk always or never being seen under some levels of a nominal variable, I attempted to obtain conditional exact estimates using Log–Xact for Windows™ (Mehta and Patel 1996). I also explored manipulating categories of discrete variables as a means of eliminating numerical problems produced by imbalanced data, thereby facilitating maximum likelihood inference.

Initially, I conducted univariate analyses to explore relationships between each independent variable and the dependent variable. The null hypothesis tested in univariate analyses was that the independent variable did not significantly affect the probability of sighting elk from a helicopter during our experimental assessment. For continuous and ordinal variables I used univariate logistic regression to assess significance and for nominal variables I used χ^2 contingency analysis. I assessed univariate significance based on *P*–values associated with the likelihood ratio χ^2 statistics (Hosmer and Lemeshow 1989). Although GRPSIZE, CANOPY, and SNOW had been collected as continuous variables, I suspected canopy cover and snow cover estimates were imprecise and that the effect of group size on sightability was minimal after some upper threshold of group size. Therefore, I also explored reclassification of these continuous variables into ordinal variables. Discrete classes were formed based on improvement of likelihood ratio χ^2 scores and ranges that I believed to be both biologically meaningful and easily applicable under actual survey conditions.

Following univariate analyses, I used multivariate logistic regression to derive a model predicting the probability of sighting elk from a helicopter (Samuel et al. 1987, Otten et al. 1993). The logistic regression model used was:

$$P = e^u / 1+e^u,$$

where P is equal to the probability of sighting elk groups from the helicopter and $u = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k$ is the linear regression of independent variables $(x_1, x_2, \ldots, x_k)$ affecting sightability.

Initially, all independent variables that were at least marginally related ($P \leq 0.25$) to the dependent variable in univariate analyses were considered candidate variables for inclusion in the multivariate model (Hosmer and Lemeshow 1989). I subsequently scrutinized multivariate coefficients for significance. I removed independent variables one at a time if they did not contribute significantly ($P \leq 0.05$) to the model. Significance was judged on the basis of P–values from the likelihood ratio χ^2 statistic for the variable and a comparison of the variable's coefficient in the multivariate model with the variable's univariate coefficient (Hosmer and Lemeshow 1989). At each step, the variable with the lowest nonsignificant P–value was eliminated. I used the Log–likelihood ratio statistic to test model significance; for each model, this tested the hypothesis that all coefficients except the constant were zero. Each time a model was reduced, I compared models with and without the variable eliminated using the G–statistic (Hosmer and Lemeshow 1989, Mehta and Patel 1996). Model goodness–of–fit was assessed with the Hosmer–Lemeshow statistic and classification tables (Hosmer and Lemeshow 1989).

Once I identified the multivariate model that appeared to include all of the important main effect independent variables, I tested the assumption that these variables were linear in the logit using the Box–Tidwell transformation (Guerro and Johnson 1982). This tested the assumption that variable x was linear in the logit by adding a $x \ln(x)$ variable to the model and assessing its significance. Nonsignificance of $x \ln(x)$ was considered evidence that x was approximately linear in the logit in its original form (Hosmer and Lemeshow 1989).

I also assessed the significance of adding the following interaction terms to the preferred main effects models: SLOPE × CANOPY, SNOW × CANOPY, SEX × CANOPY, and GRPSIZE × CANOPY. I examined the likelihood ratio χ^2 for each interaction coefficient and the significance of models with an interaction term relative to the main effects models using the G–statistic.

I developed 2 multivariate models. I treated group size, canopy cover, and snow cover as continuous variables in the first model and as ordinal variables in the second.

I used the univariate likelihood ratio χ^2 for sex × elk groups seen and missed to test the null hypothesis that adult male and female elk were equally likely to be seen during the experimental helicopter surveys. I used the significance of sex in multivariate models to test the null hypothesis that the functional relationship between the independent and dependent variables was the same for adult male and female elk. Statistically, testing this hypothesis equated to assessing whether sex was an effect modifier (Hosmer and Lemeshow 1989).

Because as few as 1–2 elk relocations were obtained from several subunits, I combined original subunits into blocks of 3–5 subunits for analyses of the spatial distribution of male and female elk. This assured that blocks did not have an excessive number of cells with expected values <5 for contingency analyses. Subunit blocks consisted of groupings of the original subunits that were similar relative to topography and predominant cover types. Blocks generally represented east–west and low elevation–high elevation clines as block number increased. I measured spatial overlap of male and female radiocollared elk relocations in the subunit blocks using Schoener's (1970) index, as applied by McCullough et al. (1989). I used χ^2 contingency analysis to test the hypothesis that the distribution of radiocollared elk among the subunit blocks was independent of sex.

I tested the hypothesis that coordinates of male and female elk relocations obtained during the sightability evaluation could have come from a common distribution using a Multi Response Permutation Procedures (MRPP) test (Mielke et al. 1981). MRPP testing was conducted using BLOSSOM software (Slauson et al. 1991). I also used univariate and multivariate logistic regression to test the hypothesis that the coordinates of elk relocations (UTM X, Y) were related to the sex of radiocollared elk.

RESULTS

I collected data from 101 radiocollared elk groups located from a helicopter. Of the 101 groups, 58 (57.4%) were groups containing at least 1 radiocollared male and 43 (42.6%) were groups containing at least 1 radiocollared female. Fifty–seven of the 58 (98.3%) groups containing radiocollared males were male–only groups. The exception involved a single adult male that was located in a small group of females and their calves. One of 43 (2.3%) groups containing radiocollared females included an unmarked branch–antlered male. Fifty elk groups (49.5%) were seen from the helicopter, and 51 groups (50.5%) were missed and relocated by telemetry. Surveyed subunits typically contained 1–5 radiocollared elk. The average time required to completely search a subunit was 36.9 min (*SD* = 13.8).

Male group sizes ($\bar{X} = 2.36$) were smaller than female group sizes ($\bar{X} = 11.1$) ($t = 7.52$, $P \leq 0.001$). Among 58 male groups, 28 (48.3%) consisted of 1 individual, and 45 (77.6%) consisted of ≤ 3 individuals. In contrast, among 43 female groups, 2 (4.7%) consisted of 1 individual and 9 (20.9%) consisted of ≤ 3 individuals. Canopy closure at sites occupied by male groups was higher than at sites occupied by female groups ($\bar{X}_{males} = 48.6\%$ CC, $\bar{X}_{females} = 28.7\%$ CC) ($t = 4.03$, $P \leq 0.001$). Sex–specific differences in activity were also apparent. Forty-three of 58 (74.1%) male groups were inactive during surveys, whereas only 8 of 43 (18.6%) female groups were inactive ($\chi^2 = 32.38$, $P \leq 0.001$).

Maximum likelihood estimates did not exist for coefficients of some of the COVTYPE design variables because all elk groups were seen under 2 of the 4 original classes. Conditional exact estimates for the design variable coefficients for COVTYPE existed, but the upper confidence limits for 2 of the 3 design variables extended to infinity. The analytical problem produced by highly unbalanced data for the nominal cover type variable was eliminated by reclassifying cover type into a binary variable (COVBIN: conifer = 0, other = 1).

The variables GRPSIZE, CANOPY, SNOW, SEX, COVBIN, and ACTIVITY were significantly ($P \leq 0.05$) related to the probability of sighting elk groups in univariate analyses (Table 1). SLOPE, consisting of 3 ordinal classes, was not useful ($P = 0.96$) for predicting whether elk groups were seen or missed.

Among ordinal intervals of 10, 15, and 20% derived from the continuous canopy closure variable, 20% intervals fit the data best, based on improvement of the likelihood ratio χ^2 scores. This ordinal canopy closure variable (CANCLASS) took on values of 1-5 and was related to the probability of sighting elk groups ($\chi^2 = 51.21$, $P \leq 0.001$). An ordinal snow cover variable (SNOWCLASS) consisting of 5 intervals of 20% (1-5) was also related to the probability of sighting elk groups ($\chi^2 = 3.75$, $P = 0.05$). An ordinal group size variable was created (GRPCLASS) that consisted of eight classes. The first 7 classes were continuous (width = 1) and an eighth class included all groups ≥ 8; this variable was related to the probability of sighting elk groups ($\chi^2 = 68.67$, $P \leq 0.001$).

There was some evidence that CANOPY and COVTYPE were correlated (Spearman's $\rho = 0.189$, $P = 0.06$). Because COVTYPE had to be reduced to a binary variable (COVBIN) to eliminate problems with unbalanced data, I opted to retain CANOPY (and its ordinal form CANCLASS) and eliminate COVBIN to maximize covariate patterns in subsequent multivariate analyses.

The initial multivariate logistic regression models contained the following independent variables: GRPSIZE (GRPCLASS), CANOPY (CANCLASS), SNOW (SNOWCLASS), ACTIVITY, and SEX. The multivariate coefficients, *P*–values, and *G*–statistics for each model iteration, along with their significance are shown in Table 2. The models containing only GRPSIZE and CANOPY (or GRPCLASS and CANCLASS) explained elk group sightability as well ($P > 0.05$) as more complex models. Using parsimony criteria, the 2-variable models were preferred ($P \leq 0.05$) to single variable models that included only GRPSIZE (or GRPCLASS) as a predictor of elk group sightability. The linear regression components of the 2 logistic models were:

$$Y = 0.240 + 0.768(GRPSIZE) - 0.072(CANOPY),$$

$$Y = 0.770 + 0.845(GRPCLASS) - 1.334(CANCLASS).$$

The coefficient for a Box–Tidwell transformed variable of the form: GRPSIZE × ln(GRPSIZE) was not significant ($\chi^2 = 0.82$, $P = 0.37$) when added to the model containing GRPSIZE and CANOPY, which supported the assumption that GRPSIZE was approximately linear in the logit. Likewise, the coefficient for CANOPY × ln(CANOPY) was not significant ($\chi^2 = 0.98$, $P = 0.32$) when added to the 2 variable model, supporting the assumption of linearity for CANOPY.

The coefficient for GRPCLASS × ln(GRPCLASS) was not significant ($\chi^2 = 0.89$, $P = 0.35$) nor was the coefficient for CANCLASS × ln(CANCLASS) ($\chi^2 = 1.53$, $P = 0.22$) when each was added to the 2 variable model containing GRPCLASS and CANCLASS. This supported the assumptions of linearity in the logit for these ordinal variables.

None of the interaction terms were significant ($P = 0.15$–0.90) when added to models containing GRPSIZE (or GRPCLASS) and CANOPY (or CANCLASS) as main effects. Models containing only the main effects variables were also preferred over each model that included an interaction term based on *G*–statistics. The final model containing GRPSIZE and CANOPY fit the data (Hosmer–Lemeshow $\chi^2 = 4.50$, $P = 0.81$) and correctly classified 88.8% of the observations. The final model using GRPCLASS and CANCLASS fit the data in an absolute sense but not as well as the continuous variable model (Hosmer–Lemeshow $\chi^2 = 8.24$, $P = 0.22$) and correctly classified 86.7% of the observations. For both models, most misclassifications were groups that were seen but were predicted to have been missed.

The 2–dimensional overlap of male and female relocations, based on Schoener's (1970) index was 67.8%. The distribution of elk relocations among the 5 subunit blocks was related to sex ($\chi^2 = 22.27$, $P \leq 0.001$). More than 70% of all elk relocations in subunit blocks 2,4, and 5 were of males. The distribution of elk among these 3 subunit blocks was independent of sex ($\chi^2 = 3.57$, $P = 0.17$). Female relocations predominated in subunit blocks 1 and 3, and relocations within these 2 blocks of subunits were independent of sex ($\chi^2 = 0.20$, $P = 0.65$). Considering subunit blocks 2, 4, 5 and 1,3 as groups, elk relocation frequencies between the 2 groups were related to sex ($\chi^2 = 19.21$, $P \leq 0.001$).

Based on MRPP testing, there was strong evidence that coordinates from radiocollared male and female elk did not come from a common distribution (test statistic = −15.83, $P < 0.0001$). The probability that a relocation came from a male elk was related to both northing ($\chi^2 = 9.09$, $P = 0.003$) and easting ($\chi^2 = 23.13$, $P \leq 0.001$) UTM coordinates. The easting coordinate alone predicted the sex of a relocated elk as well both coordinates together ($G = 2.57$, $P = 0.11$) and fit the data (Hosmer–Lemeshow $\chi^2 = 28.65$, $P \leq 0.001$, 70.4% of observations correctly classified).

DISCUSSION

The use of sightability models to reduce bias in data obtained from helicopter surveys of elk is appealing, because these models are intuitive, relatively simple to use, and because sightability has been repeatedly shown to be predicted well by only 1 or 2 independent variables (Samuel et al. 1987, Steinhorst and Samuel 1989, Otten et al. 1993, Anderson et al. 1998). Validation tests of elk sightability models have also been promising (Unsworth et al. 1990, Leptich and Zager 1993, Anderson et al. 1998). Most modelers have treated elk generically, where the probability of sighting males and females is assumed to be the same under similar levels of the factors affecting sightability. Although this seems logical, sightability functions for male and female elk could differ if sexual dimorphism affected sighting probabilities or if males and females reacted differently to helicopters (i.e., 1 sex was more likely to move or seek cover in response to helicopter noise). This research was designed to formally test the hypothesis of equal sightability.

In the univariate analysis, sex was significantly related to the probability of sighting elk groups. The univariate odds ratio estimate for sex was 9.92 (95% *CI* = 3.90–25.22), indicating that female elk groups were nearly 10 times more likely to be seen than male elk groups. The low rate of sighting male elk groups resulted from significantly smaller groups and a greater propensity for male groups to be located in heavy cover. The disparate sighting probabilities for male and female elk may also have reflected sex–specific differences in activity, which were pronounced. Because male groups were more likely to be inactive than female groups, the higher canopy closure associated with male groups may have reflected activity–specific habitat affinities rather than a generalized preference for higher canopy closure sites by males relative to females.

I rejected the null hypothesis that male and female elk groups were equally likely to be seen during the experimental surveys. Moreover, I suggest that raw sex–ratio data obtained from helicopter surveys are likely to severely biased because of systematic variation in sighting probabilities between the sexes (Czaplewski et al. 1983). Based on the magnitude of the negative sighting bias estimated for male groups, sex–ratio inference from uncorrected helicopter surveys may be considerably more biased than inference about population trend.

I found little evidence, however, that the factors affecting sightability operated differently on male and female elk groups in my experimental assessment. Sex was the least significant ($P = 0.77$) variable in the multivariate model with the most parameters. Also, sex, when forced into the final 2 variable model was highly nonsignificant for both the continuous variable model ($\chi^2 = 0.04$, $P = 0.84$) and the ordinal variable model ($\chi^2 = 0.14$, $P = 0.71$). The multivariate analysis suggested that the univariate effect of sex on the sightability of elk groups was mediated by an association of sex with one or more independent variables. Sex was significantly associated with group size and canopy closure, the primary determinants of group sighting probabilities, and also with activity. The evidence suggested that sex was a confounder in these data, but did not function as an effect modifier. Thus, I did not reject the null hypothesis that the functional relationship between variables affecting sightability and the probability of sighting elk groups was the same for male and female groups. This implies that sightability models that treat elk generically are likely to be adequate to correct helicopter survey data for the negative sighting bias associated with groups of males.

Overall, the detection rate I obtained for elk groups sighted from a helicopter (50%) was lower than the rates obtained by Samuel et al. (1987) (58%) and Otten et al. (1993) (68%). This likely reflected the higher proportion of male groups in my study and the extensive conifer cover of some subunits. Leptich and Zager (1992) recorded a slightly lower sighting rate (42%) for elk groups in another heavily forested study area in northern Idaho.

Despite some overlap in the spatial distribution of male and female elk during this evaluation, relocations of males and females within subunits were highly unbalanced for most subunits. Social segregation was pronounced. Spatial segregation by sex was also evident in the distribution of elk relocations despite the fact that males and females had been marked in the same traps. Marking males and females in the same area should have minimized the likelihood of detecting segregation. In general, elevation and conifer cover decreased in more easterly subunits, and relocations of females represented a higher proportion of all relocations in these lower, more open subunits. Correspondingly, logistic regression indicated that the probability of a relocation being from a female elk increased significantly as the easterly UTM coordinate increased.

Lone radiocollared males were repeatedly missed in subunits in which no elk were visually located. Without the aid of telemetry, I would likely have concluded these units contained no elk. These were often higher elevation, conifer–dominated subunits that still had relatively deep snow during the experimental surveys. Similarly, Leege and Hickey (1977) and Unsworth et al. (1998) found adult male elk often distributed at higher elevations and in deeper snow than females on winter range in Idaho.

It seems reasonable that extensive snowcover would increase the contrast of animals and background, thereby enhancing sightability from helicopters (Otten et al. 1993, Anderson and Lindzey 1996). However, the importance of snowcover as a factor affecting sightability has been ambiguous in previous research. Samuel et al. (1987) concluded that snowcover was not a significant predictor of elk sightability in northcentral Idaho, whereas Leptich and Zager (1992, 1993) found snowcover was positively related ($P \leq 0.05$) to the probability of sighting elk groups in northern Idaho. In my study, a snowcover variable did not significantly improve models that contained group size and canopy closure variables. However, snowcover and canopy closure were positively correlated (Pearson's $\rho = 0.28$, $P = 0.005$). Although snow may have added contrast to the sighting environment, its effect on elk group sightability was apparently influenced by its positive association with canopy closure. Elk groups were more likely to be seen in open habitats, and these areas typically had little or no snow.

The spatial distribution of males and females on winter range could be a substantial source of bias in helicopter surveys of elk. If survey boundaries reflect areas where large numbers of elk have been seen, perhaps during pre–survey reconnaissance flights, the survey area will be defined by the distribution of high–sightability groups. Groups with high sighting probabilities are larger groups in relatively open habitat. My results suggest that such groups are likely to be predominantly groups of females and calves. A relatively high proportion of the adult males in a given wintering area may be distributed peripherally to these areas occupied by female groups (Leege and Hickey 1977). Because adult males are likely to be in low–sightability groups (i.e., small groups in relatively dense cover), areas occupied primarily by males may appear to be devoid of elk during pre–survey flights. Without prior knowledge of the distribution of male elk groups, such as from telemetry, areas used mostly by males may inadvertently be excluded from survey areas.

When elk sightability models are used to estimate population sizes and sex ratios, it is likely that most of the females in the estimates will have been seen but most of the males will have been added by model corrections. Because population estimates derived from use of sightability models typically have lower precision when sighting probabilities are low (Unsworth et al. 1991, Anderson et al. 1998), the estimated number of males in a survey area may have larger coefficients of variation than the estimated number of females. This poses challenges for biologists attempting to detect changes in adult sex ratios, because tests may lack statistical power due to high variance associated with estimates of male elk numbers. If the intent is to detect small changes in adult sex ratios, greater stratification of units or increased sampling of units (i.e., increased *n*) where a high proportion of males occur may need to be employed. Variability in estimated male numbers could also be reduced by timing surveys to maximize the probability that males are active, because they may be in more open habitats when foraging. Conducting surveys as close to dawn and dusk as possible may help accomplish this. Because sightability models are designed to control extraneous variation in survey results through standardized search effort, it is inappropriate to search individual units more carefully (e.g., slower, lower, or with more closely spaced transects) because they are thought to contain males.

ACKNOWLEDGMENTS

This research was supported by grants provided by the U. S. Department of Interior–Bureau of Indian Affairs and the Rocky Mountain Elk Foundation. G. Rankel, W. P. Bradley, and T. Toman helped obtain funding. I thank fixed–wing pilot C. Dyer of Kennewick Aircraft Services and helicopter pilot M. Clarke of Diamondback Orchards Aviation for their skillful flying in support of this research.

D. Blodgett, Jr., J. Feen, and D. Sockzehigh assisted with data collection. P. Zager kindly shared his experiences in collecting and analyzing helicopter sightability data.

LITERATURE CITED

Anderson, C. R., Jr., and F. G. Lindzey. 1996. Moose sightability model developed from helicopter surveys. Wildlife Society Bulletin 24:247–259.

_____________, Jr., D. S. Moody, B. L. Smith, F. G. Lindzey, and R. P. Lanka. 1998. Development and evaluation of sightability models for summer elk surveys. Journal of Wildlife Management 62:1055–1066.

Beasom, S. L., F. G. Leon, III, and D. R. Synatzske. 1986. Accuracy and precision of counting white–tailed deer with helicopters at different sampling intensities. Wildlife Society Bulletin 14:364–368.

Bodie, W. L., E. O. Garton, E. R. Taylor, and M. McCoy. 1995. A sightability model for bighorn sheep in canyon habitats. Journal of Wildlife Management 59:832–840.

Byrne, A. E. 1993. Zag–point elk: an alternative to the four–point bull elk regulation. Pages 104–111 in R. L. Callas, D. B. Koch, and E. R. Loft, editors. Proceedings of the 1990 western states and provinces elk workshop. California Department of Fish and Game, Sacramento, California, USA.

Carpenter, L. 1991. Elk hunting regulations, the Colorado experience. Pages 16–22 in A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the Elk Vulnerability Symposium. Montana State University, Bozeman, USA.

Caughley, G. 1974. Bias in aerial survey. Journal of Wildlife Management 38:921–933.

____________. 1977. Sampling in aerial survey. Journal of Wildlife Management 41:605–615.

Cogan, R. D., and D. R. Diefenbach. 1998. Effect of undercounting and model selection on a sightability–adjustment estimator for elk. Journal of Wildlife Management 62:269–279.

Czaplewski, R. L., D. M. Crowe, and L. L. McDonald. 1983. Sample sizes and confidence intervals for wildlife population ratios. Wildlife Society Bulletin 11:121–128.

DeYoung, C. A. 1985. Accuracy of helicopter surveys of deer in south Texas. Wildlife Society Bulletin 13:146–149.

Guerro, V. M., and R. A. Johnson. 1982. Use of the Box–Cox transformation with binary response models. Biometrika 69:309–314.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. Wiley and Sons, Inc., New York, N. Y., USA.

Jakimchuk, R. D., S. H. Ferguson, and L. G. Sopuck. 1987. Differential habitat use and sexual segregation in the central arctic caribou herd. Canadian Journal of Zoology 65:534–541.

Leckenby, D., C. Wheaton, and L. Bright. 1991. Elk vulnerability–the Oregon situation. Pages 89–93 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA.

Leege, T. A., and W. O. Hickey. 1977. Elk–snow–habitat relationships in the Pete King drainage, Idaho. Wildlife Bulletin 6, Idaho Department of Fish and Game, Boise, Idaho, USA.

Leptich, D. J., and P. Zager. 1992. Couer d'Alene elk ecology project, study II: elk sightability models: elk sightability bias in relation to timbered cover types and bull elk. Job Completion Report W–160–R–20–1. Idaho Department of Fish and Game, Boise, Idaho, USA.

____________, __________. 1993. Couer d'Alene elk ecology project, study II: elk sightability models: elk sightability model validation at the Starkey Experimental Forest and Range, Oregon. Job Completion Report W–160–R–23–1. Idaho Department of Fish and Game, Boise, Idaho, USA.

Main, M. B., and B. E. Coblentz. 1990. Sexual segregation among ungulates: a critique. Wildlife Society Bulletin 18:204–210.

McCullough, D. R., D. H. Hirth, and S. J. Newhouse. 1989. Resource partitioning between sexes in white–tailed deer. Journal of Wildlife Management 53:277–283.

Mehta, C., and N. Patel. 1996. LogXact for Windows: logistic regression software featuring exact methods. Cytel Software, Corp., Cambridge, Massachussets, USA.

Mielke, P. W., K. J. Berry, P. J. Brockwell, and J. S. Williams. 1981. A class of nonparametric tests based on multiresponse permutation procedures. Biometrica 68:720–724.

Miquelle, D. G., J. M. Peek, and V. Van Ballenbergh. 1992. Sexual segregation in Alaskan moose. Wildlife Monographs 122.

National Oceanic and Atmospheric Administration. 1994. Local climatological data: annual summary with comparative data. National Oceanic and Atmospheric Administration, Washington, D. C., USA.

Neal, A. K., G. C. White, R. B. Gill, D. F. Reed, and J. H. Olterman. 1993. Evaluation of mark–resight model assumptions for estimating mountain sheep numbers. Journal of Wildlife Management 57:436–450.

Noyes, J. H., B. K. Johnson, L. D. Bryant, S. L. Findholt, and J. W. Thomas. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. Journal of Wildlife Management 60:508–517.

Otten, M. R. M., J. B. Haufler, S. R. Winterstein, and L. C. Bender. 1993. An aerial censusing procedure for elk in Michigan. Wildlife Society Bulletin 21:73–80.

Pollock, K. H., and W. L. Kendall. 1987. Visibility bias in aerial surveys: a review of estimation procedures. Journal of Wildlife Management 51:502–510.

Prothero, W. L., J. J. Spillett, and D. F. Balph. 1979. Rutting behavior of yearling and mature bull elk: some implications for open bull hunting. Pages 160–165 in M. S. Boyce and L. D. Hayden–Wing, editors. North American elk: ecology, behavior, and mangement. University of Wyoming, Laramie, USA.

Quimby, D. C., and J. E. Gaab. 1957. Mandibular dentition as an age indicator in Rocky Mountain elk. Journal of Wildlife Management 21:435–451.

Routledge, R. D. 1981. The unreliability of population estimates from repeated, incomplete aerial surveys. Journal of Wildlife Management 45:997–1000.

Samuel, M. D., and K. H. Pollock. 1981. Correction of visibility bias in aerial surveys where animals occur in groups. Journal of Wildlife Management 45:993–997.

____________, E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. Journal of Wildlife Management 51:622–630.

____________, R. K. Steinhorst, E. O. Garton, and J. W. Unsworth. 1992. Estimation of wildlife population ratios incorporating survey design and visibility bias. Journal of Wildlife Management 56:718–725.

Schoener, T. W. 1970. Non–synchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418.

Shupe, T. E., and S. L. Beasom. 1987. Speed and altitude influences on helicopter surveys of mammals in brushland. Wildlife Society Bulletin 15:552–555.

Slauson, W. L., B. S. Cade, and J. D. Richards. 1991. User manual for BLOSSOM statistical software. Midcontinent Ecological Science Center, Fort Collins, Colorado, USA.

SPSS, Inc. 1998. SPSS Base 8.0. SPSS, Inc., Chicago, Illinois, USA.

Squibb, R. C. 1985. Mating success of yearling and older bull elk. Journal of Wildlife Management 49:744–750.

Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.

Thomas, J. W. 1991. Elk vulnerability–a conference perspective. Pages 318–319 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the elk vulnerability symposium. Montana State University, Bozeman, Montana, USA.

Unsworth, J. W., L. Kuck, E. O. Garton, and B. R. Butterfield. 1998. Elk habitat selection on the Clearwater National Forest, Idaho. Journal of Wildlife Management 62:1255–1263.

____________, F. A. Leban, G. A. Sargeant, E. O. Garton, M. A. Hurley, J. R. Pope, and D. J. Leptich. 1991. Aerial survey: user's manual with practical tips for designing and conducting aerial big game surveys. Idaho Department of Fish and Game, Boise, Idaho, USA. 54 pp.

____________, L. Kuck, and E. O. Garton. 1990. Elk sightability model validation at the National Bison Range, Montana. Wildl. Soc. Bull. 18:113–115.

Zar, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Table 1. Summary of the univariate association between independent variables and the proportion of elk groups seen from a helicopter on the Toppenish Creek winter range, Washington.

Variable	n = total groups	Groups seen	Sightability	χ^2	*P*-value[a]	χ^{2b}	*P*-value[c]
% Canopy Cover				53.81	<0.001	51.21	<0.001
0-19	19	19	1.00				
20-39	26	18	0.69				
40-59	28	8	0.29				
60-79	17	5	0.29				
80-100	11	0	0.00				
% Snow Cover				11.90	0.02	3.75	0.05
0-19	40	25	0.63				
20-39	9	6	0.67				
40-59	14	2	0.14				
60-79	13	6	0.46				
80-100	25	11	0.44				
Group Size				68.04	<0.001	68.67	<0.001
1	30	2	0.07				
2	16	4	0.25				

Table 1. (continued)

Variable	n = total groups	Groups seen	Sightability	χ^2	*P*-value[a]	χ^{2b}	*P*-value[c]
Group Size							
3	7	4	0.57				
4	4	2	0.50				
5	10	8	0.80				
6	5	5	1.00				
7	4	3	0.75				
≥8	22	22	1.00				
Sex				27.56	<0.001		
Male	58	16	0.28				
Female	43	34	0.79				
Activity				51.73	<0.001		
Active	50	42	0.84				
Bedded	51	8	0.16				
Slope				0.002	0.96		
Flat	52	26	0.50				
Moderate	31	15	0.48				

Table 1. (continued)

Variable	n = total groups	Groups seen	Sightability	χ^2	*P*-value[a]	χ^{2b}	*P*-value[c]
Slope							
Steep	18	9	0.50				
Cover type				55.49	<0.001		
Conifer	61	13	0.21				
Other	40	37	0.93				

---

[a] **Univariate *P*-value of likelihood ratio χ^2 for ordinal and nominal variable forms.**

[b] **Univariate likelihood ratio χ^2 for continuous variable forms.**

[c] **Univariate *P*-value of likelihood ratio χ^2 for continuous variable forms.**

Table 2. Results of multivariate logistic regression analyses of independent variables vs. the probability of sighting elk groups from a helicopter in southcentral Washington.

		GRPSIZE	CANOPY	ACTIVITY	SNOW	SEX			
Model	Constant	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)	Likelihood ratio	G[a]	*P*
1	-0.983	0.723 (0.232)	-0.063 (0.026)	1.342 (0.907)	0.008 (0.013)	-0.306 (1.048)	88.837	0.09	0.76
2	-1.081	0.706 (0.222)	-0.061 (0.025)	1.224 (0.818)	0.009 (0.012)		88.750	0.60	0.44
3	-0.746	0.706 (0.219)	-0.057 (0.024)	1.241 (0.812)			88.146	2.31	0.13
4	0.240	0.768 (0.219)	-0.072 (0.021)				85.839	17.12	<0.001
5	-3.021	0.869 (0.183)					68.717		
1	-0.708	0.820 (0.224)	-1.083 (0.468)	1.558 (0.891)	0.090 (0.265)	-0.273 (1.016)	87.330	0.07	0.79
2	-0.794	0.801 (0.212)	-1.064 (0.461)	1.448 (0.794)	0.105 (0.260)		87.257	0.17	0.68
3	-0.529	0.795 (0.210)	-1.030 (0.453)	1.462 (0.790)			87.091	3.38	0.07
4	0.644	0.910 (0.209)	-1.338 (0.413)				83.713	15.64	<0.001
5	-3.135	0.920 (0.172)					68.076		

[a] G = Likelihood ratio [model k] – Likelihood ratio [model k + 1]).

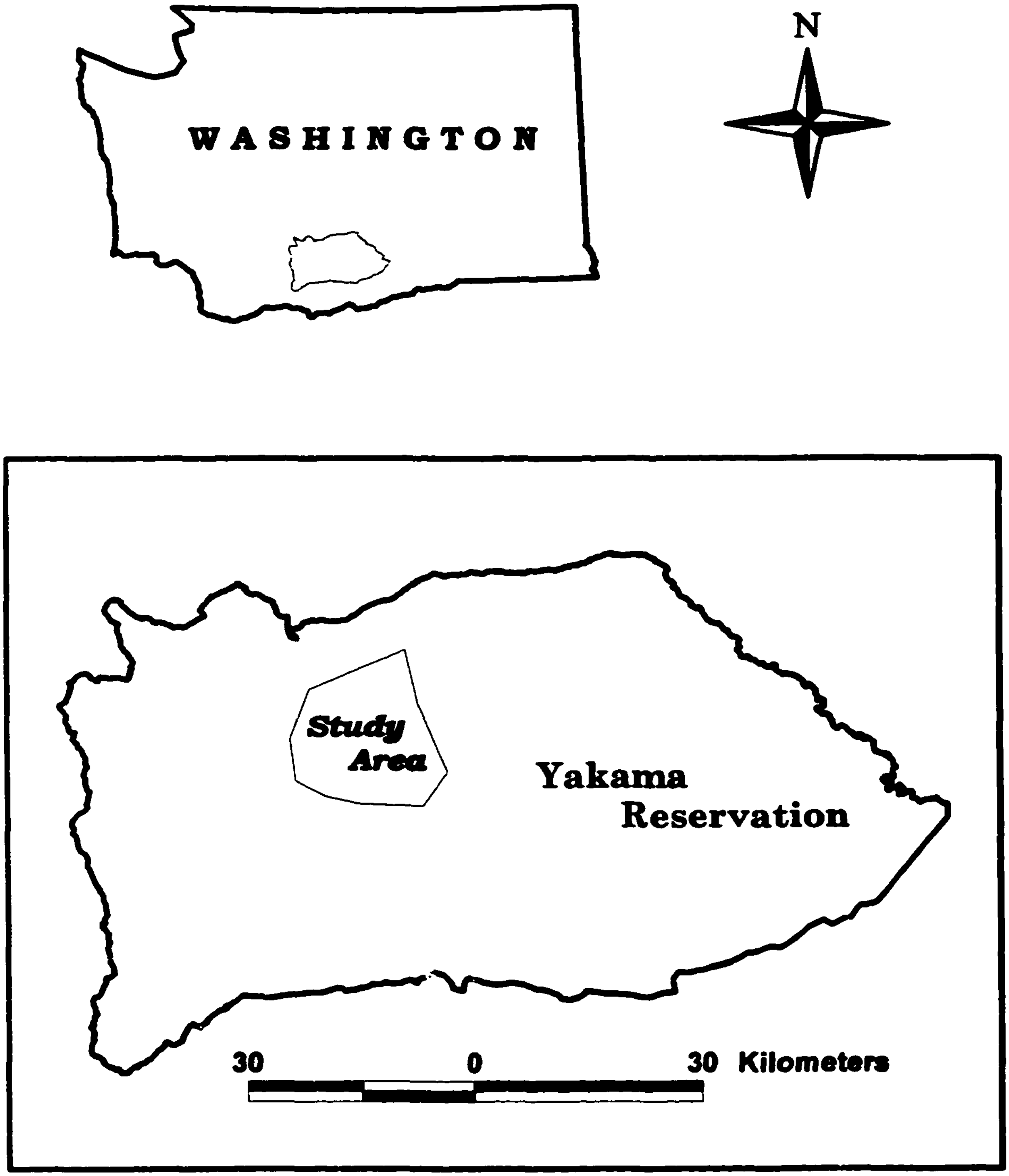

Figure 1. Location of study area and Yakama Reservation.