# BLACK BEAR DISTRIBUTION PATTERNS IN A TEMPERATE FOREST ENVIRONMENT, OLYMPIC NATIONAL PARK

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Wildlife Resources

in the

College of Graduate Studies

University of Idaho

by

Kimberly Ann Sager

March 2005

Major Professor:  R. Gerald Wright, Ph.D.

# AUTHORIZATION TO SUBMIT THESIS

This thesis of Kimberly Ann Sager, submitted for the degree of Master of Science with a major in Wildlife Resources and titled "Black bear distribution patterns in a temperate forest environment, Olympic National Park", has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

| | | |
|---|---|---|
| Major Professor | ___________________________<br>R. Gerald Wright | Date ___________ |
| Committee Members | ___________________________<br>Kurt J. Jenkins | Date ___________ |
| | ___________________________<br>John J. Beecham | Date ___________ |
| | ___________________________<br>Karen S. Humes | Date ___________ |
| Department Administrator | ___________________________<br>Kerry P. Reese | Date ___________ |
| Discipline's College Dean | ___________________________<br>Steven B. Daley Laursen | Date ___________ |

Final Approval and Acceptance by the College of Graduate Studies

___________________________ Date ___________
Margrit von Braun

# ABSTRACT

For approximately 90 years two hydroelectric dams have blocked annual returns of anadromous fish to over 113 kilometers of the Elwha River in Washington's Olympic National Park (NP). The Department of Interior now proposes to remove both dams to fully restore the Elwha River ecosystem and native anadromous fisheries. Dam removal and subsequent salmon restoration may result in altered nutrient flow dynamics throughout the watershed, with potentially profound effects on the park black bear population. To provide baseline information by which to assess the long-term ecological effects of salmon restoration on distribution patterns of bears in Olympic NP, I used Global Positioning System (GPS) radio-collar technology to describe broad-scale patterns in seasonal distribution and movements of black bears prior to dam removal. Further, due to concern over variable success of GPS collars in a temperate forest environment, I quantified systematic fix-acquisition biases of GPS radio-collars across a range of environments and subsequently developed a system for weighting GPS location data in an effort to reduce these biases. Unweighted bear location data from GPS collars were positively biased toward habitats with open canopy covers and little topographic obstruction. Therefore, weighted bear location data were used in analyses of home range and resource selection. Bear home ranges averaged 68.73 km$^2$ for males and 25.10 km$^2$ for females. Bears did not select habitats in proportion to availability. They selected meadows during all seasons, though particularly during fall, and selected hardwoods during spring. Finally, bears exhibited cyclical and predictable patterns of annual elevation change, and were closer to the Elwha River during spring than during fall. The application of weighting factors to biased bear location data provided a viable approach to reducing bias in analysis of home range and resource selection, and contributes to the current discussion over use of GPS radio-collar technology for tracking wildlife. Additionally, these data provide valuable baseline information for assessing the future effects of salmon restoration, and help Olympic NP biologists prepare for monitoring programs along the Elwha River.

# ACKNOWLEDGMENTS

First and foremost, I would like to express sincere gratitude to members of my committee for their confidence in my ability to complete this thesis and their steady support throughout all phases of the graduate process. R. Gerald Wright functioned as a wonderful and supportive major advisor, with an open-door policy that always made me feel welcome to ask questions and share stories. Gerry’s unyielding faith in me, though perhaps not always deserved, was very much appreciated and will not be forgotten. Kurt J. Jenkins provided invaluable direction and field-savvy during bear capture and GPS collar field testing, and provided insights and support throughout the data analysis and thesis-writing process. Kurt frequently put his own work aside to assist me as I struggled through the data analysis process, helping me decipher the mysteries of the statistical world. John Beecham not only served to keep me on my toes about black bear ecology, but functioned as a bear-trapping guru. John spent innumerable hours building cubbies and setting snares in an effort to teach me how to capture the wily bears of Olympic National Park. When John became frustrated, he never gave up; he just worked harder, set more elaborate snares, and invariably outsmarted the bears. Karen Humes provided GIS support, and Oz Garton, though not a formal member of this committee, was pivotal in helping design many aspects of this study.

Without the funding and support of the USGS-Forest and Rangeland Ecosystem Science Center, this project would not have been possible. The National Park Service also provided funding and staff members for this project. Finally, the National Parks and Conservation Association, Mazamas Mountaineering, and the DeVlieg Foundation supplied funding for graduate education, travel, and field-related equipment.

This project would not have gone forward without the support of staff at Olympic National Park. Kurt Jenkins, research wildlife biologist at the USGS-Olympic Field Station, and Patti Happe, wildlife biologist at Olympic NP, were instrumental in getting this project off the ground. Kurt, Patti, Gary Koehler and I conceived of this project over dinner several years ago, and Kurt and Patti's support has been unwavering since that time. Kurt wrote the grant and received the funding from USGS, while Patti supervised all phases of bear capture. She spent her valuable time pounding miles of trail and attempting to outwit the bears, and continually shared her expertise in wildlife capture and ecology. Roger Hoffman, GIS Specialist at Olympic National Park, never failed to arrive at just the right answer to any problem, field-related or otherwise. Roger helped me develop the GPS collar sampling scheme, and was always available to provide GIS help with both profound expertise and a sense of humor. Katherine Beirne, GIS Technician at Olympic National Park, created the Microsoft Access database, provided me with data while I was in Idaho, and assisted in the field. John Boetsch helped me develop my GPS probability model, and his wisdom in all matters related to data management kept me organized. Finally, I would like to thank Cat Hawkins-Hoffman, Chief of Natural Resources, for enthusiastically supporting all phases of this project.

This project benefited greatly from the dedication of various field crew members. Carrie Donnellan consistently made me laugh and see the bright side of even the most daunting problem, Dave Manson brought both good field judgment and humor to the project, and Marlon Concepcion, Mike Danisiewicz, and Brent Slone provided both light-heartedness and steadiness throughout bear capture. Multiple volunteers were willing to tromp, crawl, and push their way through the dense forests of Olympic National Park to measure vegetation, test GPS collars, and locate collars that had been slipped or released from bears. Bill Baccus exemplified dedication with his willingness to help where needed and to travel great distances to recover GPS collars. Finally, Lynn Emery packed up his mules every spring to deliver capture equipment and rancid bear bait to backcountry field stations.

Kathy Quigley, DVM, and Margaret Wild, DVM, provided valuable training, insight, and equipment for bear capture, and were always willing to respond to questions relating to animal capture procedures and animal welfare.

Staff at University of Idaho's Department of Fish and Wildlife Resources, particularly Karla Makus, Delaine Hawley, and Linda Kisha, provided encouragement and expertise in all things related to paperwork, budgets, and planning. Fellow graduate students relayed their myriad experiences with the graduate process, kept me sane when my course load seemed too daunting, and got me outside to play.

Finally, I would like to thank my parents for their faith and confidence in my abilities and their unyielding support throughout my life, as well as throughout this graduate experience. Their interest and fascination in this project brought them into the backcountry for a week where their enthusiasm was persistent, despite not seeing any bears. I also thank Steve Fradkin for his support and words of comfort and understanding during some of the more trying periods of this process.

# TABLE OF CONTENTS

**Thesis introduction**

**Chapter 1: Bias and accuracy of GPS radiotelemetry in coastal temperate forests**

**Chapter 2: Black bear distribution patterns in the Elwha River watershed of Olympic National Park**

# LIST OF TABLES

## CHAPTER 1

## CHAPTER 2

## LIST OF FIGURES

### INTRODUCTION

### CHAPTER 1

### CHAPTER 2

# LIST OF APPENDICES

## INTRODUCTION

For approximately 90 years two hydroelectric dams have blocked annual returns of anadromous fish to over 113 kilometers of the Elwha River in Washington's Olympic National Park (NP). Historically, the Elwha River supported runs of chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), pink, (*O. gorbuscha*), and chum salmon (*O. keta*), and steelhead (*O. mykiss*). The construction of the first of two dams from 1910 to 1913, about eight kilometers from the river's mouth, restricted salmon and steelhead to a small fraction of their historic range and excluded them completely from Olympic NP. The second dam, built between 1925-27, 13.7 kilometers upriver from the first dam, presented yet another impassable obstacle to anadromous fish.

The Department of Interior now proposes to remove both dams to fully restore the Elwha River ecosystem and native anadromous fisheries as authorized by the Elwha River Ecosystem and Fisheries Restoration Act of 1992. Removal of these dams, which is slated to begin in 2008, presents an unprecedented opportunity to study influences of restoring anadromous fish to one of Olympic NP's premier riverine ecosystems. Salmon and steelhead runs are estimated to increase by almost 400,000 adult fish following full restoration (NPS 1996). Researchers have begun establishing baseline values of marine-derived nutrients that are returned to Olympic NP's rivers each year by anadromous fish, thus providing the basis for monitoring ecosystem-level influences of salmon restoration on aquatic food webs and nutrient pathways (Winter et al. 2001, J. Duda, USGS, Personal Communication). Influences of this major modification of nutrient flow and food to terrestrial carnivores is poorly understood but has several implications. Perhaps most importantly, dam removal and subsequent salmon restoration may affect park black bear populations, resulting in altered nutrient flow dynamics throughout the watershed (Hilderbrand et al. 2004).

The purpose of this project is to describe broad-scale patterns in seasonal distribution and movements of black bears in Olympic NP prior to dam removal and to examine the performance of Global Positioning System (GPS) radio-telemetry in coastal temperate forests within the Pacific Northwest. The study provides baseline information by which to assess the long-term ecological effects of salmon restoration on distribution patterns of park bears. Information on the distribution of black bears will also help Olympic NP wildlife managers reduce seasonal bear/human conflicts in the Elwha backcountry and establish a long-term black bear monitoring program.

## BACKGROUND

### Use and Accuracy of GPS Telemetry

GPS telemetry is a relatively new technique in wildlife research and has been used only rarely in temperate forest environments (Janeau et al. 2001, Rodgers 2001, Taylor 2002). Dense forests and steep topography of Olympic NP pose significant challenges in the acquisition of successful GPS locations, yet the use of GPS collars presumably results in significantly more data than is generally possible with traditional VHF technology. However, it is necessary to evaluate the limitations of GPS technology in a temperate forest environment.

The GPS receiver in a telemetry collar requires unobstructed line-of-site communication with at least three satellites to establish the geographic position of the collar through triangulation. Geographic position accuracy is enhanced by both the number of satellites that can be located and used for triangulation and the position of those satellites in the sky. A minimum of three satellites is needed for triangulation, resulting in a 2-dimensional (2D) fix. Four satellites are required for a 3-dimensional (3D) fix, with the fourth satellite being used to determine the elevation of the collar. Horizontal dilution of position (HDOP) describes the configuration of satellites in the sky; a lower HDOP value indicates a better satellite configuration for triangulation while a high value suggests that satellites are more tightly grouped, and therefore less effective at triangulating. Two-dimensional fixes are less accurate than 3D fixes (D’Eon et al. 2002, Bowman et al. 2000, Edenius 1997, Moen et al. 1996, Rempel et al. 1995, Rempel and Rodgers 1997). A primary reason for this decreased accuracy is that in successive

2D fixes the elevation of the most recent 3D fix is used, thus introducing error in the horizontal position estimate (Rempel et al. 1995).

Topography and dense vegetation obstruct ground-satellite communications by influencing the proportion of sky available to the GPS receiver, thus impeding the ability of a collar to locate satellites and obtain a GPS location. Since the development of GPS-based telemetry systems, considerable research has been devoted to the study of topography and vegetation, and their effects on GPS telemetry success rates. Collars tested in boreal forests were successful 75-97% of the time, dependent on canopy cover (Dussault et al. 1999, Edenius 1997, Rempel and Rodgers 1997). In a temperate forest in southern France, 83% of fix attempts were successful (Janeau et al. 2001). Fix acquisition rates for collars on black bears in northern Ontario averaged 46%; however, the collar of a bear whose home range was in dense cover was successful 32% of the time (Obbard et al. 1998). Collars tested in the Selkirk Mountains of southeastern British Columbia had mean fix rates ranging from 70.9-100% (D'Eon et al. 2002). In heavy canopy cover in northern Minnesota (30-40 year old red pine plantations), a GPS collar on a moose acquired 5% 3-dimensional (3D) locations, 58% 2-dimensional (2D) locations, and 37% no location. It took an average of 112 seconds to obtain a fix under these dense cover conditions (Moen et al. 1996). Fix rates for collars used on grizzly bears on the Kenai Peninsula, Alaska ranged from 50-74%, but because collars attempted fixes several times per day, fixes were obtained on 97% of days (Schwartz and Arthur 1999). GPS-Simplex™ (Televilt TVP Positioning AB, Sweden) collars used on a red-deer in Belgium with four fix attempts per day had a 46% -3D fix success rate; 69% were in open areas while only 11% were in mature forest (Licoppe and Lievens 2001). The authors suggest these results may have underestimated the use of mature forests because a large proportion of mature beech forest did occur in the animal's home range.

The rate of acquiring successful fixes is related negatively to tree height (Dussault et al. 1999, Janeau et al. 2001), basal diameter, density, and canopy closure (Edenius 1997, Moen et al. 1996, Obbard et al. 1998, Rempel et al. 1995). An increase in tree density led to a decrease in GPS observation rate and an increase in the number of 2D fixes over 3D fixes (Rempel et al. 1995). In a boreal forest in Sweden, proportion of 3D locations varied inversely with canopy cover and basal area (Edenius 1997). In the Selkirk Mountains of British Columbia, canopy cover and the amount of sky unobstructed by topography were the only significant predictors of GPS collar fix-success (D'Eon et al. 2002). Basal area and DBH were excluded from the model because those variables were highly correlated with canopy cover (D'Eon et al. 2002). Snow cover on the branches of taller trees in a temperate forest in France also affected fix success negatively (Janeau et al. 2001). In contrast to the majority of studies that reported significant effects of vegetation on GPS telemetry, GPS collar performance was not affected by vegetative conditions in Mississippi, perhaps because a narrow range of vegetative characteristics existed within the controlled study site (Bowman et al. 2000). On the Kenai Peninsula, Alaska, a reduced likelihood of obtaining a successful fix was explained partially by canopy cover, but stem density, diameter and tree height did not affect fix success (Schwartz and Arthur 1999).

Animal activity may also play a role in the ability of a GPS collar to acquire a fix. GPS collars placed on free-ranging wildlife experienced lower fix-success rates than stationary collars, with the discrepancy attributed to changes in GPS antenna orientation caused by various animal behaviors (i.e. feeding and bedding; T. Graves 2004 Personal Communication, D. Heard 2004 Personal Communication). In Mississippi, GPS collars used on deer collected locations on 85% of attempts, though the ability of the collar to collect locations was affected by deer behavior. Collars on bedded deer obtained the least amount of fixes while collars on moving deer acquired the highest number of successful fixes with the lowest positional error (Bowman et al. 2000). On the contrary, a GPS collar on a moose in Minnesota was successful 88% of the time when the moose was inactive and only 69% of the time when the moose was active (Moen et al. 2001). D'Eon (2003) attributes a large amount of data loss to animal behavior when using GPS radiotelemetry and challenges future researchers to reduce bias in habitat selection studies by accounting for this loss.

Very little research with GPS collar technology has taken place in the temperate coniferous forests of the Pacific Northwest. Olympic NP biologists equipped two Roosevelt elk in an old-growth coniferous forest with GPS collars in 1999. They reported average GPS-fix acquisition success rates of about 50% (P. Happe, Olympic NP, Personal Communication).

## *Bear-Salmon Interactions*

Previous studies provide an incomplete and tenuous interpretation of what benefits Elwha River salmon restoration might confer to black bears in Olympic NP, or how the addition of salmon might influence populations or seasonal distributions of bears, bear/human conflicts in the park, or bear monitoring programs. Contrary to some expectations, salmon have not been reported to be common in the diets of black bears in

Oregon or Washington (Poelker and Hartwell 1973, Cederholm et al. 2000). These findings may reflect declining populations of salmon, or perhaps seasonal timing of spawning that overlaps considerably with the denning period of bears. It is also plausible that because fish are highly digestible, they are under-reported when using scat analysis as a basis of determining diet (Hilderbrand et al. 1996). Hand-planted carcasses of salmon were consumed frequently by black bears in selected areas of Olympic NP when carcasses were made available prior to den entry (Cederholm et al. 1989). Additionally, historical reports for the Olympic Peninsula describe instances of black bears utilizing salmon (Scheffer 1949). Over a two-day period in December, 1938, Scheffer noted numerous bear tracks and half-eaten salmon along the Calawah and Bogachiel Rivers in the western portion of the park. Further, a 1943 Washington State Game Department report states "western Washington bear are of poorer quality since their meat is sometimes tainted from feeding upon salmon" (Scheffer 1949). In a recent thorough review of salmon-wildlife relationships in Oregon and Washington, Cederholm and co-authors (2000) concluded that "salmon populations do not represent a predictable food supply to bears in Washington and Oregon….", but that "…if salmon were to be found in substantial and predictable numbers, bears in Oregon and Washington….would also establish traditional use patterns around salmon". Hilderbrand et al. 1996 further stated that "…spawning salmon are more nutrient dense than virtually any other food resource available to bears in the Pacific Northwest…"

Both brown and black bears in Alaska, British Columbia and California consume salmon during their fall spawning migrations. All radio-collared brown bears on southwest Kodiak Island used salmon streams, though annual variation in use patterns occurred depending on yearly fluctuations in salmon and berry availability (Barnes 1989). Sockeye salmon in the Wood River system of southwestern Alaska experienced density-dependent predation by brown bears, with an asymptotic increase to about 3000 salmon consumed per stream per year (Quinn et al. 2003). Movements and distribution of black bears were linked closely to salmon migrations in a southeast Alaskan stream (D. Chi. personal communication reviewed in Cederholm et al. 2000). Black bears preyed heavily upon chum and pink salmon at Olsen Creek, Alaska, and of the fishing sequences observed by the author, bears were successful 70% of the time (Frame 1974). Black bears in coastal British Columbia ate an average of 13 salmon/bear during a 45-day autumn (September to November) chum salmon spawning period, comprising 74% of the salmon entering the stream (Reimchen 2000). Finally, salmon tissue was present in 10% of black bear fecal samples collected near spawning sites in coastal California (Kellyhouse, 1975).

Several investigators have looked at selective predation by bears feeding on salmon in Alaska and British Columbia (Black bears: Frame 1974, Reimchen 2000; Brown bears: Gende et al. 2001, Quinn and Buck 2000, Quinn and Buck 2001, Quinn and Kinnison 1999, Ruggerone et al. 2000). In high-density salmon areas, both black and brown bears selected salmon based on both the sex and condition of salmon. Unspawned fish, especially females, were consumed more frequently than spawned-out salmon (Frame 1974, Gende et al. 2001, Gende et al. 2004, Ruggerone et al. 2000). However, 70-80% of salmon consumed by black bears in British Columbia were partially or completely spawned out at the time of capture (Reimchen 2000). Larger fish were generally consumed more frequently than smaller fish (Frame 1974, Gende et al. 2001, Quinn and

Buck 2001, Quinn and Kinnison 1999, Reimchen 2000, Ruggerone et al. 2000) and with the exception of Frame (1974) males were also consumed more frequently than females (Quinn and Buck 2000, Quinn and Buck 2001, Quinn and Kinnison 1999, Reimchen 2000, Ruggerone et al. 2000). Given this selective predation, it has been hypothesized that bears and other terrestrial carnivores exert a marked evolutionary pressure on salmon, potentially influencing their life history strategy as well as their morphology (Quinn et al. 2001, Willson et al. 1998).

The evidence of bear use of salmon resources across western North America suggests that removal of the Elwha dams and subsequent salmon restoration may provide a significant food resource to bears in Olympic NP. Salmon represent a lipid-rich food source for bears, particularly in the fall when hyperphagia, or intense feeding, is required (Hilderbrand et al. 1999*a*). Lipids are responsible for the significant mass gains seen in bears prior to hibernation and provide the majority of energy necessary for bear maintenance during hibernation (Hilderbrand et al. 2000). Further, because females give birth to young during this period of prolonged fasting, they must accumulate sufficient energy stores to maintain them throughout gestation and the first few months of lactation. Fat accumulation in the fall is therefore correlated with reproductive success in bear dens (Elowe and Dodge 1989, Samson and Huot 1995, Hilderbrand et al. 1999*a*, Hilderbrand et al. 2000).

Bears in Olympic NP appear to rely heavily on huckleberries (*Vaccinium spp*.) during the fall period of hyperphagia. Because berries are low in fiber, they are highly digestible (>70% dry matter digestibility; Welch et al. 1997). Daily fruit consumption by captive brown and black bears that were provided fruit ad libitum averaged 34 ± 6% of their body mass; bears that weighed between 80 and 100 kg were capable of harvesting enough berries to gain weight at their physiological maximum (Welch et al. 1997). Thus, smaller bears such as those found in Olympic NP are likely able to accumulate substantial energy reserves during good berry years. However, since huckleberries appear to provide the bulk of the yearly fall food resource in Olympic NP, bears are ultimately limited in size by bite rates, bite sizes, and berry presentation (Welch et al. 1997). They are also limited by berry production; good years provide sufficient energy reserves while meager years, particularly in the absence of an alternative food source, leave bears in poor condition. Given these limitations, the return of spawning salmon might supplement huckleberries as a lipid-rich fall food for bears in Olympic NP while providing an alternative food source. Salmon-fed wild brown bears are larger in size, have more cubs per litter, and exist at higher population densities than bears with a more vegetarian diet (Hilderbrand et al. 1999*a*). Hence, I speculate that the addition of salmon to bear diets may contribute to a change in body size, reproductive success, population density, and seasonal distribution patterns.

In addition to direct benefits to bears, salmon restoration is expected to cause a favorable shift in nutrient dynamics within the watershed, particularly within the riparian corridor. The return of salmon to their natal streams for spawning provides an ecologically significant link between marine systems and inland freshwater and terrestrial systems (Ben-David et al. 1998, Bilby et al. 1996, Willson and Halupka 1995, Willson et al. 1998). Spawning salmon increase watershed productivity by transporting marine-derived nutrients to freshwater spawning sites, as well as to terrestrial systems surrounding those sites (Willson et al. 1998). In western Washington, spawning coho salmon provided nutrient enrichment to the aquatic food web: epilithic organic matter, aquatic macroinvertebrates, and resident fishes were all enriched with marine-derived nitrogen ($^{15}N$) and carbon ($^{13}C$; Bilby et al. 1996). The proportion of salmon-contributed N in local biota ranged from 17-30%, depending on trophic category (Bilby et al. 1996). Further, 17.5% of riparian vegetation was enriched with marine-derived nitrogen (Bilby et al. 1996). The salmon-spawning portion of Sashin Creek, southeastern Alaska, was also greatly enriched with marine-derived nitrogen ($^{15}N$), which proved to be the predominate source of N in surrounding food webs (Kline et al. 1990). In 3 out of 5 riparian plant species studied on Chichagof Island, southeast Alaska, there was a decrease in $\delta^{15}N$ values with increasing distance from salmon-bearing streams (Ben-David et al. 1998). Hilderbrand et al. (1999*b*) found a similar pattern in white spruce foliage: the proportion of marine-derived nitrogen in spruce needles decreased with distance from salmon-spawning areas.

Piscivorous predators are important vectors for transporting marine-derived nitrogen away from stream environments (Ben-David et al. 1998). Bears may play especially important roles in nitrogen transfer, as they are capable of redistributing nutrients through movement of salmon carcasses, as well as through feces and urine (Cederholm et al. 1989, Gende et al. 2004, Hilderbrand et al. 1999*b*). Bears in Olympic NP transported hand-planted, tagged salmon carcasses away from streams and frequently consumed entire carcasses, only to defecate the salmon tags at a later date (Cederholm et al. 1989). Bears on Chichagof Island, Alaska, removed nearly 50% of the pink and chum salmon-derived nutrients from the stream by carrying the carcasses an average of 4.5 meters from the stream bank (Gende et al. 2004). On the Kenai Peninsula, Alaska, 15.5-17.8% of the total nitrogen in white spruce needles within 500 meters of a salmon-bearing stream was derived from salmon; of that, 83-84% was distributed by bears (Hilderbrand et al. 1999*b*). These findings suggest that nutrient dynamics in the Elwha River watershed may be greatly affected by salmon restoration, with bears serving an important role in redistributing marine-derived nutrients throughout the terrestrial system.

### *History of Bear Research and Management in Olympic NP*

Olympic NP is generally regarded as having a large population of black bears. Black bears are seemingly abundant throughout the park and seen frequently in the backcountry; however, little is known about bears within the park. Olympic NP biologists have maintained a bear observation log since 1999, which indicates bear activity throughout the park. However, this observation log is biased by inconsistent reports of bear activity. Additionally, observations are concentrated in areas of high overlap between bears and humans.

Prior to this study, the only research on black bears conducted in the park was a cooperative effort initiated in 1996 between Washington Department of Fish and Wildlife (WDFW) and Olympic NP. In that study, the Olympic Peninsula, including the park and surrounding forest lands, was one of three study areas in a statewide effort to understand black bear ecology. Ten bears were radio-equipped within Olympic NP and their movements monitored via aerial telemetry on a monthly basis. Inclement weather and difficult access was a serious impediment to data collection, so limited information was obtained about park bears. Across the Olympic Peninsula study area, mean home range size of females (28.3 km$^2$) was less that that for males (125 km$^2$; Koehler and Pierce

2003). Further, males ranged widely and unpredictably within the park, occasionally leaving the park (Koehler 1998). Sampling was not sufficient to delineate or describe seasonal distribution and movement patterns. Bears in Olympic NP were older than those captured in study areas outside the park (11 years for males and 8.5 years for females; Koehler 1998, 1999).

Bear management activities in Olympic NP were minimal until the late 1990's when escalating bear-human conflicts throughout the park, notably in the Elwha Valley, prompted the need for further action. Managers at Olympic NP relocated one bear, destroyed another, and temporarily closed popular backcountry destinations to overnight use, all in an aggressive campaign to minimize positive conditioning of bears to human food sources. Olympic NP managers closed an eleven-kilometer stretch of the Elwha valley, a popular summer hiking destination, to all human use during early summer for three consecutive years (1998-2000). The park also initiated a bear management program focused on visitor education, proper food storage methods, and bear-resistant garbage disposal.

It is not known whether the increase in bear/human conflicts was due to an increase in the bear population, variations in natural food supply, increase in habituation and food conditioning, or a combination of these factors. Data acquired during this study provide information on seasonal movement and habitat use patterns of black bears, thus serving as the foundation for answering these important management questions.

### *Long-Term Monitoring*

As a long-term solution towards reducing bear-human conflicts throughout the park, Olympic NP wishes to develop a program to monitor productivity and abundance of bears, variation in seasonal foods, and seasonal periods of bear/human conflicts in the Elwha Valley. Due to enormous difficulties and costs associated with monitoring bears in this large, inaccessible wilderness, park biologists have considered monitoring the relative abundance and productivity of bears visible on berry-producing subalpine meadows during late summer, by surveying bears that appear to concentrate in low elevations during late spring-early summer, or by employing non-invasive hair-snare techniques paired with subsequent genetic analysis. However, park managers have no information to answer the following questions: What proportion of bears use these areas of concentration? How variable are distribution patterns among years? When do bears concentrate in these areas? Further, there are valid concerns that any long-term monitoring of seasonal concentrations of bears could be affected by ecosystem-level changes in nutrient availability caused by salmon restoration activities. Answers to these questions are needed to identify optimum sampling schedules and sampling frames and to evaluate potential influences of salmon restoration on long-term black bear distribution.

## STUDY AREA

Olympic National Park, established in 1938 and 3800 km$^2$ in size, is situated on Washington State's Olympic Peninsula, in the northwest corner of the continental United States (Figure 1.0). It is bordered to the north by the Strait of Juan de Fuca, to the east by Puget Sound, and to the west by the Pacific Ocean. The park is one of the most diverse natural areas in the conterminous United States, with elevations ranging from sea level to almost 2,450 meters and annual precipitation from 40-600 cm. The western 'coastal strip' encompasses nearly 105 kilometers of wilderness coastline, and the central portion of the park comprises temperate coniferous forests, expansive river valleys, and the glacier-clad Olympic Mountains.

The Elwha River watershed is the largest on the Olympic Peninsula, encompassing 803 square kilometers, of which 83% is contained within the boundaries of Olympic NP. The Elwha River flows northwest for over 83 kilometers from its headwaters in the Olympic Mountains to the Strait of Juan de Fuca. The study area is under a maritime climatic influence, with mild, wet winters and relatively cool, dry summers.

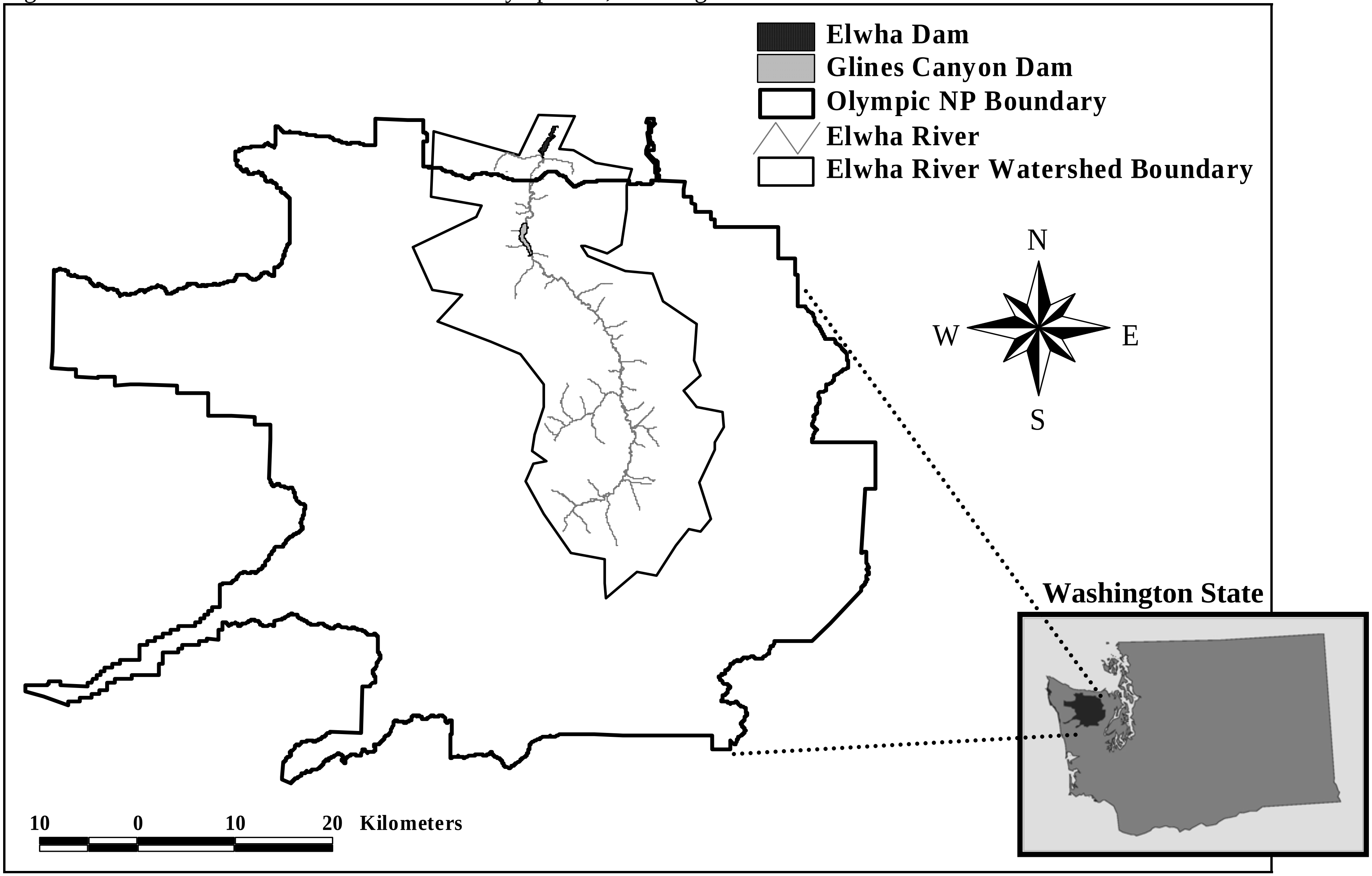
The Elwha watershed maintains a unique geographical position within Olympic NP. It lies within the transition zone between the temperate coniferous forests of the western peninsula dominated by sitka spruce (*Picea sitchensis*), and the dry coniferous Douglas fir (*Pseudotsuga menziesii*) forests of the eastern peninsula. The watershed is characterized by a range of environments, from lowland, temperate coniferous forests to high-elevation, subalpine meadows.

Below 600 meters, the watershed falls within the western hemlock (*Tsuga* *heterophylla*) zone where forests are dominated by western hemlock and Douglas fir (Henderson et al. 1989). The western hemlock zone includes some of the most productive forest lands on the Olympic Peninsula (Henderson et al. 1989). Western hemlock and western red cedar (*Thuja plicata*) are climax species within this zone, while red alder (*Alnus rubra*) is an early seral species along the riparian corridor (Henderson et al. 1989). The lower elevations of the Elwha watershed within the western hemlock zone support an array of other tree species, including Pacific madrone (*Arbutus menziesii*), grand fir (*Abies grandis*), bigleaf maple (*Acer macrophyllum*), and black cottonwood (*Populus balsamifera*). Lodgepole pine (*Pinus contorta*) and western white pine (*Pinus monticola*) may also occur (Henderson et al. 1989).

At middle elevations (600-1000 meters), the watershed falls within the silver fir (*Abies amabilis*) zone where western hemlock and Pacific silver fir forests dominate (Henderson et al. 1989). This transitional zone is characterized by forests with low to moderate productivity. Douglas fir commonly co-occurs within this zone, and Alaska yellow cedar (*Chamaecyparis nootkatensis*), western red cedar (*Thuha plicata*), mountain hemlock (*Tsuga mertensiana*), western white pine, and Pacific yew (*Taxus brevifolia*) are also regular constituents (Henderson et al. 1989).

The subalpine zone of the Elwha watershed above 1000 meters is characterized by the mountain hemlock zone to the south and west and the subalpine fir (*Abies lasiocarpa*) zone to the east (Henderson et al. 1989). Productivity of the mountain hemlock zone is considered to be low due to the duration of annual snowpack (Henderson et al. 1989). This area is dominated by mountain hemlock and subalpine fir and also includes Alaska yellow cedar and Pacific silver fir. Mountain hemlock forests are commonly associated with huckleberry species (*Vaccinium deliciosum and V. membranaceum*), which are preferred late-season bear foods. The subalpine fir zone is characterized by subalpine fir forests interspersed with Pacific silver fir and Alaska yellow cedar. This zone is also home to a number huckleberry species.

Figure 1.0. The Elwha River watershed within Olympic NP, Washington.



## PROJECT OBJECTIVES

The goal of this thesis is to describe landscape-scale patterns of black-bear distribution in Olympic NP, evaluate GPS fix-acquisition bias in a temperate forest environment, and lay the groundwork for development of population-monitoring strategies. Because I used GPS-equipped radio-collars, objectives of this study focus on large-scale questions suitable for study using remotely sensed data.

This study addresses several specific objectives and hypotheses. Due to concern over the variable likelihood of locating satellites in a temperate forest environment, a primary objective was to assess performance and observational bias of GPS radio-telemetry collars in Olympic NP. Several hypotheses relating to this objective were stated. The first was that vegetative and topographical variables would affect both location accuracy and fix acquisition rates of GPS radio-collars. Vegetative and topographical variables were also expected to affect the proportion of 3D versus 2D fixes acquired. Finally, HDOP was expected to relate to location accuracy of GPS radio-collars.

The remaining study objectives relate to landscape-scale patterns of habitat use by black bears in Olympic NP. Primary descriptive objectives were: 1) to illustrate seasonal home ranges of black bears within Olympic NP and; 2) to describe bear use of riparian areas, particularly within the Elwha River watershed. Additionally, it was hypothesized that bears utilize different elevations during different times of the year; thus, seasonal patterns of elevation distribution by black bears were examined. A final objective was to examine patterns of resource selection. Within this objective, two specific hypotheses were stated.  First, that composition of seasonal home ranges of bears differed from landscapes available.  Secondly, that bears select habitats within their home range in disproportion to availability.

## THESIS FORMAT

This thesis is divided into two main chapters. The first chapter addresses the GPS collar accuracy and bias testing component of the study. I examine GPS collar performance across the range of environments encountered in the Elwha River watershed in order to quantify habitat-related biases and inaccuracies inherent with the use of GPS telemetry collars. Based on these findings, I develop a model to predict the likelihood of a collar acquiring a location in any part of the watershed. I then propose the use of correction factors for weighting individual locations from GPS collars to minimize bias in analysis of black bear home range and habitat selection.

In the second chapter, I examine distribution patterns of black bears in the Elwha River watershed. I calculate seasonal and annual home ranges, examine patterns of elevation use, and investigate use of the Elwha River and its potential salmon-bearing tributaries. I also examine seasonal and annual patterns of resource selection. I use information gathered in chapter 1 to apply weighting factors to biased bear location data from GPS radio-collars.

# Chapter 1: Bias and accuracy of GPS radiotelemetry in coastal temperate forests

## INTRODUCTION

Wildlife research using GPS radio-telemetry yields significantly more data than was previously possible using traditional VHF radio-telemetry techniques. However, GPS telemetry is not without problems. There are two common types of error associated with GPS telemetry: data omission and spatial inaccuracy. GPS collars are variably successful in obtaining location data under different environmental conditions due to forest structure and topography. Characteristics such as canopy closure (D’Eon et al. 2002, Moen et al. 1996, Rempel et al. 1995), topographic obstruction (D’Eon et al. 2002, Frair et al. 2004,), tree height (Dussault et al. 1999, Janeau et al. 2001), percent slope (Frair et al. 2004), and vegetation type (Di Orio et al. 2003, Frair et al. 2004, Obbard et al. 1998) reduce the likelihood of a GPS receiver contacting satellites, and therefore, acquiring and storing a location. Because wilderness areas are not homogenous in terms of terrain and forest attributes, data loss occurs disproportionately across the landscape. This systematic omission of data introduces bias in the estimation of animal home range and resource selection patterns (D’Eon et al. 2002, D’Eon 2003, Di Orio et al. 2003, Frair et al. 2004).

The second type of GPS collar error, spatial inaccuracy, appears to be a function of poor satellite configuration (i.e. high ‘Dilution of Precision’ [DOP]; D’Eon et al. 2002, Edenius 1997), satellite availability (2D versus 3D locations; Bowman et al. 2000, D’Eon et al. 2002, Di Orio et al. 2003, Edenius 1997, Rempel et al. 1995), or habitat attributes

(Di Orio et al. 2003, D'Eon et al. 2002, Rempel et al. 1995). Because dilution of precision is a numeric indicator of satellite geometry with a higher DOP constituting poor measurement results, it is a good predictor of position accuracy. Similarly, the number of satellites available for a collar to acquire a GPS location has consequences for collar accuracy. Because only three satellites are used to triangulate a 2-dimensional (2D) fix and four satellites are required for a 3-dimensional (3D) fix, 2D fixes are less accurate than 3D fixes (D'Eon et al. 2002, Bowman et al. 2000, Edenius 1997, Moen et al. 1996, Rempel et al. 1995, Rempel and Rodgers 1997). A primary reason for this decreased accuracy is that in successive 2D fixes the elevation of the most recent 3D fix is used, thus introducing error in the horizontal position estimate (Rempel et al. 1995). Whatever their cause, errors in GPS locations could cause biases in analysis of resource selection of bear data, depending on their magnitude and the degree of habitat heterogeneity in the study area. These biases may be minimized by placing error buffers around animal locations acquired from GPS collars (Moen et al. 1997, Rettie and McLoughlin 1999).

Accuracy and bias of GPS telemetry have been studied previously in coniferous forests of North America (D'Eon et al. 2002, Di Orio et al. 2003, Moen et al. 1997, Schwartz and Arthur 1999), but never in mature coastal temperate forests of the Pacific Northwestern United States. Olympic NP posed unique problems for GPS radio-collars due to its steep terrain and heavily forested valleys, and I suspected that influences of forest overstories were potentially greater than ever previously studied. Due to concerns about inconsistent fix-success rates and spatial inaccuracy of GPS radio-collars in the mountainous terrain and dense temperate forests of Olympic NP, I examined GPS collar performance across the range of environments encountered in the Elwha River watershed to quantify habitat-related bias. I examined influences of environment on GPS collar performance by placing test collars throughout the watershed, recording information about the surrounding topography and vegetation, and modeling the effects of these habitat characteristics on GPS collar fix-acquisition success and spatial accuracy. Specifically, I developed a model to predict the likelihood of a collar acquiring a location in any part of the Elwha River watershed. Further, I established correction factors to weight individual locations from GPS collars, thereby laying the groundwork for minimizing bias in analysis of black bear home range and habitat selection data.

# METHODS

## *Field Methods*

### <u>*Assessing bias and success rates of GPS-telemetry collars:*</u>

I examined potential biases and performance of GPS Simplex™ (Televilt TVP Positioning AB, Lindesberg, Sweden) radio-collars by placing collars at randomly chosen locations near trail systems in the Elwha Valley and Hurricane Ridge areas of Olympic NP. Success rate, or the rate at which GPS collars successfully acquire positional fixes, was assumed to vary according to habitat and landscape features present within bear's home ranges. I examined several variables for their ability to predict the likelihood of successfully obtaining satellite fixes in different habitats utilized by bears. These variables also provided a basis for weighting bear locations derived from GPS radio-telemetry in the subsequent analyses of home range and resource selection.

The GIS Specialist at Olympic NP assisted with the identification and development of two categorical variables for use in establishing sampling locations: canopy cover and "satellite view". Both categorical variables were available from Olympic NP's Geographic Information System. I determined percent of overstory vegetative cover for each 25 X 25m pixel in the Elwha watershed based on GIS habitat layers. I then partitioned percent of canopy cover into 4 categories: 0-10% cover (includes all meadow types and shrub layers), 11-40% cover, 41-70% cover, and 71-100% cover.

I defined the potential satellite view associated with each pixel as the portion of available sky that is traversed by GPS satellites and unobstructed by topography. To determine satellite view, from the center point of each pixel, 48 points were evaluated for their potential to “see” satellites, 1-5 points in each cardinal and semi-cardinal direction (i.e. SE aspect at 15, 30, 45, 60 and 75 degrees above the horizon, etc) (Figure 1.1). Because few GPS satellites are present in the northern sky of the Pacific Northwest (from approximately 315° [NW] to 45° [NE]), fewer sample points were distributed in that part of the sky (Figure 1.1). I rated satellite view of each pixel as the percentage of 48 potential satellite views not obscured by topographic relief. Based on the graphical representation of the numbers of pixels and the proportion of the 48 views that each pixel in the Elwha watershed could “see”, I classified potential satellite view into 4 categories: lowest satellite view (0-60% of potential satellite views are not obstructed by topography), moderate-low satellite view (60-75% of potential satellite views are not obstructed), moderate-high (75-90%) and highest (90-100%) (Figure 1.2, Table 1.1).

I sampled sixty-three locations from the 4 satellite view and 4 cover-type categories, resulting in 3-4 randomly selected replicates from each of 16 different possible sampling combinations (Table 1.2). My goal was to sample 4 replicate stands of each of the 16 habitat combinations (64 stands total), with approximately equal sampling effort at low (<1000 meters) and high (>1000 meters) elevations in the Elwha River valley and Hurricane Ridge areas, respectively. For logistical reasons, I randomly selected sample sites from within 1 km of roads or trails, and in some instances, were selected based on their proximity to bear trapping locations. Due to safety concerns, I successfully completed GPS collar testing in 63 of the 64 stands.

I programmed test collars to attempt a GPS fix either four times per day ($n=3$) or once each hour ($n=60$) and placed them at the pre-selected locations for at least one 24-hour period. All collars were placed approximately 0.5-1-m above ground with the GPS

Figure 1.1. Typical daily satellite availability in the Elwha watershed, Olympic NP. The variable "satellite view" represents the proportion of 48 satellite views available from any point within the watershed.

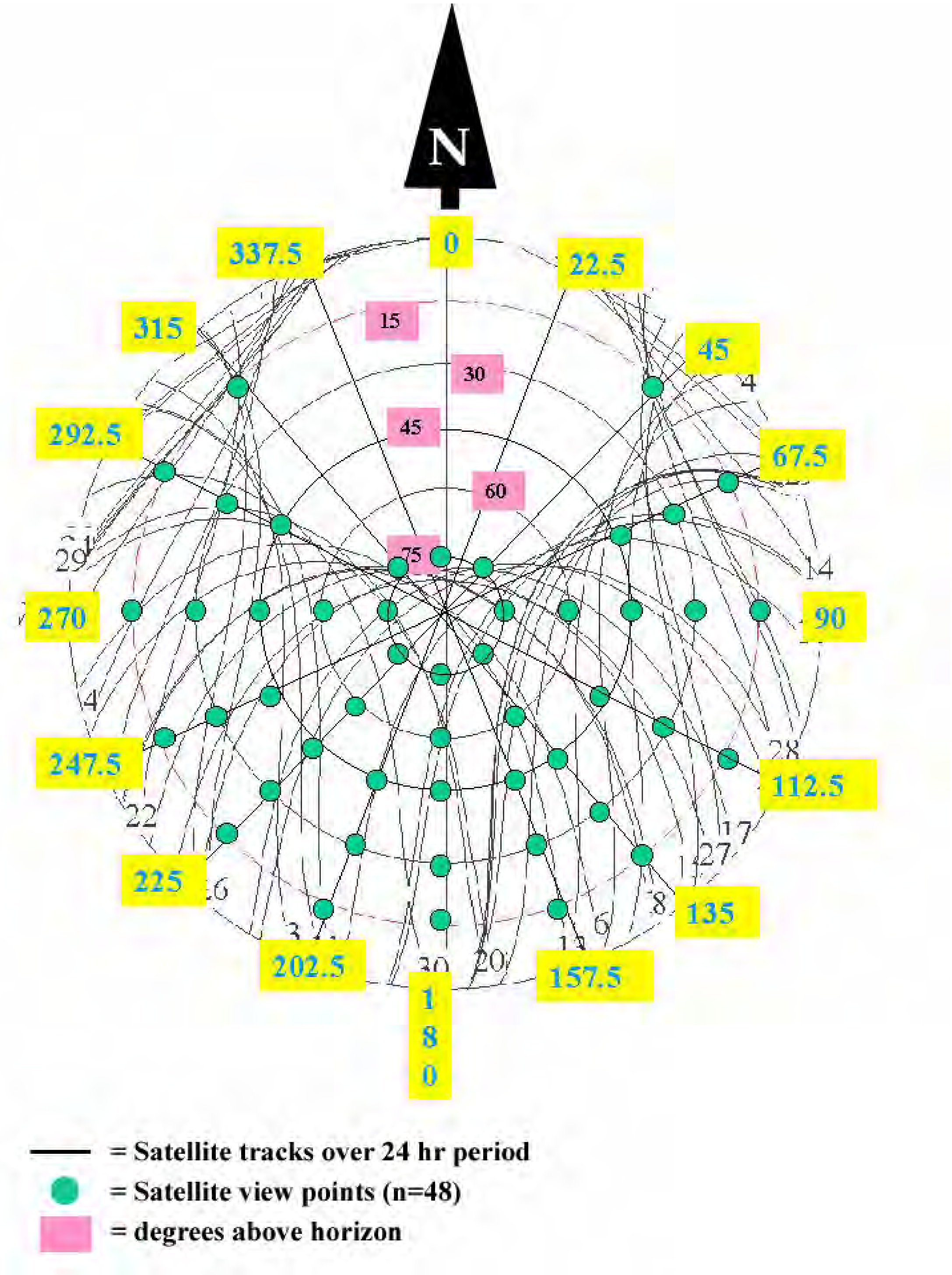


Figure 1.2. Number of 25 x 25 meter pixels (cells) and the proportion of each of 48 potential satellite views that can be seen from each of those pixels in the Elwha watershed, Olympic NP.

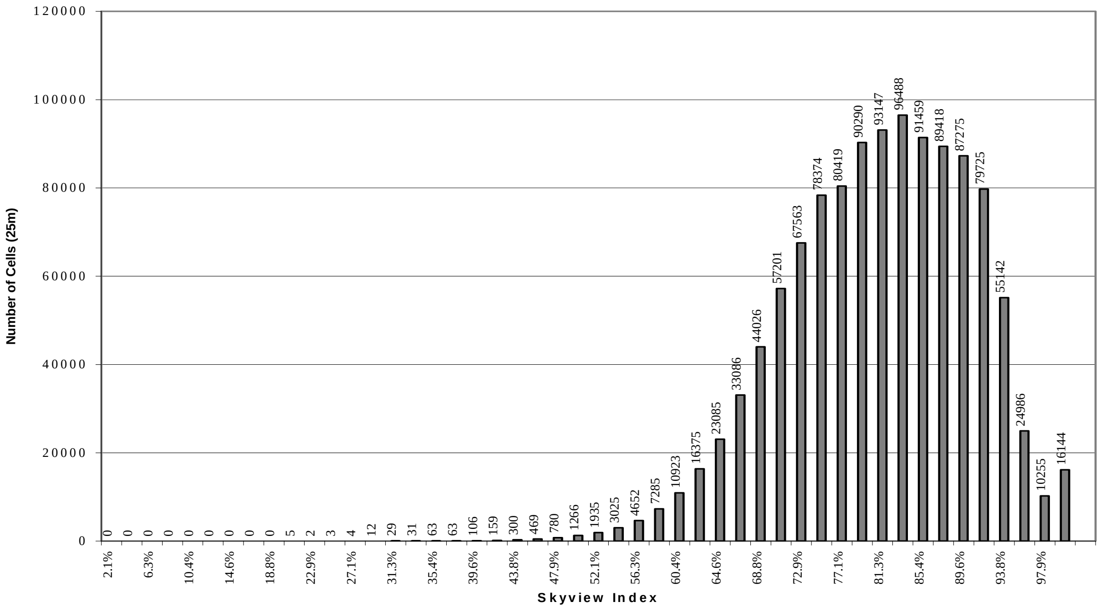


Table 1.1. Classification scheme for four categories of satellite view in Olympic NP, including number of pixels in the Elwha watershed that fell within each class of satellite view, and the number of satellite view 'points' that each class represented.

| **Number of pixels** | **Potential satellite views** | **Satellite view points (*n*/48)** |
|---|---|---|
| 31,112 | 20-60% | 10-28 |
| 319,710 | 60-75% | 29-35 |
| 628,496 | 75-90% | 36-42 |
| 186,252 | 90-100% | 43-48 |

Table 1.2. Canopy cover and satellite view combinations used to determine test site locations for examining bias of GPS radio-collars, Olympic NP.

| **Class level** | **Canopy cover** | **Satellite view (# points visible[1])** |
|---|---|---|
| 1 | >70% | 43-48 points |
| 2 | 41-70% | 43-48 points |
| 3 | 11-40% | 43-48 points |
| 4 | <10% | 43-48 points |
| 5 | >70% | 36-42 points |
| 6 | 41-70% | 36-42 points |
| 7 | 11-40% | 36-42 points |
| 8 | <10% | 36-42 points |
| 9 | >70% | 29-35 points |
| 10 | 41-70% | 29-35 points |
| 11 | 11-40% | 29-35 points |
| 12 | <10% | 29-35 points |
| 13 | >70% | 10-28 points |
| 14 | 41-70% | 10-28 points |
| 15 | 11-40% | 10-28 points |
| 16 | <10% | 10-28 points |

[1] 'Visible' refers to points not obstructed by topography.

antenna facing upward, towards the sky. Collars programmed to attempt a fix four times per day had been programmed for placement on bears and were used for testing during the bear-trapping period. Collars programmed to attempt 24 GPS fixes per day were programmed primarily for testing.

At each sampling site, I measured and recorded the following vegetation and landscape features: cover type (deciduous forest, coniferous forest, mixed forest or unforested), slope, aspect, basal area, percent canopy cover (including relative cover of deciduous and coniferous forest components), tree height of modal trees, tree density, and diameter at breast height (DBH). I obtained remotely-sensed data for each site and derived forest structure and forest cover-related variables from Pacific Meridian Resources GIS data (Pacific Meridian Resources Vegetation and Landform Database Development, September 30, 1996).

I measured slope, aspect, and basal area from the center of each selected site. Slope and aspect were measured with a magnetic compass, and basal area with a “Cruz-All” at the 5, 10 or 20 factor, depending on the forest type. I measured canopy cover with a spherical densiometer in four cardinal directions from the plot center. Due to problems encountered during 2002 with overestimating canopy cover using a spherical densiometer (Cook et al. 1995), I also began using a GRS Densitometer at each site for comparison purposes. The GRS Densitometer was used to measure the vertical intercept cover of plot center, and at 7.5m, 15m and 22.5m from plot center in each cardinal and semi-cardinal direction (for a total of 25 points). The heights of 4 trees that best represented the overstory canopy were measured using a laser range finder from plot center. I used the point-center-quarter method to measure tree density, average tree diameter and basal area (Mueller-Dumbois and Ellenberg 1974). I measured distances and diameter at breast height of the nearest tree in each of 4 quadrants (N→E, E→S, S→W, W→N) identified around 9 points at each radio-collar test location. The sampling points were the test-collar location itself and 8 points, each 30 m from this central point in each of the semi-cardinal directions. All measurements were taken in the summer during the "leaf-on" season to avoid problems associated with variable deciduous cover. The “leaf-on” season from April to October represents the majority of annual time during which bears are active. A tree was defined as any live tree greater than 10 cm in DBH.

### *Assessing accuracy of GPS-telemetry collars:*

To measure location accuracy of GPS collars, I selected 16 sites from the original 63 sites that represented the range of conditions and fix-success rates observed in the Elwha River valley and at Hurricane Ridge. These 16 sites were selected in the 2004 season based on data acquired from test collars during 2002 and 2003. Of the 63 sites sampled during those years, I examined the range of successful 2D and 3D GPS telemetry fixes to determine which sites had the best and worst fix-success rates, respectively. I selected the 4 least successful sites (18-42% overall fix-success; 0-10% of fixes 3D) and the 4 most successful sites (100% overall fix-success; 64-73% of fixes 3D) to adequately sample endpoints of the observed range. I then systematically selected another 8 sites that fell between these two extremes (48-94% overall fix-success; 0-31% of fixes 3D).

At each of the 16 sites selected, I placed two GPS collars and left them to collect location data for at least 48 hours. Each collar was programmed to attempt fixes at 30 minute intervals. The first collar was placed at approximately the same location and orientation as during the previous year's testing of location success. The second collar was placed within 30 meters of the first, but at a less-optimal site that approximated a bear bedding site (i.e., under a large tree). The purpose for the placement of the latter collar was to examine the potential influences of collar orientation and microsite characteristics associated with behavior of bears. I placed these collars upright at the base of a tree in a configuration approximating a bedding bear ($n=12$). If the habitat was open and did not contain a bedding site, I positioned the collar on its side with the antenna facing the slope ($n=4$). At each collar location, I measured a variety of habitat variables: slope and aspect using a magnetic compass with built-in clinometer, canopy cover using a spherical densiometer, and DBH, distance and azimuth of the closest tree.

I used a GPS Pathfinder® Pro XR by Trimble (Trimble Navigation Limited, Sunnyvale, CA) to average at least 2000 points and record a differentially corrected UTM coordinate at the center of each site. This coordinate was considered the reference location on the ground. The Pro XR is considered to provide locations with sub-meter accuracy (Trimble Navigation Limited, Sunnyvale, CA).

## ***Statistical Methods***

### Quantifying bias of GPS-telemetry collars:

I used logistic regression (Hosmer and Lemeshow 2000) to model location success as a function of environmental characteristics. Location success was a binary variable recorded as successful or unsuccessful each time a GPS test collar attempted to acquire a fix. Location success was treated as the dependent variable in the logistic regression procedure. Habitat attributes measured at the site or obtained from remotely sensed data formed the pool of predictor variables in the model. Statistical analyses were performed using SAS 8.0 software (SAS Institute 1996). I treated individual fixes as independent sample units in the analysis. I acknowledge that fixed terrain and vegetative attributes within each site may reduce independence; however, the range of satellite availability changed throughout each day and produced highly variable location success among hours within sites. This was evidenced by the inconsistent success of GPS collars over a 24 hour testing period; acquisition of a single fix did not necessarily result in attainment of additional fixes. Logistic regression model parameters are robust generally to violations of the independence assumption despite overestimated precision (Burnham and Anderson 2002: p. 67). Further, I found no evidence of overdispersion in location success data that would indicate a noteworthy lack of independence in the data set and raise concerns over potentially biased precision estimates (Burnham and Anderson 2002).

### *MODEL BUILDING*

I developed an *a priori* set of candidate models composed of a global model and its reduced forms. The parameters contained in the global model were chosen *a priori* based on landscape variables known from previous studies to affect GPS collar location success (D’Eon et al. 2002, Di Orio et al. 2003, Frair et al. 2004, Moen et al. 1996). I excluded variables that were not significant in univariate tests ($P > 0.10$) and eliminated one variable from each pair of correlated variables (Pearson $r > 0.5$). Potential covariates were overstory canopy cover class, tree size class (DBH in cm), satellite view, relative cover of deciduous trees, tree density, slope, aspect, basal area, tree height, elevation, and the interaction between satellite view and canopy cover class. Half of the variables were remotely sensed. Though I measured overstory canopy cover and DBH at each test site, remotely sensed forms of these variables were more appropriate for predictive purposes. Additionally, although I used 4 class levels of overstory canopy cover for test site determination, I further reduced this to 3 classes for analytical purposes (0-10% and 11-40% canopy cover were combined to become 0-40% canopy cover). For the two categorical variables (canopy cover class and tree size class), I coded the most open classes, or those least likely to influence whether or not the collar successfully acquired a fix, as the reference category.

I calculated the variance inflation factor, $\hat{c}$ (Pearson's $\chi^2$ divided by the degrees of freedom) to evaluate model fit and to determine whether I needed to apply a quasi-likelihood variance expansion term for overdispersed data (if $\hat{c}$ was substantially larger than 1; Burnham and Anderson 2002). Once model adequacy was established, I used Akaike's information criterion (AIC), Akaike differences ($\Delta_i$) and Akaike weights ($w_i$) to identify the most parsimonious model for examining GPS collar success as a function of environmental covariates.

The most parsimonious model was used to predict the probability of a GPS collar successfully obtaining fixes under various conditions. Because this model was subsequently used to reduce bias in bear location data, I was limited to selecting the best model which contained only remotely-sensed covariates. The logistic model used for predicting the probability that a GPS collar would successfully obtain a fix over a variety of environmental conditions is:

$$P_{success} = \frac{\exp(u)}{1+\exp(u)}$$

where $P_{success}$ is the probability of successfully acquiring a GPS location and

$$u = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i$$

is the linear regression equation of variables derived from logistic regression. $B_0$ is the model intercept and $\beta_1 \ldots . \beta_i$ are regression coefficients estimated for parameters $x_1 \ldots . x_i$ (Hosmer and Lemeshow 2000).

I used ArcView 3.3 (ESRI GIS and Mapping Software, Redlands, California) to develop a data layer which used remotely sensed data from test sites to attribute $P_{success}$ coefficients to each pixel in Olympic NP based on the terrain and forest attributes. I also calculated an associated weighting factor for each $P_{success}$ coefficient (1/ $P_{success}$) and created a second layer which provided a weighting factor for each 25 X 25 m pixel in Olympic NP for use in subsequent analyses of bear data.

### *Quantifying accuracy of GPS-telemetry collars:*

I calculated location error as the Euclidean distance (m) between the GPS Pathfinder® Pro XR reference coordinate at each site and the coordinates obtained by the GPS collar at the same site. I examined location error separately for 2D and 3D fixes. A 2D fix resulted when three satellites were used for triangulation, while 3D fixes required four satellites, with the fourth satellite being used to determine the elevation of the collar. Because I sometimes moved collars over a wide elevational gradient in a short period of time and 2D locations used the elevation of the most recent 3D fix, I further divided the 2D fixes into two classes. One class, 2D-quality2, represented the first 2D fixes acquired at a new site, before a new 3D fix was obtained. Another class, 2D-quality1, represented 2D fixes obtained at a new site after attaining a 3D fix at that same site. I hypothesized that accuracy of fixes would be ranked 3D> 2D-quality1> 2D-quality2.

### *Examining the effect of DOP on location error:*

I used non-linear regression to examine the effect of DOP on GPS collar location error for 3D, 2D-quality1 and 2D-quality2 satellite fixes.

### *Examining the effect of environmental characteristics on location error:*

I used stepwise multiple linear regression to investigate the effect of terrain and habitat attributes on GPS collar location error. I selected model covariates by including only those variables that were not correlated (Pearson $r > 0.6$), resulting in the inclusion of relative cover of deciduous trees, overstory canopy cover, average DBH, and satellite view. With the exception of satellite view, each variable was ground-measured and continuous. Due to confounding effects of large elevation changes between some of the collar testing sites, I included only 3D and 2D-quality1 fixes in this analysis.

## RESULTS

### *Test collar success rates:*

GPS collars tested in Olympic NP successfully acquired locations at each of the 63 GPS collar testing sites examined. Mean fix-success rate ranged from 37.5% to 94.0% across all combinations of canopy cover and terrain conditions (Table 1.3). Success rates at individual locations ranged from 17.8-100% (Table 1.3). Of 1727 total fixes acquired at 63 test sites, 21.7% were 3D and 78.3% were 2D.

### *Bias of GPS-telemetry collars:*

Preliminary univariate logistic regression models indicated that canopy cover class (Wald $\chi^2$ = 41.4999-78.1930, $P$<0.0001), tree size class (Wald $\chi^2$ = 41.1526-74.6842, $P$<0.0001), satellite view (Wald $\chi^2$ = 143.3982, $P$<0.0001), relative cover of deciduous trees (Wald $\chi^2$ = 23.8493, $P$<0.0001), aspect (Wald $\chi^2$ = 0.0531-47.1781, $P$<0.0001), basal area (Wald $\chi^2$ = 8.6469, $P$=0.0033), tree height (Wald $\chi^2$ = 52.9376, $P$<0.0001), and elevation (Wald $\chi^2$ = 92.5936, $P$<0.0001) were significant predictors of whether a GPS collar successfully acquired a location. Slope (Wald $\chi^2$ = 0.0334, $P$=0.8549), and tree density (Wald $\chi^2$ = 0.1761, $P$=0.6747), did not significantly affect the probability of a GPS collar acquiring a fix. Subsequent test for correlation resulted in deletion of the following variables from further consideration: relative cover of deciduous trees, aspect, basal area, and tree height. Based on the *a priori* considerations, univariate tests, and correlations between variables, the resultant global model contained the following variables: overstory canopy cover class, tree size class, satellite view, elevation, and an

Table 1.3. Characteristics of 63 sites where GPS collars were tested in Olympic NP, and percentage of successful location attempts.

| | | | **Elevation (m)** | | **% location success** | |
|---|---|---|---|---|---|---|
| **% canopy cover[1]** | **% of satellite views available** | **Number of trial sites** | **Range** | **Mean ± SE** | **Range** | **Mean ± SE** |
| 0-40 | 90-100 | 6 | 442.9 - 1587.5 | 1146.8 ± 221.2 | 78.3 - 100.0 | 94.0 ± 3.5 |
| 0-40 | 75-90 | 10 | 110.7 - 1737.5 | 1061.0 ± 204.8 | 61.5 - 100.0 | 93.6 ± 3.7 |
| 0-40 | 60-75 | 2 | 393.7 - 1484.9 | 939.3 ± 545.6 | 36.0 - 92.9 | 64.4 ± 28.4 |
| 41-70 | 90-100 | 4 | 388.9 - 1489.3 | 1088.9 ± 351.2 | 62.5 - 79.2 | 69.9 ± 4.9 |
| 41-70 | 75-90 | 7 | 79.1 - 1494.9 | 644.5 ± 233.8 | 60.0 - 100.0 | 86.2 ± 5.0 |
| 41-70 | 60-75 | 4 | 534.5 - 1543.0 | 980.9 ± 256.3 | 19.2 - 100.0 | 60.3 ± 17.6 |
| 41-70 | 50-60 | 1 | | 219.7 | | 54.2 |
| 71-100 | 90-100 | 6 | 513.3 - 1749.1 | 1010.3 ± 189.5 | 60.0 - 100.0 | 87.3 ± 5.1 |
| 71-100 | 75-90 | 12 | 126.8 - 1270.6 | 502.9 ± 105.6 | 17.8 - 91.0 | 69.2 ± 6.8 |
| 71-100 | 60-75 | 9 | 213.5 - 1281.6 | 433.6 ± 103.3 | 44.7 - 87.5 | 59.7 ± 4.8 |
| 71-100 | 50-60 | 2 | 197.9 - 610.9 | 404.4 ± 206.5 | 33.3 - 41.7 | 37.5 ± 4.2 |
| | | | | | **Mean of means:** | 70.6 ± 5.4 |

interaction term between canopy cover class and satellite view.

Overall, the global model was significant ($P<0.0001$). Further, the variance inflation factor was close to one ($\hat{c} = 1.0282$), indicating acceptable model structure and a lack of overdispersion (Burnham and Anderson 2002). Thus, I did not make a quasi-likelihood adjustment for variance inflation.

The highest ranked multiple logistic regression model included the following variables: canopy cover class, satellite view, elevation, and interaction terms for canopy cover X satellite view ($w_i = 0.896$; Table 1.4). That model contained only remotely-sensed variables; therefore, I was able to use it to estimate success rate of each location derived from telemetered bears. An examination of AIC differences between the most parsimonious model and lesser-ranked models failed to find strong support for any other model (Table 1.4). AIC differences between 0-2 indicate a well supported model while $\Delta_i$ between 4-7 suggest considerably less support and $\Delta_i > 10$ are indicative of a model with essentially no support (Burnham and Anderson 2002). Therefore, the second-ranked model containing tree size class was only weakly supported ($\Delta_i = 4.702$; Table 1.4).

The best model resulted in significant coefficients ($p \leq 0.10$) for the 41-70% canopy cover class, satellite view, elevation, and the satellite view X 41-70% canopy cover interaction term (Table 1.5).

Logistic model predictions for $P_{success}$ from 63 test sites ranged from 34.6% to 98.2% (Figure 1.3) and were relatively consistent with the actual collar success rates of 17.8% to 100%. $P_{success}$ increased linearly with increasing numbers of satellite views, and was greatest for open forest vegetation (Figure 1.3). Satellite view had the greatest influence on $P_{success}$ in the 71-100% canopy cover class (Figure 1.3).

Table 1.4. Comparison and ranks of logistic regression models for GPS collar fix-success bias. GPS collars were tested at 63 sites in Olympic NP. Models are shown in order of rank, and include K (# of parameters in model, including intercept and error term), -2 log likelihood (-2LL), Akaike's information criterion (AIC), AIC difference ($\Delta_i$), and AIC weight ($w_i$). * Interaction term.

| **Rank** | **Parameters included in the model** | **K** | **-2 LL** | **AIC** | **$\Delta_i$** | **$w_i$** |
|---|---|---|---|---|---|---|
| 1 | CAN[1], SAT[2], ELEV[3], CAN*SKY | 8 | 2037.855 | 2053.855 | 0.000 | 0.896 |
| 2 | CAN, SAT, SIZE[4], ELEV, CAN*SKY | 11 | 2036.557 | 2058.557 | 4.702 | 0.085 |
| 3 | CAN, SAT, ELEV | 6 | 2049.689 | 2061.689 | 7.834 | 0.018 |
| 4 | CAN, SAT, SIZE, ELEV | 9 | 2048.933 | 2066.933 | 13.078 | 0.001 |
| 5 | CAN, SAT, CAN*SKY | 7 | 2062.643 | 2076.643 | 22.788 | 0.000 |
| 6 | CAN, SAT, SIZE, CAN*SKY | 10 | 2059.325 | 2079.325 | 25.470 | 0.000 |
| 7 | CAN, SAT | 5 | 2072.094 | 2082.094 | 28.239 | 0.000 |
| 8 | CAN, SAT, SIZE | 8 | 2070.619 | 2086.619 | 32.764 | 0.000 |
| 9 | SAT, ELEV | 4 | 2094.945 | 2102.945 | 49.090 | 0.000 |
| 10 | CAN, ELEV | 5 | 2113.393 | 2123.393 | 69.538 | 0.000 |

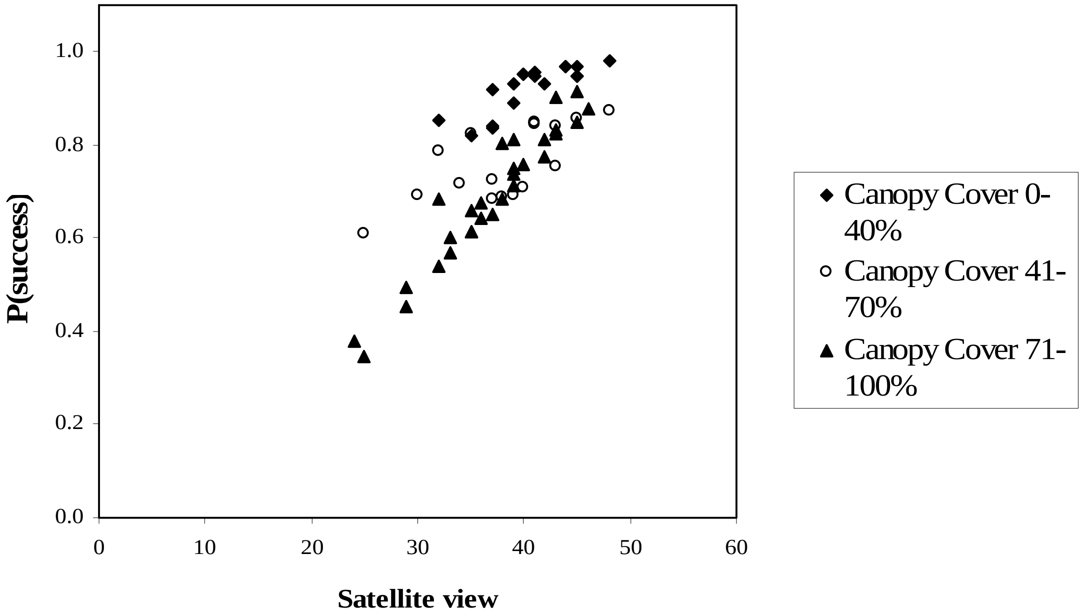
[1] Canopy cover (0-40%, 41-70%, 71-100%), [2] Satellite view, [3] Elevation, [4] Tree size (0-23 cm, 24-53 cm, 54-81 cm, 82-122 cm)

Table 1.5. Highest-ranked logistic regression model for predicting the probability of a GPS radio-collar acquiring a fix as a function of environmental characteristics in Olympic NP ($N_{\text{fix attempts}} = 2198$, Wald $\chi^2 = 194.52$, $P < 0.0001$).

| **Variable** | **β** | **SE** | ***P*** |
|---|---|---|---|
| Intercept | -3.4972 | 1.6140 | 0.0303 |
| Canopy cover 41-70%[1] | 3.0130 | 1.7846 | 0.0914 |
| Canopy cover 71-100% | 0.0293 | 1.6941 | 0.9862 |
| Satellite view | 0.1366 | 0.0411 | 0.0009 |
| Elevation (dm) | 0.000059 | <.0001 | <.0001 |
| Satellite view * Canopy cover 41-70% | -0.1046 | 0.0457 | 0.0220 |
| Satellite view * Canopy cover 71-100% | -0.0280 | 0.0433 | 0.5177 |

[1] Canopy cover 0-40% = Reference

Figure 1.3. Satellite view versus probability of a GPS collar successfully acquiring a location for 3 levels of overstory canopy cover. Probability of success calculated from highest ranked logistic regression model, which included variables canopy cover, satellite view, elevation, and canopy cover*satellite view interaction terms.



I input coefficients from the most parsimonious model into the map calculator in ArcView and calculated $P_{success}$ and associated weighting factors for pixels throughout Olympic NP. $P_{success}$, when extrapolated throughout the park, ranged from approximately 0.152 to 1.0 (Figure 1.4). Weighting factors ranged from 1.0 to 6.59 (Figure 1.5).

### *Effect of behavior on location success rate:*

Collars paired with test collars under conditions simulating bear bed sites (under large trees) received, on average, 10.5% fewer fixes than optimally configured collars (Table 1.6).

### *Accuracy of GPS-telemetry collars:*

Both GPS collars and the Pathfinder® Pro XR successfully acquired locations at 15 of the 16 accuracy testing sites. Of the 1705 total GPS locations acquired, 32.9% were 3D and 67.1% were 2D (Table 1.7). Three-dimensional fixes were more accurate than either level of 2D fixes, and 2D-quality1 fixes were more accurate than 2D-quality2 fixes (Table 1.7). Ninety-five percent of 3D fixes were within 17.72 m of the reference coordinate while 95% of 2D fixes were within 74.33 m and 583.10 m for 2D-quality1 and 2D-quality2 fixes, respectively (Table 1.7). Overall, 95% of 2D fixes were within 264.64 m of the reference coordinate and 95% of all fixes combined were within 182.53 m of the true location (Table 1.7). Large location errors reported for the 100th percentile (2230.12 m) were rare (Table 1.7). When collars were moved over greater elevations, the first 2D fixes (2D-quality2) at a new site had greater location errors than when the collars had remained at a relatively constant elevation (Figure 1.6).

Figure 1.4. Probability of a GPS collar acquiring a fix for each 25 X 25m pixel in Olympic NP. $P_{success}$ calculated based on GPS collar testing at 63 sites in the Elwha watershed and at Hurricane Ridge.

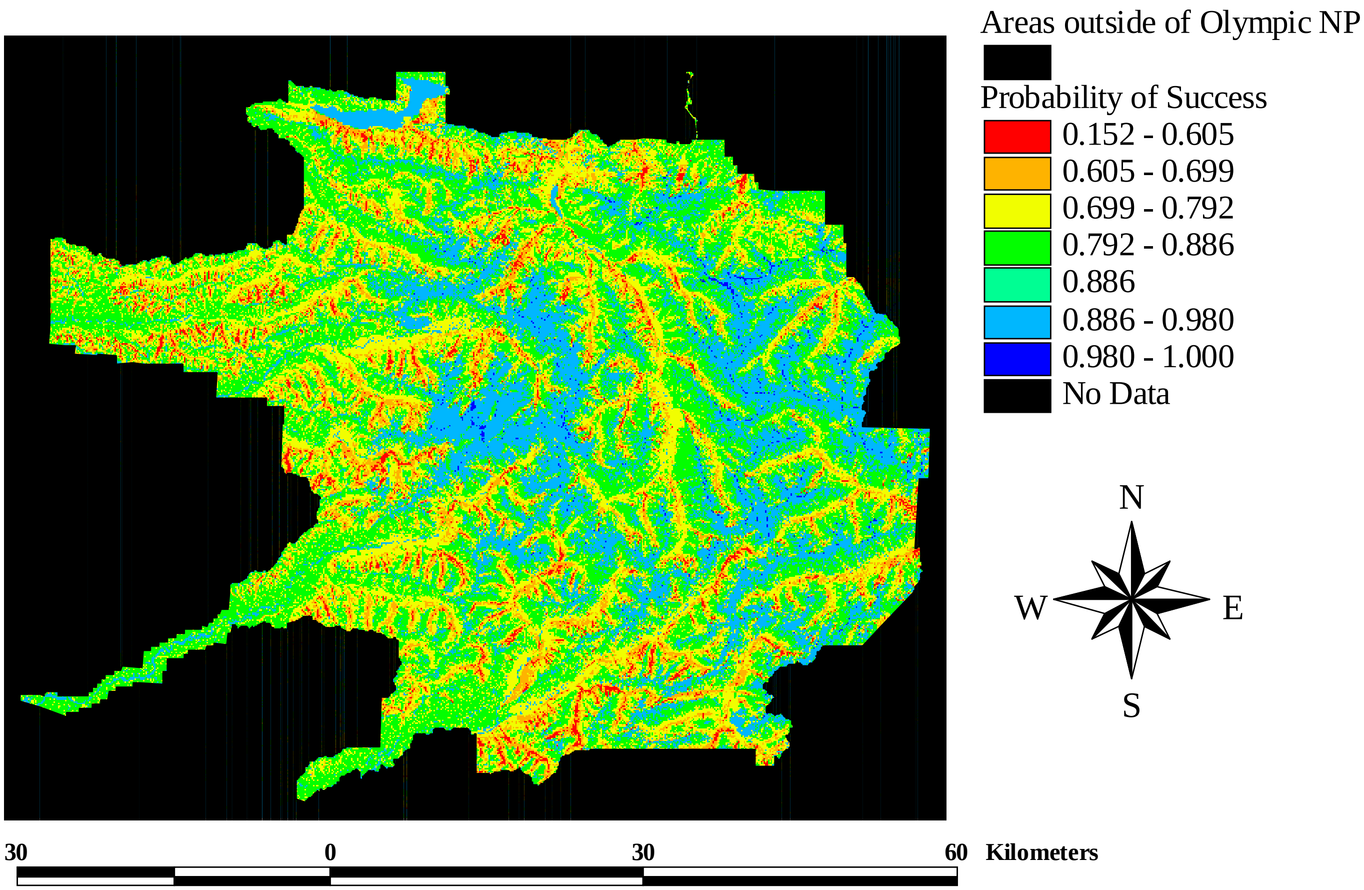


Figure 1.5. Weighting factors for each 25 X 25m pixel in Olympic NP. Weighting factors calculated based on GPS collar testing at 63 sites in the Elwha watershed and at Hurricane Ridge. Weighting factor = $1/P_{success}$.

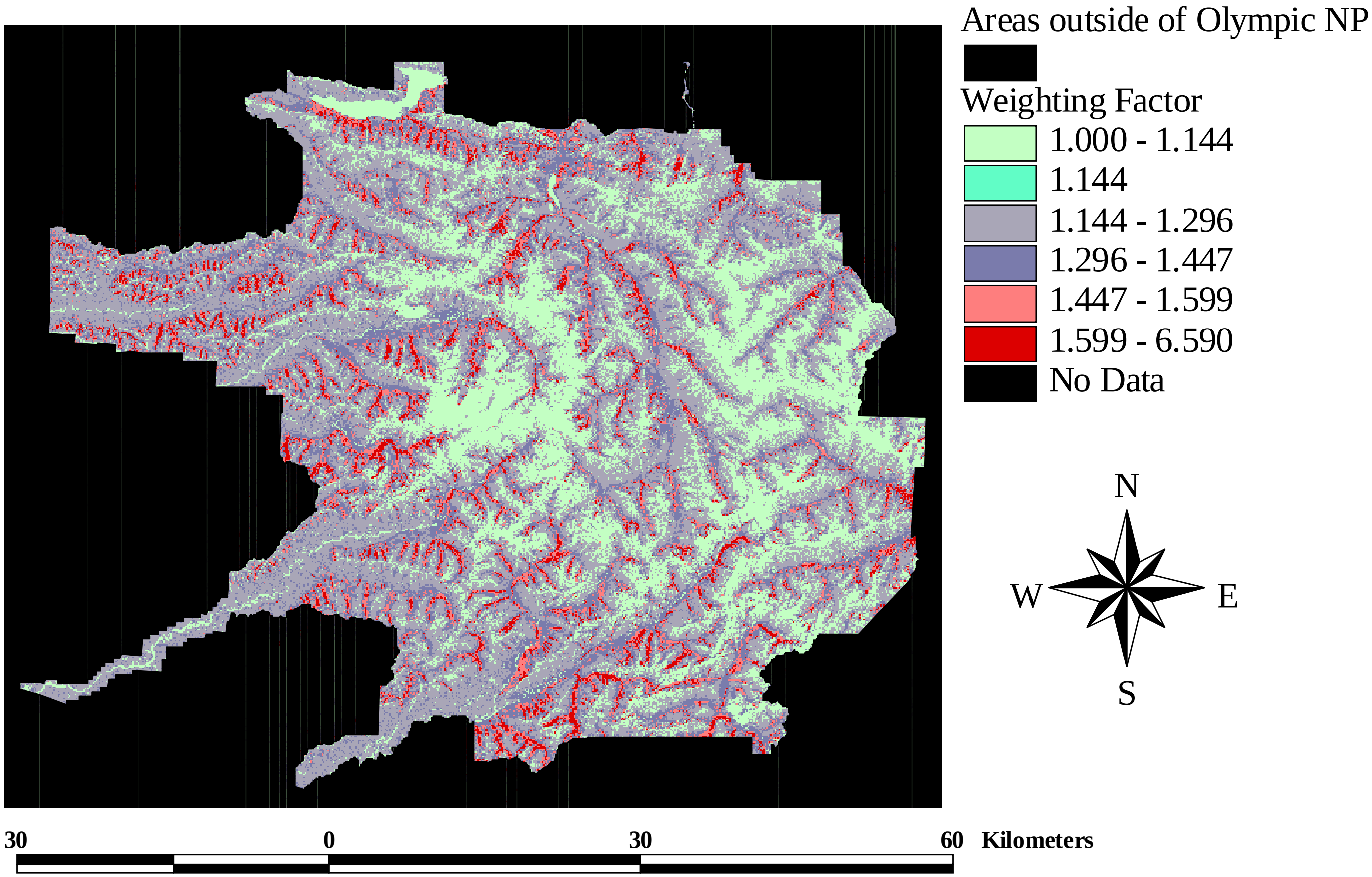


Table 1.6. Comparisons of GPS collar success rates at optimally configured test sites and sites designed to approximate a bedded bear. Collars failed prematurely at 4 of the 16 test sites, so data is exhibited for remaining 12 sites.

| **Optimally configured collar** | | | **Bedded bear simulation** | | | |
|---|---|---|---|---|---|---|
| **# fix attempts** | **# successful fixes** | **% location success** | **# fix attempts** | **# successful fixes** | **% location success** | **Difference between collar configuration types (%)** |
| 86 | 83 | 96.51 | 86 | 84 | 97.67 | -1.16 |
| 148 | 148 | 100.00 | 146 | 118 | 80.82 | 19.18 |
| 374 | 374 | 100.00 | 374 | 346 | 92.51 | 7.49 |
| 91 | 91 | 100.00 | 91 | 76 | 83.52 | 16.48 |
| 296 | 218 | 73.65 | 296 | 181 | 61.15 | 12.50 |
| 133 | 112 | 84.21 | 133 | 89 | 66.92 | 17.29 |
| 82 | 74 | 90.24 | 95 | 90 | 94.74 | -4.49 |
| 93 | 81 | 87.10 | 93 | 75 | 80.65 | 6.45 |
| 109 | 98 | 89.91 | 109 | 97 | 88.99 | 0.92 |
| 243 | 24 | 9.88 | 243 | 30 | 12.35 | -2.47 |
| 238 | 41 | 17.23 | 238 | 30 | 12.61 | 4.62 |
| 286 | 155 | 54.20 | 286 | 13 | 4.55 | 49.65 |
| | | | | **Mean difference:** | | **10.54** |

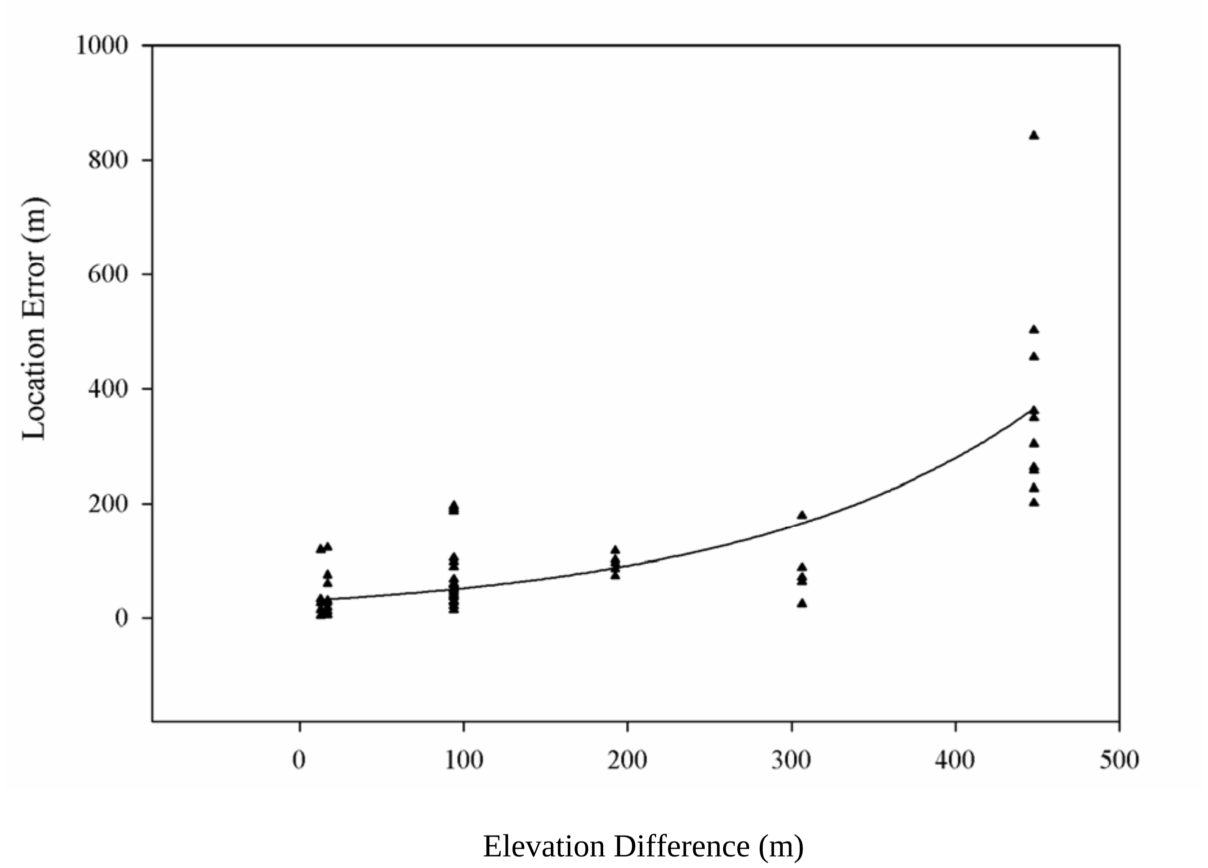
Table 1.7. Mean, median, and frequency percentiles for location errors of GPS collars tested in a temperate forest environment, Olympic NP.

| | | | **Location error (m)** | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Fix type**[a] | ***n***[b] | **% of fixes** | **Mean ± SE** | **50%** | **90%** | **95%** | **99%** | **100%** |
| 3D | 561 | 32.9 | 9.24 ± 0.26 | 9.43 | 15.81 | 17.72 | 31.58 | 73.41 |
| 2D-qual1 | 982 | 57.6 | 30.38 ± 3.30 | 13.04 | 43.86 | 74.33 | 576.72 | 2036.28 |
| 2D-qual2 | 162 | 9.5 | 206.63 ± 20.93 | 122.64 | 416.94 | 583.10 | 1534.17 | 2230.12 |
| 2D-all | 1144 | 67.1 | 55.34 ± 4.48 | 15.26 | 112.54 | 264.64 | 721.34 | 2230.12 |
| All | 1705 | 100 | 40.17 ± 3.05 | 10.82 | 65.19 | 182.53 | 583.10 | 2230.12 |

[a] 3D = 3-dimensional fix; 2D-1 = 2-dimensional fix where previous 3D was at same site; 2D-2 = 2-dimensional fix where previous 3D was at a different site.

[b] *n* = Number of fixes acquired by collars placed for at least 24 hours at 15 different sites; each collar attempted 2 fixes per hour.

Figure 1.6. Elevation differences between consecutive test sites (*n* = 6) and associated location errors of the first 2D fixes at a new site. 2D fixes shown here represent fixes obtained without the benefit of a previous 3D fix at the same site.



*Effect of DOP on location error:*

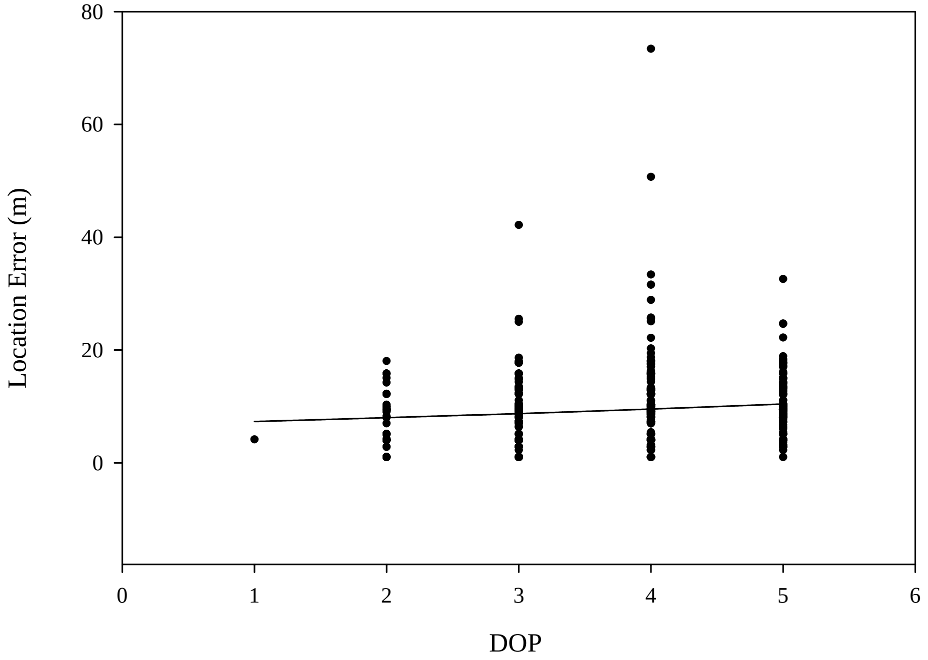
Significant relationships occurred between DOP and location error for all types of GPS fixes collected at 15 collar testing sites (3D: $R^2=0.702$, $F_{2,561}=659.19$, $P\leq0.0001$; 2D: $R^2=0.146$, $F_{2,1144}=97.29$, $P\leq0.0001$; 2D-quality1: $R^2=0.093$, $F_{2,982}=50.10$, $P\leq0.0001$; 2D-quality2: $R^2=0.444$, $F_{2,162}=63.76$, $P\leq0.0001$; Figure 1.7). Increasing DOP resulted in an increase in location error across all fix qualities examined (Figure 1.7). Three-dimensional fixes ranged across DOP classes 1 to 5, with 32.44% of fixes occurring at a DOP of 4 and 100% of fixes having location errors of less than 100 m (Table 1.8). The highest quality 2D fixes occurred across a range of DOP classes from 1-11, with 96.54% of fixes having location errors of less than 100 m; the majority of those fixes occurred at a DOP of 5 or less (Table 1.9). Lower quality 2D fixes (2D-quality2) also occurred across a range of DOP classes from 1-11; however, only 43.83% of locations were within 100 m of the reference coordinate (Table 1.10). Several 2D-quality2 fixes (6.17%) were greater than 500m from the reference coordinate, and of those, the majority occurred at a DOP of 5 or greater (Table 1.10). Approximately 1.02% of 2D-quality1 fixes were also greater than 500 m from the reference coordinate; however, those fixes were more evenly distributed across all ranges of DOP (Table 1.9).

*Effect of landscape characteristics on location error*:

Stepwise multiple regression resulted in a significant model which included variables overstory canopy cover and satellite view as significant predictors of location error ($R^2=0.019$, $F_{2,1542}=15.01$, $P\leq0.0001$). The significant parameter estimate for overstory canopy cover ($\beta=0.29918$, $P\leq0.0001$) indicated that location error increased with increasing canopy cover.  Further, as the number of available satellite views in the sky increased, there was an associated decrease in location error ($\beta=-1.29293$, $P \leq 0.0001$).

Figure 1.7. Dilution of position (DOP) versus location error for each fix-type at 15 sites designed to test accuracy of GPS telemetry collars in Olympic NP.

***3D fixes*** ($R^2$=0.702, $F_{2,561}$=659.19, *P*≤0.0001)



***2D fixes*** ($R^2$=0.146, $F_{2,1144}$=97.29, *P*≤0.0001)

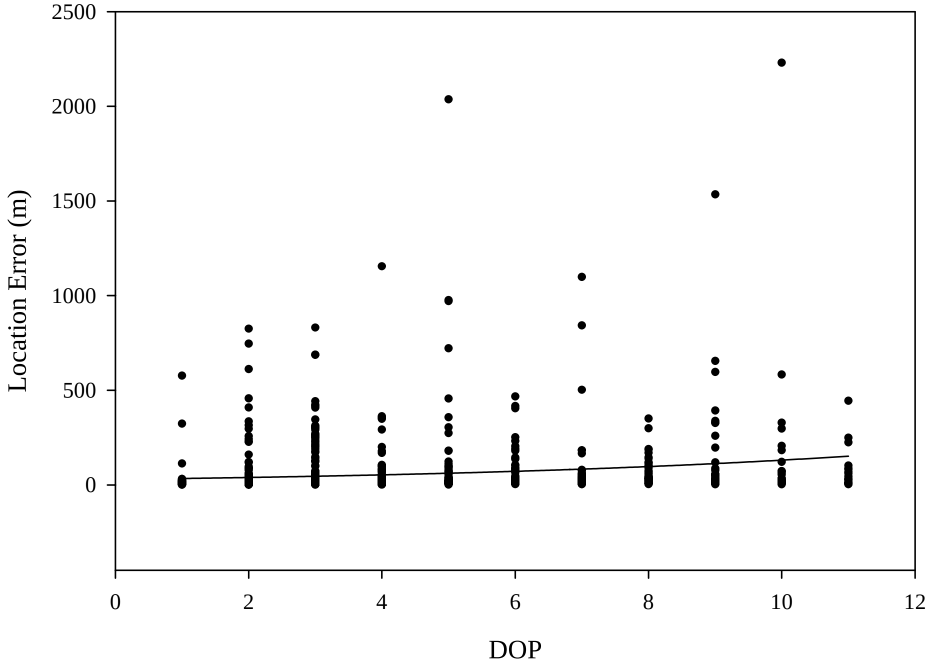
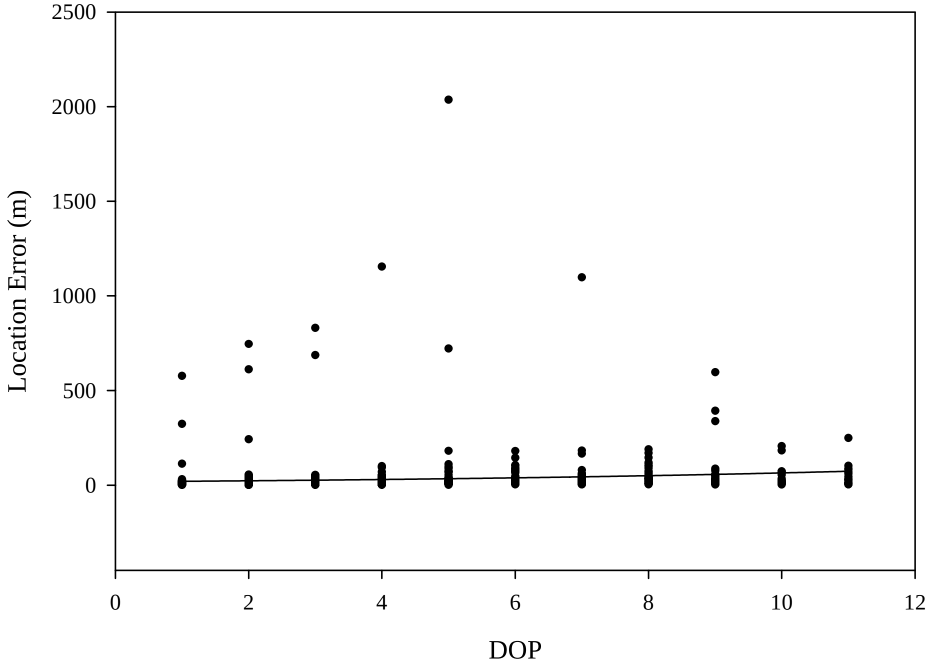


Figure 1.7. Continued.

***2D-quality1*** ($R^2$=0.093, $F_{2,982}$=50.10, $P \leq 0.0001$)



***2D-quality2*** ($R^2$=0.444, $F_{2,162}$=63.76, $P \leq 0.0001$)

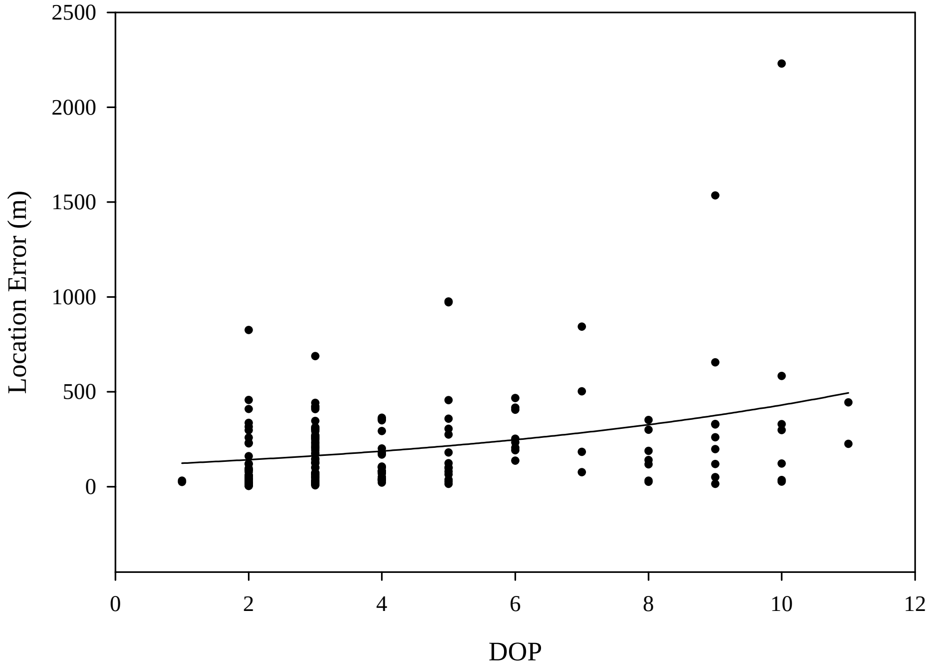


Table 1.8. Percent of 3D fixes at different levels of dilution of position (DOP) and their associated location errors for GPS locations collected at 15 test sites in Olympic NP.

| | DOP | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Location Error** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **Totals** |
| **≤ 100 m** | 0.18 | 18.18 | 26.38 | 32.44 | 22.82 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 100.00 |
| **100-200 m** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **200-500 m** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **>500 m** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

Table 1.9. Percent of 2-dimensional (2D-quality 1) fixes at different levels of dilution of position (DOP) and their associated location errors for GPS locations collected at 15 test sites in Olympic NP.

| | **DOP** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Location Error** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **Totals** |
| **≤ 100 m** | 8.45 | 31.87 | 19.35 | 11.10 | 7.23 | 4.99 | 3.87 | 4.18 | 2.24 | 1.53 | 1.73 | 96.54 |
| **100-200 m** | 0.10 | 0.00 | 0.00 | 0.00 | 0.20 | 0.41 | 0.20 | 0.71 | 0.00 | 0.10 | 0.10 | 1.83 |
| **200-500 m** | 0.10 | 0.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.20 | 0.10 | 0.10 | 0.61 |
| **>500 m** | 0.10 | 0.20 | 0.20 | 0.10 | 0.20 | 0.00 | 0.10 | 0.00 | 0.10 | 0.00 | 0.00 | 1.02 |

Table 1.10. Percent of 2-dimensional (2D-quality 2) fixes at different levels of dilution of position (DOP) and their associated location errors for GPS locations collected at 15 test sites in Olympic NP.

| | **DOP** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Location Error** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **Totals** |
| **≤ 100 m** | 1.23 | 15.43 | 12.35 | 6.17 | 4.32 | 0.00 | 0.62 | 1.23 | 1.23 | 1.23 | 0.00 | 43.83 |
| **100-200 m** | 0.00 | 1.85 | 5.56 | 3.70 | 1.23 | 1.23 | 0.62 | 1.85 | 1.23 | 0.62 | 0.00 | 17.90 |
| **200-500 m** | 0.00 | 4.94 | 12.96 | 2.47 | 2.47 | 3.70 | 0.00 | 1.23 | 1.85 | 1.23 | 1.23 | 32.10 |
| **>500 m** | 0.00 | 0.62 | 0.62 | 0.00 | 1.23 | 0.00 | 1.23 | 0.00 | 1.23 | 1.23 | 0.00 | 6.17 |

## DISCUSSION

Collar fix-success rates of 17.8-100% (mean = 75.9 ± 2.9) were relatively consistent with success rates reported in other studies that examined fix-success rates across a range of environments (Frair et al. 2004: 12.8-100% [mean across collar brands, vegetation, and topography: 67.6-99.7%]; Rempel et al. 1995: 10-97%). However, they were much lower than were reported in several other studies (D'Eon 2002: 71-100%, Edenius 1997: 69-100%, Moen et al. 1996: 63-97%), perhaps reflecting differences in forest structure and terrain attributes between areas, differences in collar brands used for testing, or a combination of both factors. Random collar error may also have been a factor, as fix-success rates of individual collars may vary (D'Eon et al. 2002, Frair et al. 2004). Collar brand was identified as a significant predictor of location success when 3 collar brands were tested and compared across a range of conditions; Televilt collars had lower fix-success rates than either Lotek- or ATS-brand collars (Frair et al. 2004).

Tests from paired collars in Olympic NP resulted in clear differences in fix-success rates between ideally configured collars and those placed directly under trees or laying on their sides. The 10.5% increase in GPS location success in ideally configured testing locations over sites that mimicked bear beds suggests that animal behavior is an important factor reducing fix-success. Effects of animal behavior reducing fix acquisition rates were identified recently in several controlled experiments (Bowman et al. 2000, Moen et al. 2001, T. Graves 2004 Personal Communication, D. Heard 2004 Personal Communication). It was not possible to attribute bear behavior to each fix acquired in this study; however, future research would benefit from the ability to correlate animal behavior with individual fix likelihood.

GPS collars tested in Olympic NP acquired substantially lower proportions of 3D fixes (22%) than reported previously (D'Eon et al. 2002: 92.4%; Di Orio et al. 2003: 64% 3D fixes from Lotek and 90% from ATS; Moen et al. 2001: 63% when moose inactive, 32% when moose active). This incongruity may be a function of collar brand, different collar programming schemes, or differences in habitat attributes between areas. In Olympic NP, I programmed test collars to search for satellites for 240 seconds during each fix attempt. However, once the GPS unit in a collar had contacted 3 satellites, it recorded a 2D fix and looked for additional satellites for only 20 more seconds (Simplex Project Manager Manual, Version 1.2.5, Televilt TVP Positioning). It is possible that greater success in acquiring 3D fixes could be achieved if the GPS receiver continued to look for satellites for the duration of the 240 second period. This, however, would have had negative consequences for collar longevity, as batteries would have failed sooner. In addition to potentially different programming schedules, GPS collars may have had difficulty contacting satellites due to the steep rugged terrain and dense old-growth coniferous forests that characterize Olympic NP. I suspect that mature coastal forests found in Olympic NP represent one of the most difficult environments for using GPS telemetry.

Results from AIC model selection generally corroborated previous studies that reported important effects of overstory canopy cover and satellite view on fix acquisition rates of GPS-telemetry collars (D'Eon et al. 2002, Frair et al. 2004, Moen et al. 1996, Rempel et al. 1995). Unlike previous studies, I also identified elevation as a significant predictor of GPS collar fix-success. A positive coefficient in the final logistic regression model for the elevation variable indicated that as elevation increased, so did the probability of a GPS collar acquiring a fix. Though elevation was examined in other studies as it related to location error (D'Eon et al. 2002), few published studies have found elevation to predict success of GPS collar fix-acquisition. Elevation likely influenced tree height, density, and size and therefore acted as a surrogate for these forest attributes when predicting fix-acquisition success. At higher elevations where forests were characterized by smaller, less dense stands of trees, fix acquisition rates were enhanced independent of tree canopy cover.

Unobstructed satellite views and open canopies were associated with the greatest probabilities of successfully acquiring telemetry fixes. A significant interaction between the effects of satellite view and canopy cover, however, complicated the interpretation of either variable independently (Figure 1.3). The interaction of canopy cover classes 41-70% and 71-100% at a point where approximately 83% of satellite views are visible suggests that the effect of canopy cover was reduced under conditions of low topographic obstruction and high satellite view. This may reflect the relative importance of satellite view versus canopy cover. Under conditions of high satellite views, the effect of unobstructive topography overrides that of canopy cover. Conversely, under conditions of low satellite views, the influence of forest canopy was greater.

Predictions of $P_{success}$ from the fitted logistic regression model closely approximated fix-success rates of collars tested on the ground. However, the model fit was poorest under conditions of low $P_{success}$. GPS collars at 4 out of 63 test sites had actual success rates lower (17.8% - 33.3%; Table 1.3) than the lowest predicted success rate (34.6%; Figure 1.3). Three of those 4 sites were found under the densest canopy cover class, and none were located in areas with high satellite view availability.  They were among the "worst-case" scenario sites found in Olympic NP, and though I suspect bears do not frequent these types of habitats I recognize the possibility of overestimating the $P_{success}$ coefficient in areas with dense forests and steep terrain.

On average, accuracy of GPS collars used for testing in Olympic NP was similar to what has been reported in the literature.  However, in several extreme cases, errors were substantially larger than have been reported previously, perhaps reflecting random error, differences in collar brands, or differences in habitat and terrain attributes between study areas.  At the 95th percentile, GPS locations in Ontario had errors of 242.4 m and 120.1 m for 2D and 3D locations, respectively (Rempel et al. 1995), while in the Selkirk Mountains of southeastern British Columbia 95% of locations were within 98.5 and 26.2 meters of the true location (D'Eon et al. 2002).  The errors reported by Rempel et al. (1995) were similar to the 264.64 m reported here for 2D fixes, but far greater than the 17.72 m that I reported for 3D errors.  Three-dimensional location errors reported in this study were nearer those reported by D'Eon et al. (2002).  However, the highest 2D errors reported in Ontario and British Columbia were 649.8 m and 545.1 m, respectively, while in Olympic the largest error was substantially greater at 2230.12 m.  The greatest error reported by Di Orio et al. (2003) was 702 m for a Lotek collar.

By reducing 2D fixes acquired at GPS collar testing sites in Olympic NP into two additional classes, 2D-quality1 and 2D-quality2, I was able to examine the effect of substantial elevation changes on location accuracy of consecutive fixes.  A shift in elevation between consecutive GPS locations clearly influenced location error, with greater elevation shifts resulting in greater errors.  Because 2D locations were established using the elevation from a previous 3D fix, 2D fixes acquired without the benefit of a previous 3D location at a similar elevation had substantially greater location errors than those with a 3D reference elevation.  Di Orio et al. (2003) acknowledged the possibility for this discrepancy, but differences in location errors between classes of 2D fixes have rarely been quantified.  This finding has consequences for other research on GPS collar accuracy and should be addressed in future study designs.  Further, there are implications for analysis of animal movement data, particularly data from wide-ranging animals that frequently travel vast distances over a wide elevation gradient.

Similar to D'Eon et al. (2002), I found that location error increased with increased canopy cover and decreased availability of open sky for viewing satellites.  It is probable that the heavily forested and steep terrain of Olympic NP may have had a greater effect on GPS collar location error than in many other areas, which may explain why location errors were greater in Olympic NP than in many other areas.

## RESEARCH IMPLICATIONS

My findings on fix-acquisition success rates and location errors of GPS telemetry in Olympic NP have several implications for black bear research. GPS data collected from test collars were biased towards habitats with open forest overstories and little topographic obstruction, suggesting that animal movement data will also be biased towards these habitat types. Furthermore, GPS location data contained spatial inaccuracies that will lead to further biases in animal movement data, particularly during analysis of resource selection. Each of these types of bias has potential to cause misclassification of home range and resource selection patterns by bears. Therefore, it is important that they are minimized before subsequent inferences from bear location data are made.

Within Olympic NP, predictive logistic regression models based on remotely-sensed independent variables allowed for quantification of $P_{success}$ and associated weighting factors across a variety of habitats. These weighting factors, which weight telemetry locations as the inverse of $P_{success}$, provide a viable option for minimizing bias associated with the systematic loss of data that occurs when using GPS radio-collars. Though there is mounting evidence that animal behavior may represent bias that is not accounted for (Bowman et al. 2000, Moen et al. 2001, T. Graves 2004 Personal Communication, D. Heard 2004 Personal Communication), the application of weighting factors to GPS locations on the basis of their probability of detection shows promise as a tool to reduce bias in estimation of home range and habitat selection by black bears.

Spatial inaccuracies in location data from GPS radio-telemetry collars may also reduce reliability of home range and resource selection estimates. Several researchers have proposed options for reducing this type of bias: removing data points based on DOP (D’Eon et al. 2002, Moen et al. 1996) or fix-type (2D vs. 3D; D’Eon et al. 2002), or by including error buffers around data points (Moen et al. 1997, Rettie and McLoughlin 1999). However, due to what appears to be a random association between DOP and location error for many fixes collected by test collars in Olympic NP, I cannot visually or analytically identify a DOP value that will reliably extract inaccurate GPS locations. Further, because 2D fixes are less accurate than 3D fixes, it has been suggested that 2D fixes could be rejected from further analysis (D’Eon et al. 2002). However, the authors acknowledged that deleting 2D locations could introduce additional unknown bias, and they cautioned against omitting 2D fixes unless absolutely necessary. Because this additional bias would not be quantifiable and because collars in Olympic NP received a large proportion of 2D fixes, deleting these locations is not a practical option in Olympic NP.

Finally, researchers have proposed placing error buffers around GPS locations in an effort to minimize biases associated with inaccurate location data (Moen et al. 1997, Rettie and McLoughlin 1999). I recommend buffering each bear location with a 180-m error radius, which encompasses an estimated 95% of all location errors in Olympic NP. This will address issues of GPS accuracy while retaining an appropriate scale of analysis that allows for correct interpretation of resource selection analyses.

# Chapter 2: Black bear distribution patterns in the Elwha River watershed of Olympic National Park

## INTRODUCTION

Black bears are important components of ecosystems and may function as flagship or umbrella species within the context of ecosystem management and biodiversity conservation programs (Simberloff 1999). In the western United States, black bears have both ecological and management significance. Bears may be key predators of ungulate neonates such as elk (Bull et al. 2001), moose (Ballard 1999) and deer (Bull et al. 2001, Kunkel and Mech 1994). They also function as seed dispersers (Auger et al. 2002) and are important vectors of nutrient transport from marine to terrestrial systems by feeding on salmon runs and subsequently depositing feces and salmon carcasses on land (Cederholm et al. 1989, Gende et al. 2004, Hilderbrand et al. 1999*b*).

In addition to their ecological significance, black bears pose unique management challenges. Within national parks, bears have a long and varied history of interaction and conflict with humans. Historically, contact between bears and humans was commonplace, with visitors feeding bears along roadsides and observing bears as they fed in open-pit dumps (Wright 1992). Management practices have evolved considerably since the days of open-pit dumps, and bears in national parks today are managed as wild populations (Wright 1992). NPS biologists are mandated to preserve natural abundances, diversities, dynamics, distributions, and behaviors of native animal populations (NPS 2001). As a response to this mandate, aggressive educational campaigns and stringent food- and garbage-storage regulations have diminished negative interactions between humans and bears (Wright 1992). However, instances of conflict are still common in some areas, and persistent enforcement of these management practices and continued scientific research are necessary to effectively manage bear and human conflicts in national parks (Wright 1992).

Despite the ecological and management significance of black bears, very little research has been conducted in Washington. Most research has focused on supplemental feeding programs aimed at reducing conifer damage by bears on managed timberlands (Partridge et al. 2001, Ziegltrum 2004). Few studies have investigated home range and habitat selection patterns in coastal, mountainous regions of the Pacific Northwest (Koehler and Pierce 2003, Lyons et al. 2003). The one study that was conducted in Olympic NP (Koehler 1998, 1999) was hampered by poor weather for carrying out telemetry flights necessary with the use of VHF telemetry transmitters. Therefore, very little data were obtained for bears within Olympic NP. Since that study, an increased interest in basic bear biology and the establishment of a black bear management plan in Olympic NP have prompted the need for further research on black bear distribution patterns.

Contemporary research on black bears in Olympic NP is particularly important in light of future dam removal activities in the Elwha River watershed. Removal of the Elwha dams and subsequent salmon restoration provides an unparalleled opportunity to study the effects of altered nutrient cycles on black bears within the watershed. The major influx of nutrients associated with salmon restoration has the potential to alter seasonal bear movements, affect patterns of resource selection, and influence home range size and location. As a result, bears may act as vectors of nutrient transport and may affect both riparian and upland vegetation within the watershed.

Objectives of this chapter are to examine distribution patterns of black bears in the Elwha River watershed of Olympic NP. I calculated seasonal and annual home ranges, examined patterns of elevation use, and investigated use of the Elwha River and its potential salmon-bearing tributaries. Finally, I examined seasonal and annual patterns of resource selection. I employed GPS radio-collar technology to investigate these patterns, and used information gathered in chapter 1 to apply weighting factors to biased bear location data from GPS radio-collars. Very few studies have attempted to reduce bias in analysis of GPS radio-telemetry data (D’Eon 2003, Frair et al. 2004), and I demonstrate a viable option for applying correction factors in the analysis of animal home range and distribution.

## METHODS

### ***Field Methods***

### <u>Animal Capture:</u>

Bears were captured by a crew of field employees consisting of National Park Service (NPS), United States Geological Survey (USGS), and Beringia South research personnel and field technicians. Our objective was to capture a minimum of 12 adult bears in the Elwha watershed between 2002-04 and equip each bear with a GPS Simplex™ (Televilt TVP Positioning AB, Lindesberg, Sweden) radio-collar. Each collar was coded with a unique color combination for easy visual identification and each bear was marked with a numbered and color-coded ear tag in each ear.

We captured black bears of both sexes using two methods: Aldrich-style foot snares in a cubby set (Johnson and Pelton 1980) or, in some instances, free-range darting. Cubby sets were baited using road-killed deer or elk, a manufactured scent lure, or rotting commercial meat scraps. Once a bear was restrained in a foothold snare, we used a syringe pole or Dan-Inject$^{TM}$ $CO_2$ darting rifle to deliver the immobilizing agent. We immobilized free-ranging bears with a Dan-Inject$^{TM}$ remote delivery system. The Dan-Inject$^{TM}$ $CO_2$ rifle was ideal because the range and impact force of the dart was adjustable. Capture crews consisted of a minimum of three people, with each crew member having primary responsibility for administering drugs, recording data, or monitoring the well- being of the immobilized bear.

Olympic NP's Black Bear Observation database indicated that bears used low-elevation, front-country areas of the Elwha watershed heavily during early spring.

Further, we suspected that bears traveled up-valley as spring progressed and snow continued to melt. Therefore, we concentrated capture efforts during early May of each year in front-country areas of the Elwha valley. Spring trapping consisted of setting, baiting, and checking snares, as well efforts to dart free-ranging bears. We built cubbies and pre-baited each site 1-2 weeks before beginning spring trapping so that bears would become accustomed to the shapes and smells surrounding snares. During each of the three study years, we set approximately 8-15 snares in the lower Elwha valley in May. During June of 2002 and 2003, we moved the capture operation 11.5 miles up the main Elwha River trail and set 8 snares in areas around Elkhorn Cabin. Finally, throughout July and August we trapped in the lower Elwha valley or at Hurricane Ridge, depending on reports of bear activity in either area.

We anesthetized captured bears with a mixture of Ketamine hydrochloride (HCL; 4.4 mg/kg) and Xylazine HCL (2.2 mg/kg) or with Telazol® (tiletamine HCl and zolazepam HCl; 7.0 mg/kg) (Kreeger 1997). We took the utmost care to ensure the stability and comfort of each bear by monitoring its vital signs throughout the procedure, adjusting its position as necessary, and administering long-term care drugs. We determined gender, reproductive condition, and physical condition of each bear. We also visually estimated weight of each bear, estimated age by examining tooth-wear, and recorded morphological measurements (LeCount 1986). We collared and ear-tagged every adult bear, and placed a microchip (containing identification code) in the shoulder of each animal. Finally, we collected biological samples: we attempted to extract a first upper premolar from each bear for age estimation from cementum annuli, obtained blood and tissue samples for future DNA analysis, and collected hair samples for isotopic analysis of dietary sources of nitrogen and carbon.  The analysis of stable isotope ratios has been used to determine proportions of terrestrial animal, salmon, and plant material in the diets of bears (Hilderbrand et al. 1996, Hilderbrand et al. 1999, Jacoby et al. 1999). Though not a part of this thesis, dietary baselines derived from this study will permit future monitoring and comparisons over time after salmon are restored to the Elwha River.

All capture protocols were reviewed and accepted by the Animal Use and Welfare Committee at Oregon State University, which reviews live animal research sponsored by the USGS- Forest and Rangeland Ecosystem Science Center.

### *GPS Collar Radio-telemetry:*

We instrumented each immobilized bear with a 950-g GPS-Simplex™ 1D radio-collar.  Each collar was also equipped with VHF capability, mortality and activity sensors, and a drop-off mechanism.  We programmed each radio-collar to attempt to obtain a location fix 4 times daily (2002 and 2003) or 3 times daily (2004) during spring-summer-fall and once daily during the denning period (1 November-31 March).  During each location attempt, the collar attempted to find satellites over a 240-second interval (180-seconds in 2004).  Once three satellites were located (thereby obtaining a 2D fix), the collar continued looking for additional satellites for 20 additional seconds.  If unsuccessful at locating a fourth satellite, the collar stored the 2D fix; otherwise, a 3D fix was obtained and stored.  The collar never attempted to acquire satellites once the allotted search time had passed.

Location data were stored in the collar’s short-term memory until they could be downloaded remotely at a later date with the use of a specialized receiver (RX-900 Receiver, Televilt TVP Positioning AB, Lindesberg, Sweden). A successful fix attained the following data: date, time, latitude, longitude, dilution of position (DOP), and whether the fix was 2D or 3D. Most commonly, I downloaded data from fixed-wing aircraft. Every collar was programmed to transmit stored data via its VHF transmitter at pre-determined times during May, July, and September. Within each of these months, the collars were programmed to send the same set of data on four separate occasions, each a week apart and at the exact same time (i.e. on any given Tuesday during a data transmission period, a collar may send data at 0915, another at 1015, and another at 1215). This allowed for flight completion during favorable weather, and allowed for several chances to download data in the event of technical problems. The collar had no way of “knowing” whether or not the data were received; it sent the data regardless of whether it was received or not. In the event that remote retrieval of a data set failed during all four attempts, the data were stored in long-term memory until the collar could be recovered. Further, several collars placed on bears in 2003 and 2004 were capable of “on-demand” data downloads. These data downloads required use of a specialized transmitter which sent a VHF signal to the collar, thereby initiating a data download.

Collars placed on bears were scheduled to release approximately 16 months after their initial deployment. Each collar deployed in 2002 was programmed to drop-off in late September 2003; collars deployed in 2003 were programmed to drop-off in late September 2004; and collars deployed in 2004 were programmed to drop-off in late September, 2006. Finally, collars placed on bears in 2003 and 2004 were capable of releasing “on-demand” in the event of an early collar failure or other unexpected circumstance. We attempted to recover every GPS radio-collar released during the course of the project by locating them from a fixed-wing aircraft and then either hiking to them or retrieving them from a helicopter landing zone. This component of the study was completed during September or October of 2003 and 2004.

### ***Analytical Methods***

#### Home Range Analysis:

I estimated black bear annual and seasonal home ranges using the fixed kernel method with likelihood cross-validation for choosing kernel width (J. Horne, University of Idaho, Personal Communication). Kernel estimators are nonparametric and are therefore the best method to use when estimating animal home ranges from data that are multi-modal and non-normal (Seaman et al. 1999, Seaman and Powell 1996). Worton (1989) first suggested using kernel methods as a nonparametric means of estimating an animal’s home range (i.e. utilization distribution), and stated the adaptive kernel method would produce the best results. However, in computer simulations, fixed kernel density estimates using least squares cross-validation for choosing the smoothing parameter outperformed both adaptive kernel and harmonic mean estimates when the true area and shape of multimodal, two-dimensional distributions was known (Powell et al. 1997, Seaman and Powell 1996). Ultimately, Worton (1995) also found that fixed kernel estimators were less biased than the harmonic mean method. Fixed kernel estimates gave not only the most accurate estimate of home range area, but also had the smallest variance (Powell et al. 1997).

Selection of appropriate kernel size (smoothing parameter) is very important for reducing bias in the home range estimate, and least squares cross-validation has been shown previously to be the preferred method for making this selection (Seaman et al. 1999, Seaman et al. 1998, Powell et al. 1997, Seaman and Powell 1996, Worton 1995). However, J. Horne and E.O. Garton (University of Idaho, Personal Communication) have recently shown that likelihood cross-validation outperformed least squares cross-validation, particularly at small sample sizes. Likelihood cross-validation is based on minimizing the Kullback-Leibler distance between the known and estimated utilization distributions (Silverman 1986). When likelihood cross-validation was used for choosing the smoothing parameter, estimated utilization distributions were less variable than when least squares cross-validation was used (J. Horne and E.O. Garton, Personal Communication).

Because sample size affects bias and precision of the home range estimate, it is important to establish a minimum sample size for home range analyses (Seaman et al. 1999). Seaman et al. (1999) suggested a minimum sample size of 30 independent observations per animal, though preferably at least 50 observations, for input into a fixed kernel estimator. Furthermore, J. Horne and E.O. Garton (Personal Communication) found that the likelihood cross-validation method resulted in a better fit than least-squares cross-validation in the estimation of home ranges based on small sample sizes (i.e. $\leq 40$). However, in an examination of three home range estimators including kernel estimators, Girard et al. (2002) suggested that up to 300 locations per animal may be needed for annual home ranges and 30-100 locations for seasonal home ranges. Given these recommendations and the use of likelihood cross-validation for selecting kernel size, I selected a minimum sample size of 30 GPS relocations per bear for seasonal home range analysis. Annual home ranges contained substantially more locations.

I used a Visual Basic program created by J. Horne (University of Idaho) to calculate 95% fixed kernel home ranges. The program used likelihood cross-validation for selection of kernel width. Further, the program allowed for input of weighted bear points based on their probability of detection (see Chapter 1). The following kernel home range equation was used to estimate the probability density at any point (*x*, *y*) in space:

$$\hat{f}(x,y) = \frac{\left[\sum_{i=1}^{n} \frac{\beta_i}{2\pi n h^2} \exp\left(-\frac{d_i^2}{2h^2}\right)\right]}{\sum_{i=1}^{n} \beta_i}$$

where $h$ is the smoothing parameter calculated with likelihood cross-validation, $d_i$ is the distance between the $i^{th}$ observation and the $x$, $y$-coordinate, and $\beta_i$ is the weighting factor for each location ($1/P_{success}$; J. Horne, Personal Communication).

I calculated both composite and seasonal home ranges for each GPS radio-collared bear. Composite home ranges included the pooled locations from all seasons and years downloaded from a particular bears' GPS collar. Seasonal home ranges, corresponding with spring and fall, were subsets of composite home ranges. Dates for seasonal home ranges were determined according to an examination of annual bear activity patterns and resource availability in Olympic NP. Like Unsworth et al. (1989), I defined the spring season as encompassing the period from den emergence through the breeding season (June), while the fall season included the period between July and den entry, when berries were widely available. Furthermore, the fall season encompassed the period that salmon are expected to spawn in the Elwha watershed after dam removal and subsequent salmon restoration, making this season useful for future comparison purposes (NPS 1996).

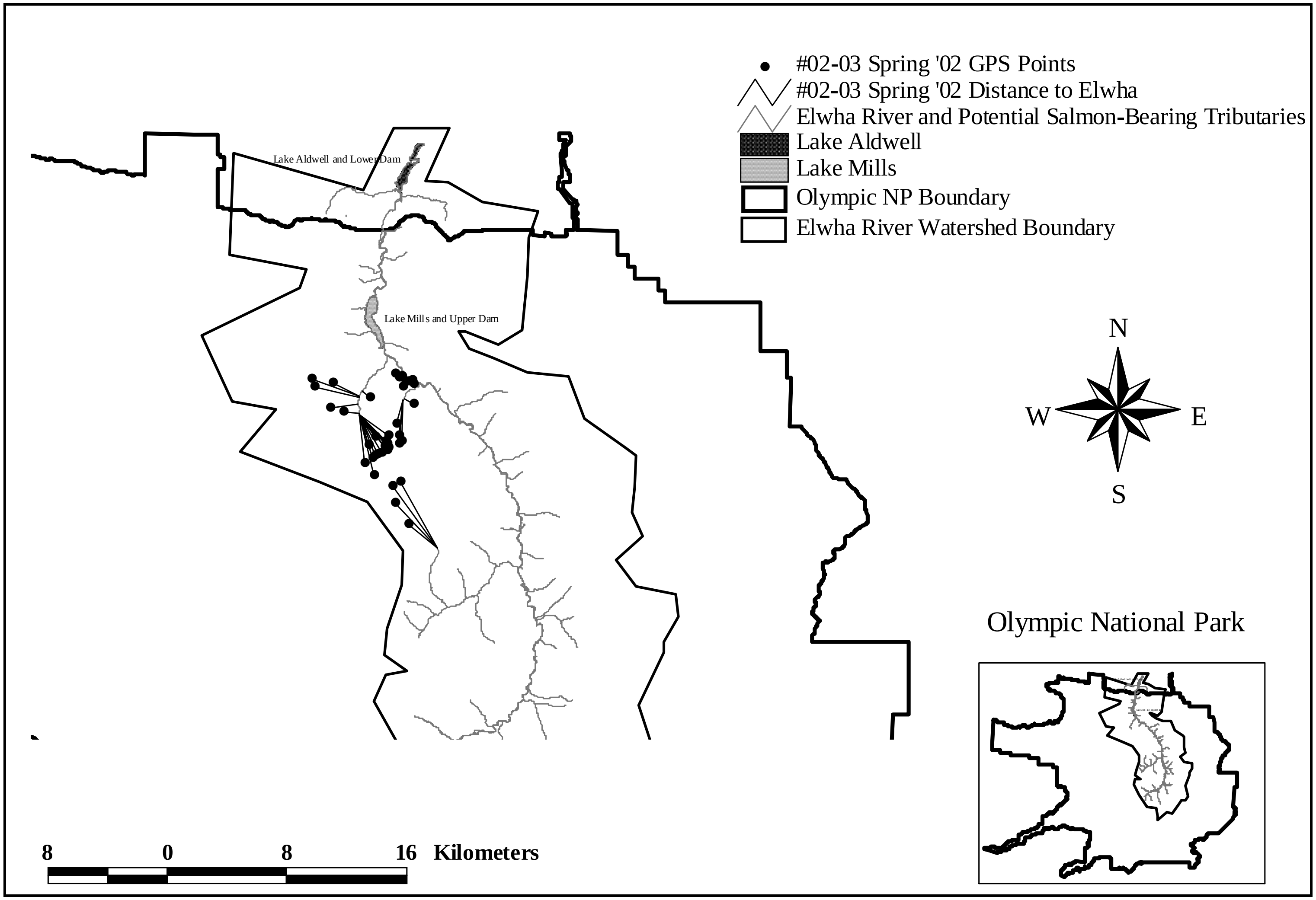
### *Seasonal patterns in elevation distribution:*

To determine if bears exhibited seasonal shifts in elevation, I used ArcView to assign elevation data to each bear coordinate. Each bear point was then weighted according to its probability of detection. I computed mean elevations for each bear during each week. I then computed a weekly mean (±SE) for all radio-collared bears combined (*n* = 11), and graphically represented these data using SigmaPlot for Windows Version 8.0 (SPSS, Inc.).

### *Distance to Elwha River and tributaries:*

Because I was interested in examining bear use of the Elwha River watershed prior to removal of the Elwha dams, I examined bear distance to the Elwha across all seasons and years. I used ArcView to digitize a polygon of the Elwha River watershed, and defined the watershed as the Elwha Basin bounded by Low Divide to the south, by mountain ridges on the east and west, and by Lake Aldwell to the north. I used the GeoProcessing Wizard in ArcView to clip the USGS-derived hydrography layer and contain it within the watershed boundaries. I then deleted segments of the river and its tributaries that are not predicted to support runs of spawning salmon after river restoration (NPS 1996; Figure 2.1). I used the Animal Movement Extension for ArcView 2.0 (USGS-BRD, Alaska Science Center- Biological Science Office) to conduct spider distance analyses for each bear. These provided straight-line distances between potential

Figure 2.1. Example of spider distance analysis for examining distance of GPS radio-collared black bears to potential salmon-bearing streams in the Elwha river watershed, Olympic NP. Data shown here for bear # 2002-03 for one spring season.



Elwha salmon-bearing waters and each bear point (Figure 2.1). Though many of the bear points fell outside the boundary of the watershed, and in some cases were found along other major rivers, I retained all bear points for this level of analysis. The Elwha watershed was considered to be the main study area; because I was interested in collecting baseline data on bear use of the watershed, it was important to examine how bears moved in relation to the watershed and potential salmon-bearing portions of the Elwha.

After conducting spider-distance analyses on all bear points, I weighted each point and associated distance by the inverse of the point's probability of detection. I analyzed temporal differences in distances of bears to the Elwha River at two scales. First, I examined seasonal differences in bear use of the Elwha River corridor. To determine if seasonal differences existed, I grouped points and their associated distance-to-Elwha measurements by season (spring and fall). I conducted descriptive statistics and calculated a mean and standard error for distance measurements for each bear during each season. In several cases where bears remained collared over multiple years, I pooled spring and fall from different years. This resulted in one data set corresponding to spring and fall for each bear. I then conducted a paired two-sample t-test to test for differences in mean distance-to-Elwha measurements between spring and fall seasons.

At a finer resolution of temporal scale, I evaluated weekly patterns of use throughout the year. I computed mean (±SE) distance-to-Elwha measurements for each bear during each week. I then computed a weekly mean for all radio-collared bears combined, and graphically represented these data using SigmaPlot.

*Resource selection analysis:*

I examined habitat selection patterns of GPS radio-collared black bears at two nested spatial scales, each providing greater spatial resolution for identification of resource selection patterns. This hierarchical approach for examining usage versus availability was first proposed by Johnson (1980). I examined resource use by bears at two levels of Johnson's (1980) proposed selection hierarchies: second-order selection and third-order selection. As defined by Johnson (1980), second-order selection determines the placement of an individual's home range while third-order selection pertains to the individual's usage of various habitat components within the home range.

At the broadest scale of selection (second-order), I investigated factors influencing seasonal home range placement for individual bears by comparing proportions of cover type classes found within error circles (i.e. buffers) that I inscribed around individual bear locations to proportions of habitat types available in the study area. The study area was defined as the minimum convex polygon (MCP) encompassing the aggregate of all collared bear home ranges (Thomas and Taylor 1990, Manly et al. 1993). Though numerous researchers (i.e. Aebischer et al. 1993, Lyons et al. 2003) have examined the factors affecting home range placement by comparing the proportions of cover type classes contained within the home range (rather than individual locations) to the proportion of those available on the study area, White and Garrott (1990) dismissed this approach as biased. They argue that it confounds errors in home range estimates, assumes that home ranges are used uniformly by animals, and ignores the fact that by its nature a home range already represents prior selection.

To determine habitat selection at a finer level of resolution, I examined black bear use of habitats within their individual composite and seasonal home ranges (third-order selection). I compared proportions of cover types within error circles inscribed around individual bear locations to proportions of cover types available within 95% composite seasonal fixed kernel home ranges (Thomas and Taylor 1990, Manly et al. 1993).

At both orders of selection, I defined use as the proportion of cover type classes occurring within 180-m error radii of the estimated animal locations. I chose a 180-m radius buffer for two reasons. First, 180 m accounted for 95% of the GPS telemetry error quantified in the first part of the study (Table 1.6), as well as errors in digital habitat coverages. Secondly, Rettie and McLoughlin (1999) demonstrated that placing buffers around individual animal locations reduced inaccuracies and biases inherent in many telemetry-based habitat selection studies, and revealed the importance of habitat mosaics in resource selection by wildlife (Rettie and McLoughlin 1999).

I determined the vegetative composition of available habitats within the study area, within individual home ranges, and within error buffers around individual location points using the Pacific Meridian Resources (PMR) GIS coverage for Olympic NP. To improve interpretability and power of the analysis, I reduced the original 25 cover type classes to 8 cover type classes based on similarity in plant attributes and community composition (Table 2.1).

Table 2.1. Vegetation cover classes and associated PMR[1] vegetation types used for resource selection analyses.

| **Cover class** | **Vegetation Types** |
|---|---|
| 1 | Water/Rock/Snow |
| 2 | All meadow types |
| 3 | Heather/Shrub/<25% any species |
| 4 | Douglas Fir (PSME) and Lodgepole Pine (PICO) |
| 5 | Mountain Hemlock (TSME) and Subalpine Fir (ABLA) |
| 6 | Western Hemlock (TSHE), Sitka Spruce (PISI), Western Red Cedar (THPL), Conifer mix |
| 7 | Pacific Silver Fir (ABAM) and Alaska Yellow Cedar (CHNO) |
| 8 | Hardwoods: Big Leaf Maple (ACMA), Red Alder (ALRU), Hardwood mix |

[1] Pacific Meridian Resources

### *GIS METHODOLOGY*

To determine available habitat for the analysis of second-order selection, I used the Animal Movement Extension for ArcView to calculate the MCP on an aggregate of all bear locations combined. I used the Grid Analyst Extension to extract the vegetation layer so that it was contained within the boundaries of the MCP. Finally, I used the XTools Extension to calculate and summarize the number of hectares for each cover type found within the MCP.

To establish resource availability for analysis of third-order selection, I used 95% fixed kernel home ranges. Where seasonal home ranges from multiple years were available, I computed a combined seasonal home range prior to analysis so that each bear was represented by one spring and one fall seasonal range, as well as the composite home range. Home ranges were hand-digitized to form polygons and I used the Geoprocessing Wizard in ArcView to intersect home ranges with the vegetation layer. I used XTools to calculate and summarize the total area of each cover type for spring, fall, and composite home ranges. This provided a measure of availability for analysis of third-order selection from which I calculated proportion of available cover types in each home range.

I created error buffers of 180-m radius around each bear location using ArcView, resulting in an area of 10.17 hectares around each bear point. I buffered points within three temporal groupings for each bear: composite locations, combined spring locations, and combined fall locations. I used the Geoprocessing Wizard to intersect bear buffers with the vegetation overlay so that, depending on the level of habitat heterogeneity, each buffer was comprised of one to several cover types. The proportions of cover types in each buffer summed to 1.0. I used the XTools extension in ArcView to calculate the area of each cover type contained within each buffer. This provided a measure, in hectares, of the cover type composition of each buffer.

Without the application of weighting factors to correct for GPS bias, buffers were biased towards more open and less steep habitat types. Therefore, I bias-corrected each point by multiplying the point-specific weighting factor by the number of hectares of each cover type that comprised the buffer. For example, assume that 4 of the 8 available habitat types were found within one 10-hectare buffer. If each habitat comprised 2.5 hectares of area within the buffer, and the weighting factor for that point was 2, the resultant weight would be 2.5 * 2 = 5 hectares used for each of the 4 cover types. This is akin to assuming the point was selected 2 times. Once each buffered bear point was bias-corrected, I used XTools to summarize the total number of weighted hectares in each habitat type. This was completed for each bear and each time frame (composite, spring, fall). I was then able to calculate the weighted proportional use for each habitat type.

### *COMPOSITIONAL ANALYSIS*

At both scales of selection, I used compositional analysis to compare proportions of habitats used by bears (i.e., within weighted error buffers) to proportion of habitats available and to develop a ranking of cover type preferences (Aebischer et al. 1993). Compositional analysis uses the animal, rather than the individual GPS location, as the sampling unit (Aebischer et al. 1993). This ameliorates the problem of autocorrelation of points, but as a consequence requires that the number of animals be considered the sample size. Because Aebischer et al. (1993) suggested an absolute minimum of 6 animals for compositional analysis, though preferably 10, I pooled data obtained from 2 individual females and 8 males prior to analysis. I had at least 1 spring and 1 fall data set for each of these bears. Although I pooled males and females prior to analysis, I graphically displayed use of habitats separately for males and females.

I input proportional use and availability data derived from GIS into Resource Selection software (Resource Selection for Windows, Version 1.00, 1999, Fred Leban). Values of 0% corresponding to non-utilized cover types were replaced with 0.1% (Aebischer et al. 1993). Significance was set at $\alpha = 0.10$.

## RESULTS

### *Animal capture:*

We captured a total of 18 different bears over 3 field seasons; additionally, 4 bears were caught more than once for a total of 22 bear captures (Table 2.2). Five bears were free-range darted, while 17 were captured in Aldrich snares (Table 2.2). Sixteen of the captured bears were male, and only 2 were female (Table 2.2). Each of the 2 females were captured and collared in 2002, and were recaptured in 2004 (Table 2.2). Of 18 bears caught, 15 different bears were equipped with GPS radio-collars (Table 2.2). Four recaptured bears were equipped twice with GPS collars, for a total deployment of 19 GPS collars over the course of the study (Table 2.2).

Excluding one yearling male, each bear was sexually mature at the time of capture (Table 2.2). During 2002, one female was in estrus (bear 2002-08) and another had 2 cubs-of-the-year (bear 2002-10; Table 2.2). Subsequent observations of bear 2002-10 revealed that her cubs remained with her throughout 2002 and 2003. This is contrary to common knowledge of black bear reproductive biology, which suggests that cubs remain with their mothers only during their first 16 months (Pelton 2003). In 2003, incidental observations of bear 2002-08 indicated that she had one cub-of-the-year. This cub did not appear to remain with her in 2004, as evidenced by the fact that she was alone when recaptured during that year. When recaptured in 2004, both females were in estrus (Table 2.2).

Bears captured in Olympic NP varied by age and size. Based on estimates of tooth-wear, captured bears ranged in age from approximately one year to over 16 years old,

Table 2.2. Cumulative summary of black bears captured and tagged in Olympic NP, 2002-2004.

| **Animal #** | **Capture date** | **Capture method** | **Capture location** | **Collar type** | **Sex** | **Breeding status** |
|---|---|---|---|---|---|---|
| 2002-01 | 5/15/2002 | Snare | Lower Elwha | VHF | M | Testes descended |
| 2002-02 | 5/16/2002 | Free-ranged | Lower Elwha | VHF | M | Testes descended |
| 2002-03 | 5/19/2002 | Snare | Lower Elwha | GPS | M | Testes descended |
| 2002-04 | 5/28/2002 | Snare | Lower Elwha | GPS | M | Testes descended |
| 2002-05 | 6/3/2002 | Snare | Lower Elwha | GPS | M | Testes descended |
| 2002-06 | 6/17/2002 | Snare | Upper Elwha | GPS | M | Testes descended |
| 2002-07 | 6/18/2002 | Snare | Upper Elwha | GPS | M | Testes descended |
| 2002-08 | 7/18/2002 | Snare | Hurricane Ridge | GPS | F | In estrus |
| 2002-09 | 8/6/2002 | Snare | Hurricane Ridge | None | M | Testes not fully descended |
| 2002-10 | 8/7/2002 | Free-ranged | Hurricane Ridge | GPS | F | 2 cubs of the year |
| 2003-01 | 5/9/2003 | Free-ranged | Lower Elwha | GPS | M | Testes descended |

Table 2.2. Continued.

| Animal # | Capture date | Capture method | Capture location | Collar type | Sex | Breeding status |
|---|---|---|---|---|---|---|
| 2003-02 | 5/28/2003 | Snare | Upper Elwha | GPS | M | Testes descended |
| 2003-03 | 6/3/2003 | Snare | Upper Elwha | GPS | M | Testes descended |
| 2003-04 | 7/16/2003 | Snare | Lower Elwha | GPS | M | Testes descended |
| 2002-02 | 5/11/2004 | Free-ranged | Lower Elwha | GPS | M | Testes descended |
| 2004-02 | 5/13/2004 | Snare | Lower Elwha | GPS | M | Testes descended |
| 2004-03 | 5/16/2004 | Snare | Lower Elwha | GPS | M | Testes descended |
| 2004-04 | 5/18/2004 | Snare | Lower Elwha | GPS | M | Testes descended |
| 2004-05 | 5/24/2004 | Snare | Lower Elwha | GPS | M | Testes descended |
| 2002-08 | 5/31/2004 | Free-ranged | Hurricane Ridge | GPS | F | In estrus |
| 2002-10 | 6/5/2004 | Snare | Hurricane Ridge | GPS | F | In estrus |
| 2003-02 | 7/9/2004 | Snare | Hurricane Ridge | GPS | M | Testes descended |

though the majority were greater than 8 years old (Table 2.3). Captured bears ranged in size from approximately 100 to 300 pounds and were variable in overall condition and measures of neck, chest, and shoulder size (Table 2.3). We did not document any natural or capture-related mortality during the study.

Collared bears entered their winter dens as early as October and as late as December. They emerged from their dens between early March and early May (Table 2.4). The two females entered their dens later than males (December) and also emerged from their dens after the males (late April and early May).

### *GPS collar performance:*

We experienced inconsistent success with GPS collars placed on black bears. Of the 19 GPS collars deployed during the study, 5 large male bears shed their collars; 3 of those collars provided some level of data before they were shed (Table 2.5). Another 8 collars experienced some type of failure. These failures ranged from complete and immediate failure to failure of the VHF or GPS component several months after deployment (Table 2.5). Of the 8 failed collars, data were retrieved from 5 (Table 2.5). Ultimately, bear movement data were collected from 11 different bears over the course of the study. Of those, 10 bears provided data for at least 1 spring and 1 fall and are the basis for many of the subsequent analyses.

Four collars that acquired data were not recovered either because the VHF signal had failed or we could not locate them. I obtained data from those collars through remote downloads of the data and not through physical recovery of the collar (Table 2.5). Additionally, the 2 collared females are each still equipped with their second GPS collar

Table 2.3. Physical data of 18 black bears captured in Olympic NP, 2002-2004.

| **Animal #** | **Sex** | **Estimated ages (years)** | **Estimated weight (lbs.)** | **Physical condition** | **Neck size (cm)** | **Chest size (cm)** | **Shoulder height (cm)** | **Total length (cm)** |
|---|---|---|---|---|---|---|---|---|
| 2002-01 | M | 8 3/4-15 3/4 | 275-300 | Good | 75 | 114 | 72 | 182 |
| 2002-02 | M | 8 3/4-15 3/4 | 250 | Good | 58 | 88 | 80 | 160 |
| 2002-03 | M | 8 3/4-15 3/4 | 200 | Good | 68 | 200 | 71 | 169 |
| 2002-04 | M | 8 3/4-15 3/4 | 175 | Fair | 68 | 97 | 74 | 165 |
| 2002-05 | M | 8 3/4-15 3/4 | 150 | Fair | 54 | 92 | 79 | 175 |
| 2002-06 | M | 4-7 | 175-200 | Fair | 56 | 96 | 80 | 82 |
| 2002-07 | M | 8 3/4-15 3/4 | 175 | Fair | 56 | 104 | 77 | 171 |
| 2002-08 | F | 8 3/4-15 3/4 | 120 | Fair | 49 | 78 | 66 | 142 |
| 2002-09 | M | 1 | 100 | Fair | 46 | 70 | 57 | 145 |
| 2002-10 | F | 8 3/4-15 3/4 | 125 | Fair | 45 | 75 | 65 | 143 |

Table 2.3.  Continued.

| **Animal #** | **Sex** | **Estimated ages (years)** | **Estimated weight (lbs.)** | **Physical condition** | **Neck size (cm)** | **Chest size (cm)** | **Shoulder height (cm)** | **Total length (cm)** |
|---|---|---|---|---|---|---|---|---|
| 2003-01 | M | 8 3/4-15 3/4 | 225 | Good | 57 | 93 | 82 | 169 |
| 2003-02 | M | 8 3/4-15 3/4 | 250 | Good | 62 | 99 | 80 | 175 |
| 2003-03 | M | 8 3/4-15 3/4 | 275 | Good | 68 | 107 | 86 | 80 |
| 2003-04 | M | 8 3/4-15 3/4 | 150 | Fair | not taken | not taken | not taken | not taken |
| 2004-02 | M | 16 3/4 + | 175 | Fair | 57 | 91 | 81 | 173 |
| 2004-03 | M | 8 3/4-15 3/4 | 170 | Good | 63 | 94 | 73 | 162 |
| 2004-04 | M | 10 | 250 | Good | 68 | u[2] | u | 169 |
| 2004-05 | M | 16 3/4 + | 150 | Good | 61 | 101 | 91 | 160 |

Table 2.4. Approximate hibernation dates for 6 bears in Olympic NP, 2002-2004. Data from bears with collars that functioned properly over a winter period.

| **Animal #** | **Approximate den entry date** | **Approximate den exit date** |
|---|---:|---:|
| 2002-05 | 11/17/2002 | 3/31/2003 |
| 2002-06 | 11/24/2002 | 3/29/2003 |
| 2002-08[1] | 12/8/2002 | 5/9/2003 |
| 2002-10[1] | 12/2/2002 | 4/29/2003 |
| 2003-01 | 10/8/2003 | 3/30/2004 |
| 2003-04 | 11/30/2003 | 3/10/2004 |

[1] Females; all others are males.

Table 2.5. Status of radio-collars on all tagged bears, Olympic NP, 2002-2004.

| **Animal #** | **Capture date** | **Collar type** | **Collar status** | **Collar recovered?** | **Some level of data collection?** |
|---|---|---|---|---|---|
| 2002-01 | 5/15/2002 | VHF[1] | Removed by bear within 2 days | Yes | No |
| 2002-02 | 5/16/2002 | VHF[1] | Removed by bear immediately | Yes | No |
| 2002-03 | 5/19/2002 | GPS | Removed by bear, 7/18/02 | Yes | Yes- Directly downloaded |
| 2002-04 | 6/9/2002 | GPS | GPS-component failed, 9/2002; collar failed to drop-off in 9/2003 | No | Yes- Remotely downloaded |
| 2002-05 | 6/3/2002 | GPS | Dropped-off, 9/2003 | Yes | Yes- Directly downloaded |
| 2002-06 | 6/17/2002 | GPS | Dropped-off, 9/2003 | Yes | Yes- Directly downloaded |
| 2002-07 | 6/18/2002 | GPS | Malfunctioned immediately | No | No |
| 2002-08 | 7/18/2002 | GPS | Collar failed to drop-off in 9/2003, but dropped-off late (12/2003) | Yes | Yes- Directly downloaded |
| 2002-09 | 8/6/2002 | None | N/A; Yearling bear | N/A | N/A |
| 2002-10 | 8/7/2002 | GPS | Dropped-off, 9/2003 | Yes | Yes- Directly downloaded |
| 2003-01 | 5/9/2003 | GPS | Failed, 8/2004 | No | Yes- Remotely downloaded |

Table 2.5. Continued.

| Animal # | Capture date | Collar type | Collar status | Collar recovered? | Some level of data collection? |
|---|---|---|---|---|---|
| 2003-02 | 5/28/2003 | GPS | GPS-component failed, 9/2003 | Yes- recapture | Yes- Directly downloaded |
| 2003-03 | 6/3/2003 | GPS | Removed by bear, 9/2003 | Yes | Yes- Directly downloaded |
| 2003-04 | 7/16/2003 | GPS | Dropped-off, 9/2004 | No | Yes- Remotely downloaded |
| 2002-02 | 5/11/2004 | GPS | VHF component failed, 7/2004 | No | No |
| 2004-02 | 5/13/2004 | GPS | GPS component failed, 7/2004 | No | No |
| 2004-03 | 5/16/2004 | GPS | Removed by bear, 7/2004 | No | Yes- Remotely downloaded |
| 2004-04 | 5/18/2004 | GPS | Removed by bear after 1 week | Yes | No |
| 2004-05 | 5/24/2004 | GPS | Removed by bear within 1 day | Yes | No |
| 2002-08 | 5/31/2004 | GPS | Still functioning on bear | N/A | Yes- Remotely downloaded |
| 2002-10 | 6/5/2004 | GPS | Still functioning on bear | N/A | Yes- Remotely downloaded |
| 2003-02 | 7/9/2004 | GPS | GPS component failed, 9/2004 | Yes | Yes- Directly downloaded |

[1] VHF collar placed on bear because GPS collars too small.

of the study; therefore, 2004 data for these bears were downloaded remotely. Comparisons between data received from remote downloads and data received directly from recovered collars revealed that remote data downloads captured only a portion of the stored data (mean = 66.24% ± 2.24). The data downloading process was tenuous, with the VHF signal often wavering outside the ranges of signal-strength parameters necessary for successful data retrieval. When this occurred, data lines were lost in transmission and not received by the RX-900 receiver. Though this resulted in loss of data, an examination of remotely transmitted data revealed that the loss was not systematic, but rather random. Given this, I pooled remotely and directly downloaded data for all analyses.

Collars that were recovered and from which I downloaded data directly to a computer (*n* = 7) attempted a total of 5392 fixes while on bears; 2015 fixes were successful, resulting in an average fix success rate of 38.97 ± 3.71% (Table 2.6). Three-dimensional fixes were acquired on 507 occasions, for a mean 3D fix success rate of 23.26 ± 4.08% (Table 2.6).

### *Home range analysis:*

Bears in the Elwha watershed, particularly males, ranged widely (Appendix 1). They frequently left the Elwha River watershed for extended periods of time, especially during the breeding and fall huckleberry-foraging seasons. However, they all returned to the Elwha during late fall and remained there until spring.

Composite and seasonal home ranges were calculated for 10 bears (Appendix 1). Due to battery-life limitations of GPS collars, dropped and failed collars, and different

Table 2.6. Number of successful GPS locations from 7 collared bears in Olympic NP, including 3D fix rates. Data downloaded directly from recovered collars.

| **Bear #** | **Total # successful fixes** | **Total # of fix attempts** | **% fix success** | **Total # 3D fixes** | **% 3D fix success** |
|---|---|---|---|---|---|
| 2002-03 | 79 | 240 | 33% | 12 | 15% |
| 2002-05 | 398 | 967 | 41% | 165 | 41% |
| 2002-06 | 506 | 1343 | 38% | 122 | 24% |
| 2002-08 | 322 | 1059 | 30% | 50 | 16% |
| 2002-10 | 303 | 987 | 31% | 40 | 13% |
| 2003-02 | 142 | 344 | 41% | 27 | 19% |
| 2003-03 | 265 | 452 | 59% | 91 | 34% |
|  |  |  | **Mean ± SE** |  | **Mean ± SE** |
| **Totals** | 2015 | 5392 | 38.97 ± 3.71 | 507 | 23.26 ± 4.08 |

capture dates for each bear, the range of dates available for seasonal home range analyses varied (Table 2.7). This, coupled with variable GPS collar fix-success, resulted in unequal numbers of fixes available for use in home range analyses (Table 2.7).

Home range sizes of male bears were highly variable. Composite 95% fixed kernel home ranges for males ranged in sized from 49.72 to 104.18 $km^2$ (mean = 68.73 ± 6.27 $km^2$; Tables 2.8 and 2.9). Seasonal home ranges of males varied in size from 26.62 to 119.71 $km^2$ during spring (mean = 60.49 ± 11.66 $km^2$) and 19.55 to 95.17 $km^2$ during fall (mean = 50.91 ± 7.77 $km^2$; Tables 2.8 and 2.9).

Female bears had smaller and less variable home ranges than males. Female composite home ranges were less than half the size of male home ranges, and averaged 25.10 ± 5.05 $km^2$ (Table 2.9). Spring home ranges averaged 5.76 ± 0.21 $km^2$ while fall home ranges averaged 16.45 ± 3.55 $km^2$ (Table 2.9).

### *Seasonal patterns in elevation distribution:*

Bears in Olympic NP followed a cyclical annual pattern of elevation use. The pattern was predictable among the three years of the study, with bears using low elevations in the early spring, followed by mid- to high-elevations during summer and fall, and finally returning to lower elevations prior to den entry (Figure 2.2). Locations of bears ranged from 271-1399 m during spring (approximately March 10 – June 30). Fall locations (July 1 – December 8) ranged from a low of 753 m to a peak elevation of 1687 m.

Table 2.7. Seasonal home range dates of 10 GPS radio-collard bears and number of fixes acquired during those dates.

| **Bear #** | **Year** | **Season** | **Begin Date** | **End Date** | **# Fixes**[1] |
|---|---|---|---:|---:|---:|
| 2002-03 | 2002 | Spring | 5/21/2002 | 6/28/2002 | 39 |
| 2002-03 | 2002 | Fall | 7/1/2002 | 7/19/2002 | 42 |
| 2002-04 | 2002 | Spring | 6/12/2002 | 6/30/2002 | 18 |
| 2002-04 | 2002 | Fall | 7/1/2002 | 9/5/2002 | 107 |
| 2002-05 | 2002 | Spring | 6/4/2002 | 6/30/2002 | 42 |
| 2002-05 | 2002 | Fall | 7/1/2002 | 11/17/2002 | 317 |
| 2002-05 | 2003 | Spring | 3/31/2003 | 5/22/2003 | 40 |
| 2002-06 | 2002 | Spring | 6/18/2002 | 6/30/2002 | 21 |
| 2002-06 | 2002 | Fall | 7/1/2002 | 11/24/2002 | 298 |
| 2002-06 | 2003 | Spring | 3/29/2003 | 6/30/2003 | 43 |
| 2002-06 | 2003 | Fall | 7/1/2003 | 9/7/2003 | 145 |
| 2002-08 | 2002 | Fall | 7/19/2002 | 12/8/2002 | 203 |
| 2002-08 | 2003 | Spring | 5/9/2003 | 6/30/2003 | 68 |
| 2002-08 | 2003 | Fall | 7/1/2003 | 7/29/2003 | 52 |
| 2002-08 | 2004 | Spring | 6/2/2004 | 6/29/2004 | 24 |
| 2002-08 | 2004 | Fall | 7/1/2004 | 9/16/2004 | 23 |
| 2002-10 | 2002 | Fall | 8/7/2002 | 12/2/2002 | 136 |
| 2002-10 | 2003 | Spring | 4/29/2003 | 6/30/2003 | 121 |

Table 2.7. Continued.

| **Bear #** | **Year** | **Season** | **Begin Date** | **End Date** | **# Fixes** |
|---|---|---|---:|---:|---:|
| 2002-10 | 2003 | Fall | 7/2/2003 | 8/1/2003 | 48 |
| 2002-10 | 2004 | Spring | 6/7/2004 | 6/30/2004 | 19 |
| 2002-10 | 2004 | Fall | 7/1/2004 | 9/21/2004 | 53 |
| 2003-01 | 2003 | Spring | 5/10/2003 | 6/30/2003 | 67 |
| 2003-01 | 2003 | Fall | 7/2/2003 | 10/8/2003 | 209 |
| 2003-01 | 2004 | Spring | 3/30/2004 | 6/30/2004 | 66 |
| 2003-01 | 2004 | Fall | 7/1/2004 | 7/29/2004 | 51 |
| 2003-02 | 2003 | Spring | 5/29/2003 | 6/30/2003 | 47 |
| 2003-02 | 2003 | Fall | 7/1/2003 | 8/22/2003 | 95 |
| 2003-02 | 2004 | Fall | 7/9/2004 | 7/31/2004 | 19 |
| 2003-03 | 2003 | Spring | 6/4/2003 | 6/30/2003 | 49 |
| 2003-03 | 2003 | Fall | 7/1/2003 | 9/24/2003 | 216 |
| 2003-04 | 2003 | Fall | 7/16/2003 | 11/30/2003 | 170 |
| 2003-04 | 2004 | Spring | 3/10/2004 | 5/10/2004 | 25 |
| 2004-03 | 2004 | Spring | 5/28/2004 | 6/29/2004 | 17 |

[1] No home ranges computed if <30 fixes available.

Table 2.8. Ninety-five percent fixed kernel home range sized of 10 GPS collared black bears in Olympic NP. Composite ranges combine all GPS locations acquired over all years and all seasons.

| **Bear #** | **Sex** | **Year** | **Home range season** | **95% fixed kernel home range size (km$^2$)** | **# GPS locations available** |
|---|---|---|---|---|---|
| 2002-03 | M | 2002 | Composite | 61 | 81 |
| | | 2002 | Spring | 57 | 39 |
| | | 2002 | Fall | 46 | 42 |
| 2002-04 | M | 2002 | Composite | 61 | 125 |
| | | 2002 | Spring | * | 18 |
| | | 2002 | Fall | 60 | 107 |
| 2002-05 | M | 2002-2003 | Composite | 80 | 399 |
| | | 2002 | Spring | 72 | 42 |
| | | 2002 | Fall | 54 | 317 |
| | | 2003 | Spring | 27 | 40 |
| 2002-06 | M | 2002-2003 | Composite | 71 | 507 |
| | | 2002 | Spring | * | 21 |
| | | 2002 | Fall | 20 | 298 |
| | | 2003 | Spring | 120 | 43 |
| | | 2003 | Fall | 65 | 145 |
| 2002-08 | F | 2002-2004 | Composite | 30 | 370 |
| | | 2002 | Fall | 28 | 203 |
| | | 2003 | Spring | 6 | 68 |
| | | 2003 | Fall | 9 | 52 |
| | | 2004 | Spring | * | 24 |
| | | 2004 | Fall | * | 23 |

Table 2.8. Continued.

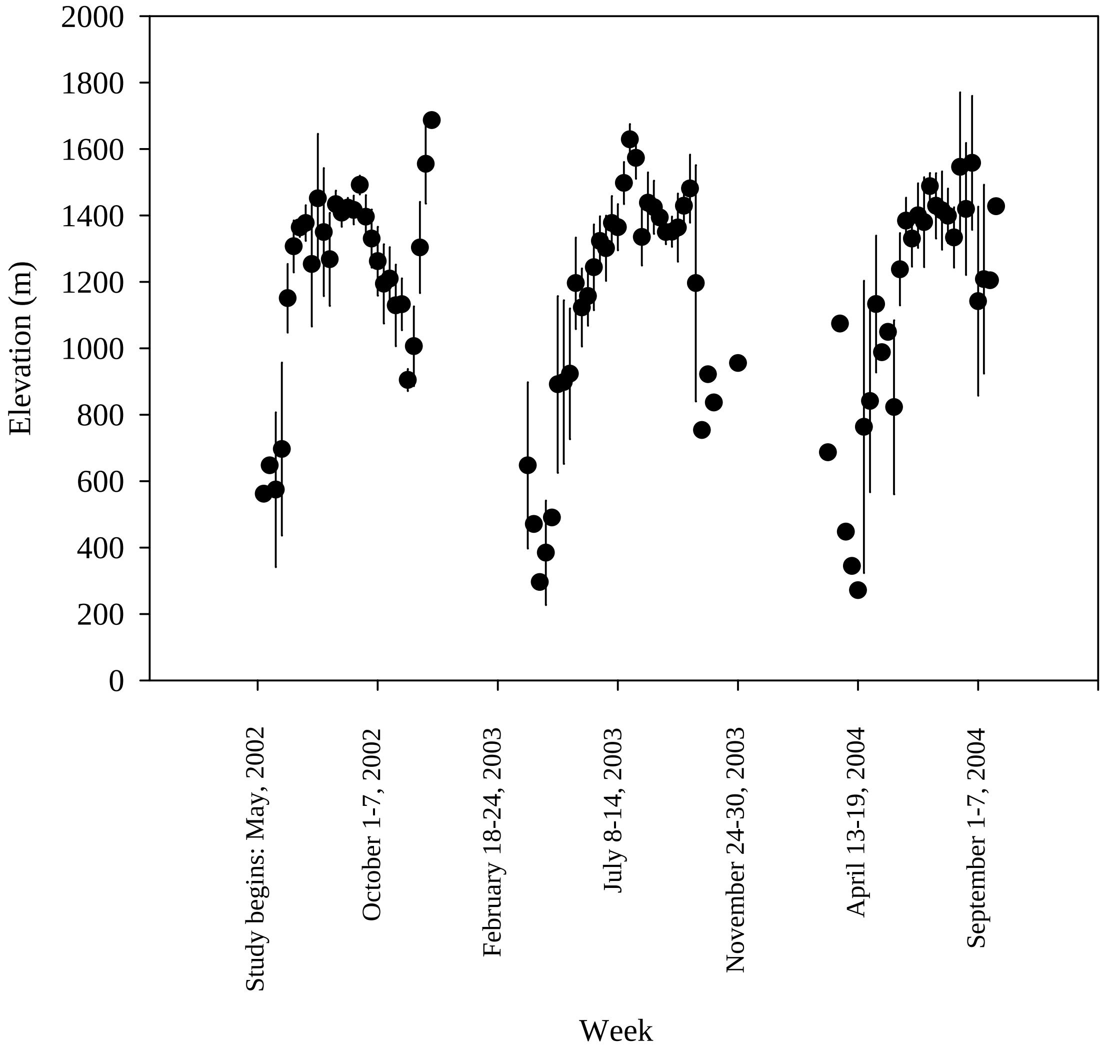
| **Bear #** | **Sex** | **Year** | **Home range season** | **95% fixed kernel home range size ($km^2$)** | **# GPS locations available** |
|---|---|---|---|---|---|
| 2002-10 | F | 2002-2004 | Composite | 20 | 377 |
| | | 2002 | Fall | 19 | 136 |
| | | 2003 | Spring | 6 | 121 |
| | | 2003 | Fall | 9 | 48 |
| | | 2004 | Spring | * | 19 |
| | | 2004 | Fall | 18 | 53 |
| 2003-01 | M | 2003-2004 | Composite | 51 | 393 |
| | | 2003 | Spring | 49 | 67 |
| | | 2003 | Fall | 29 | 209 |
| | | 2004 | Spring | 37 | 66 |
| | | 2004 | Fall | 22 | 51 |
| 2003-02 | M | 2003-2004 | Composite | 72 | 162 |
| | | 2003 | Spring | 29 | 47 |
| | | 2003 | Fall | 78 | 95 |
| | | 2004 | Fall | * | 19 |
| 2003-03 | M | 2003 | Composite | 104 | 265 |
| | | 2003 | Spring | 94 | 49 |
| | | 2003 | Fall | 95 | 216 |
| 2003-04 | M | 2003-2004 | Composite | 50 | 195 |
| | | 2003 | Fall | 39 | 170 |
| | | 2004 | Spring | * | 25 |

*indicates that no home range calculated due to insufficient sample size (≤30 GPS locations)

Table 2.9. Mean kernel home ranges of 10 black bears in Olympic NP. Home ranges are fixed-kernel estimates for bears with ≥ 30 relocations over all seasons and all years.

| **Sex** | **Home range** | **# of bears** | **Home range size (mean km$^2$)** | **SE** |
|---|---|---|---|---|
| Male | Composite | 8 | 68.73 | 6.27 |
| | Spring | 6 | 60.49 | 11.66 |
| | Fall | 8 | 50.91 | 7.77 |
| Female | Composite | 2 | 25.10 | 5.05 |
| | Spring | 2 | 5.76 | 0.21 |
| | Fall | 2 | 16.45 | 3.55 |

Figure 2.2. Mean (± SE) weekly elevations of 11 GPS radio-collared black bears in Olympic NP, May 1, 2002 to September 20, 2004.



### *Distance to Elwha River and tributaries:*

Bears were located farther from the Elwha and its potential salmon-bearing tributaries during fall than during spring ($p = 0.0024$; Table 2.10). They averaged 4323 m from the river or its tributaries during fall, and were located an average of 2713 m from the river during spring (Table 2.10).

Bears in Olympic NP exhibited a cyclical seasonal pattern in their proximity to the Elwha River and its potential salmon-bearing tributaries (Figure 2.3). In early spring, bears were most frequently located near the river or one of its tributaries. As summer progressed, they traveled farther from the river, and were located at the greatest distances from the river in late summer (August to September; Figure 2.3). Bears returned to areas closer to the river prior to denning (Figure 2.3).

### *Resource selection analysis:*

Analysis of second-order selection revealed that bears in Olympic NP did not use habitats within the study area in proportion to availability. When all points during a year were combined, compositional analysis detected a significant departure from random use ($\lambda = 0.0385$, $\chi^2_7 = 32.58$, $P < 0.0001$), indicating bears did not establish home ranges at random within the study area. I also found significant habitat selection during the spring ($\lambda = 0.1053$, $\chi^2_7 = 22.51$, $P < 0.05$) and fall ($\lambda = 0.0410$, $\chi^2_7 = 31.94$, $P < 0.0001$) seasons.

Compositional analysis of second-order selection resulted in ranking matrices that ordered habitat types in order of greatest to least use (Figure 2.4, Table 2.11). These

Table 2.10. Mean distances of 10 bears to the Elwha River and its main tributaries that are expected to support salmon runs after dam removal. Data included for bears with GPS locations from at least 1 fall and 1 spring season.

| | Spring | | | Fall | | |
|---|---|---|---|---|---|---|
| **Bear #** | **# seasons** | **Mean distance (m)** | **SE** | **# seasons** | **Mean distance (m)** | **SE** |
| 2002-03 | 1 | 2069 | · | 1 | 4072 | · |
| 2002-04 | 1 | 1872 | · | 1 | 3656 | · |
| 2002-05 | 2 | 1390 | 747 | 1 | 5017 | · |
| 2002-06 | 2 | 1349 | 170 | 2 | 2567 | 1171 |
| 2002-08 | 2 | 3285 | 200 | 3 | 3573 | 211 |
| 2002-10 | 2 | 2985 | 404 | 3 | 2906 | 227 |
| 2003-01 | 2 | 5685 | 307 | 2 | 9626 | 1235 |
| 2003-02 | 1 | 3941 | · | 2 | 3438 | 563 |
| 2003-03 | 1 | 2256 | · | 1 | 4379 | · |
| 2003-04 | 1 | 2307 | · | 1 | 3993 | · |
| Overall means[1] | 10 bears | 2714 | 420 | 10 bears | 4323 | 629 |

[1] Seasonal means differ significantly (one-tail T-test: $p = 0.0024$)

Figure 2.3. Mean (± SE) weekly distances of 11 GPS radio-collared black bears to portions of the Elwha River expected to support salmon after full restoration, Olympic NP, May 1, 2002 to September 20, 2004.

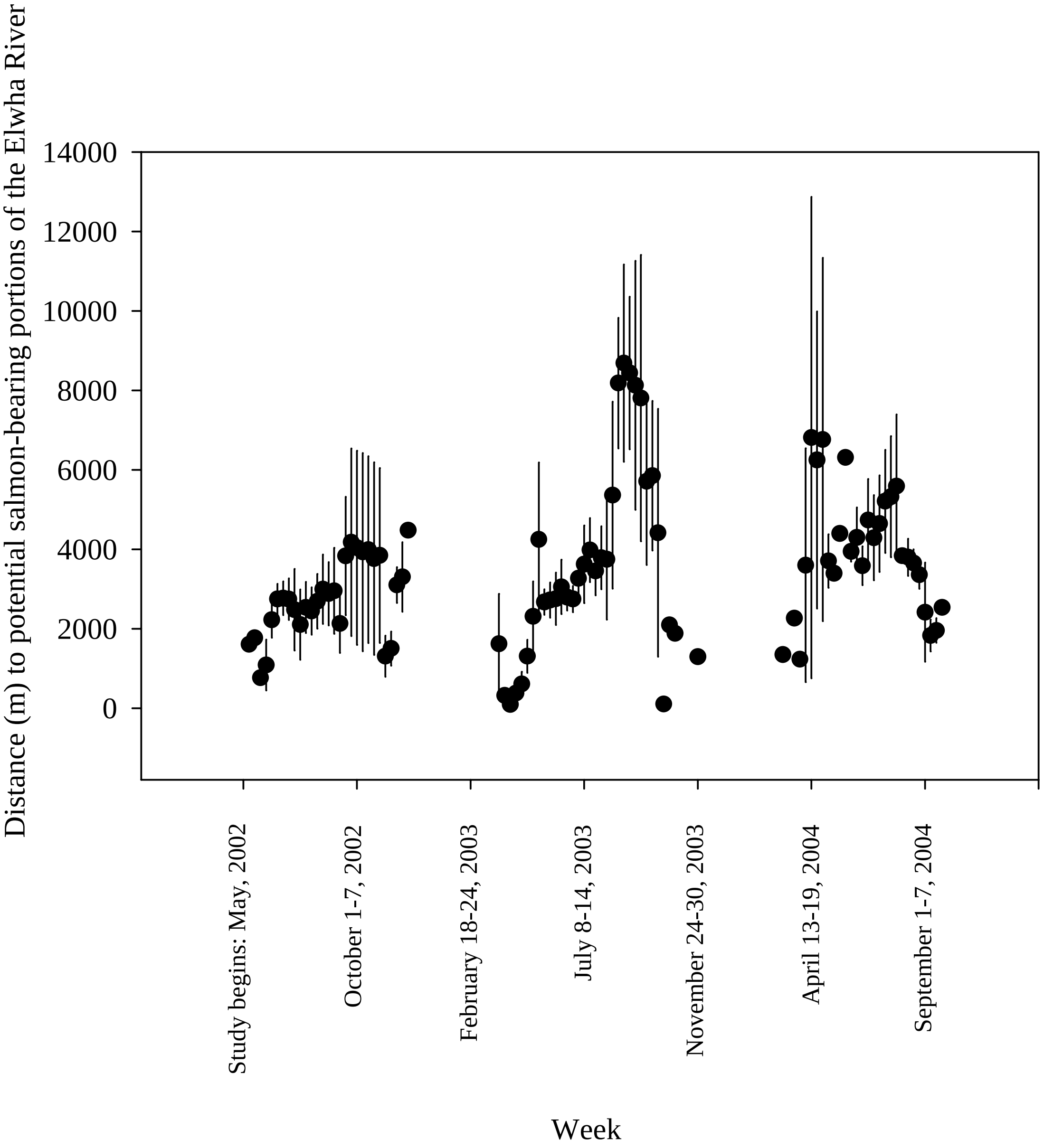
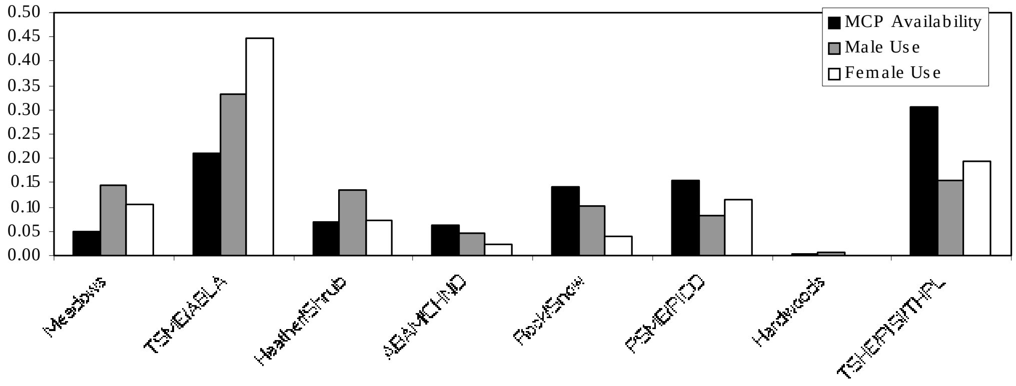
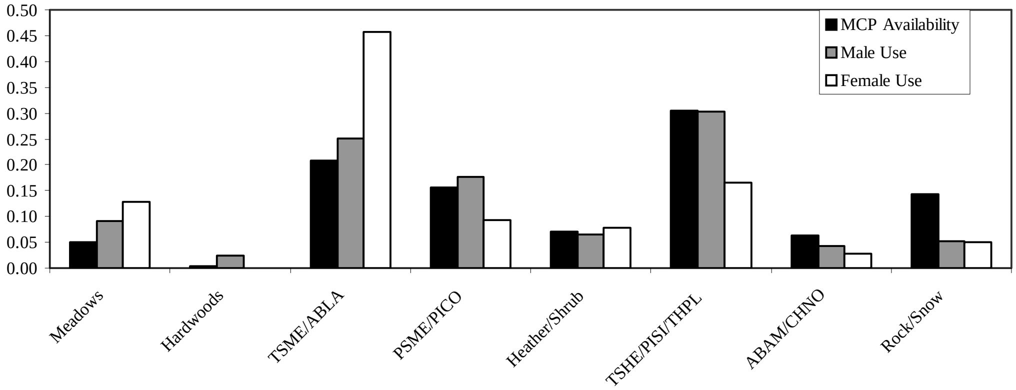


Figure 2.4. Second-order selection by black bears in Olympic NP. Vegetation types* are arranged from left to right according to decreasing preference during composite, spring, and fall seasons.

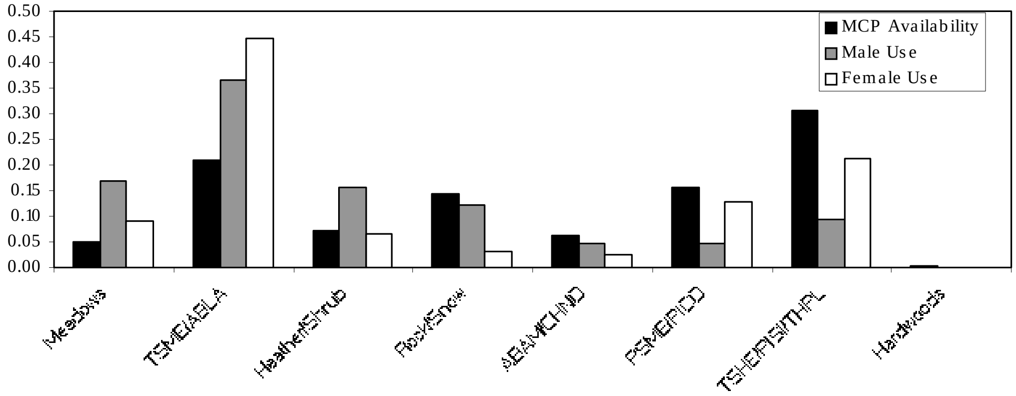
**Composite**



**Spring**



**Fall**



*Tree species codes may be found in Table 2.1.

Table 2.11. Ranked cover types resulting from second-order compositional analysis of black bear data in Olympic NP. Cover type classes are ranked from highest use (7) to least use (0). If two cover classes share a common letter within a column, then there was not a significant difference between use of those classes ($P$ = 0.10).

| **Rank** | **Cover class[1]** | **Rank differences between cover classes** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| ***Composite*** | | MD | T/A | H/S | A/C | R/S | P/P | HW | T/P |
| 7 | Meadows (MD) | a | | | | | | | |
| 6 | TSME/ABLA (T/A) | | b | c | | | | | |
| 5 | Heather/Shrub (H/S) | | b | c | | | | | |
| 4 | ABAM/CHNO (A/C) | | | | d | e | f | g | h |
| 3 | Rock/Snow (R/S) | | | | d | e | f | g | h |
| 2 | PSME/PICO (P/P) | | | | d | e | f | g | |
| 1 | Hardwoods (HW) | | | | d | e | f | g | h |
| 0 | TSHE/PISI (T/P) | | | | d | e | | g | h |
| ***Spring*** | | MD | HW | T/A | P/P | H/S | T/P | A/C | R/S |
| 7 | Meadows (MD) | a | b | c | d | e | f | | |
| 6 | Hardwoods (HW) | a | b | c | d | e | f | g | |
| 5 | TSME/ABLA (T/A) | a | b | c | d | e | f | | |
| 4 | PSME/PICO (P/P) | a | b | c | d | e | f | | |
| 3 | Heather/Shrub (H/S) | a | b | c | d | e | f | | |
| 2 | TSHE/PISI (T/P) | a | b | c | d | e | f | | |
| 1 | ABAM/CHNO (A/C) | | b | | | | | g | h |
| 0 | Rock/Snow (R/S) | | | | | | | g | h |
| ***Fall*** | | MD | T/A | H/S | R/S | A/C | P/P | T/P | HW |
| 7 | Meadows (MD) | a | | | | | | | |
| 6 | TSME/ABLA (T/A) | | b | c | | | | | |
| 5 | Heather/Shrub (H/S) | | b | c | | | | | |
| 4 | Rock/Snow (R/S) | | | | d | e | f | g | |
| 3 | ABAM/CHNO (A/C) | | | | d | e | f | | |
| 2 | PSME/PICO (P/P) | | | | d | e | f | g | h |
| 1 | TSHE/PISI (T/P) | | | | d | | f | g | h |
| 0 | Hardwoods (HW) | | | | | | f | g | h |

[1] Tree species codes may be found in Table 2.1.

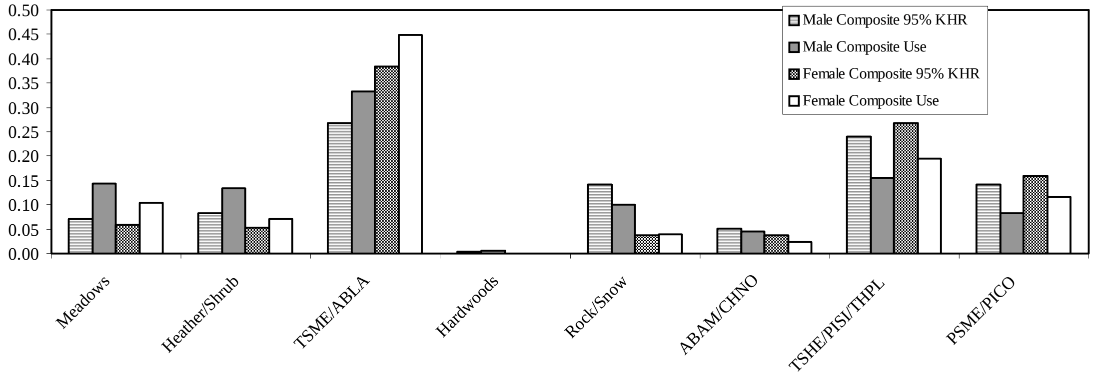
matrices revealed that bears consistently selected meadow types during spring, fall, and across seasons (Figure 2.4, Table 2.11). However, during spring, use of meadow types was similar to use of several other cover types (Table 2.11), perhaps reflecting less selection during spring due to the wide elevation gradient covered by male bears during the breeding season. Rock and snow and ABAM/CHNO were least selected during spring (Figure 2.4). During fall, bears selected meadows, followed in importance by subalpine forest (TSME/ABLA) and heather/shrub types. Rock and snow, several forest types and hardwoods were least selected during fall (Figure 2.4, Table 2.11). Though sample sizes were not sufficient to warrant separate analyses of habitat selection by males and females, the limited sample of females tended to select TSME/ABLA forests to a greater degree than males during each season.

Bears did not select habitat types within their individual composite and seasonal home ranges at random, as indicated by analysis of third-order selection. At the scale of the composite home range, I found a significant difference between habitats used and those available to bears ($\lambda = 0.0226$, $\chi^2_7 = 37.90$, $P < 0.0001$). Within seasonal home ranges, proportional use of cover types was significantly different from proportion of cover types available during the spring ($\lambda = 0.0898$, $\chi^2_7 = 24.10$, $P < 0.05$) and fall ($\lambda = 0.0141$, $\chi^2_7 = 42.59$, $P < 0.0001$) seasons.

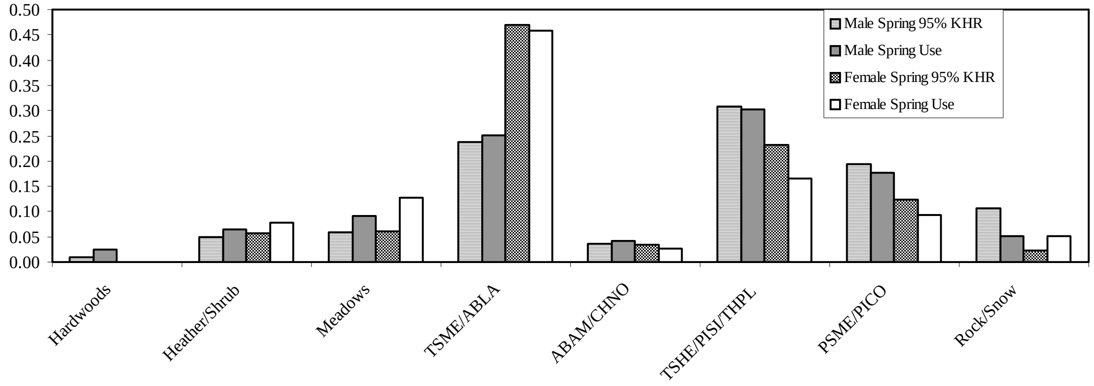
Ranking matrices for third-order selection of habitat types were similar to those resulting from second-order selection, but with some important differences. Within home ranges, meadow types were ranked first within composite and fall home ranges, but third within spring home ranges (Figure 2.5, Table 2.12). This result substantiates the finding in analysis of second-order selection that availability of meadow types is important to

Figure 2.5. Third-order selection by black bears in Olympic NP. Vegetation types* are arranged from left to right according to decreasing preference during composite, spring, and fall seasons.

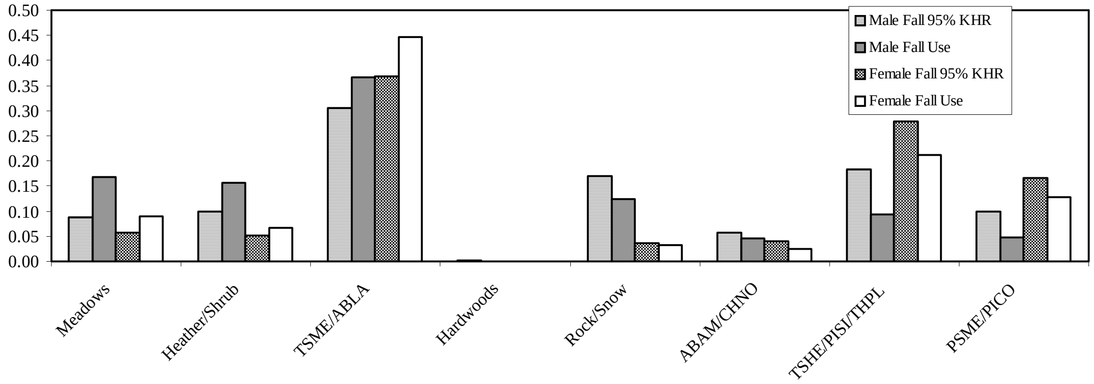
**Composite**



**Spring**



**Fall**



*Tree species codes may be found in Table 2.1.

Table 2.12. Ranked cover types resulting from third-order compositional analysis of black bear data in Olympic NP. Cover type classes are ranked from highest use (7) to least use (0). If two cover classes share a common letter within a column, then there was not a significant difference between use of those classes ($P = 0.10$).

| **Rank** | **Cover class**[1] | **Rank differences between cover classes** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| ***Composite*** | | MD | H/S | T/A | HW | R/S | A/C | T/P | P/P |
| 7 | Meadows (MD) | a | | | | | | | |
| 6 | Heather/Shrub (H/S) | | b | | | | | | |
| 5 | TSME/ABLA (T/A) | | | c | d | | | | |
| 4 | Hardwoods (HW) | | | c | d | e | f | | |
| 3 | Rock/Snow (R/S) | | | | d | e | f | g | |
| 2 | ABAM/CHNO (A/C) | | | | d | e | f | | |
| 1 | TSHE/PISI (T/P) | | | | | e | | g | |
| 0 | PSME/PICO (P/P) | | | | | | | | h |
| ***Spring*** | | HW | H/S | MD | T/A | A/C | T/P | P/P | R/S |
| 7 | Hardwoods (HW) | a | b | c | | | | | |
| 6 | Heather/Shrub (H/S) | a | b | c | | | | | |
| 5 | Meadows (MD) | a | b | c | d | e | f | g | |
| 4 | TSME/ABLA (T/A) | | | c | d | e | f | g | |
| 3 | ABAM/CHNO (A/C) | | | c | d | e | f | g | h |
| 2 | TSHE/PISI (T/P) | | | c | d | e | f | g | h |
| 1 | PSME/PICO (P/P) | | | c | d | e | f | g | h |
| 0 | Rock/Snow (R/S) | | | | | e | f | g | h |
| ***Fall*** | | MD | H/S | T/A | HW | R/S | A/C | T/P | P/P |
| 7 | Meadows (MD) | a | b | | d | | | | |
| 6 | Heather/Shrub (H/S) | a | b | c | d | | | | |
| 5 | TSME/ABLA (T/A) | | b | c | d | | | | |
| 4 | Hardwoods (HW) | a | b | c | d | e | f | | |
| 3 | Rock/Snow (R/S) | | | | d | e | f | | |
| 2 | ABAM/CHNO (A/C) | | | | d | e | f | | |
| 1 | TSHE/PISI (T/P) | | | | | | | g | h |
| 0 | PSME/PICO (P/P) | | | | | | | g | h |

[1] Tree species codes may be found in Table 2.1.

bears when they select home ranges; however, meadows are not selected during all times of the year. Hardwoods were the highest ranked cover type within spring home ranges (Figure 2.5, Table 2.12). This selection signifies the importance of hardwoods, despite their scarcity, when bears first emerge from winter dens. Females had available to them, and used, more subalpine forest habitat during spring than males (Figure 2.5). Similar to second-order selection, rock and snow and several forest types were least selected during spring (Figure 2.5). During the fall season, bears selected meadows, heather/shrub, and subalpine forests within their home ranges, and tended to select Douglas fir and hemlock forests least (Figure 2.5).

## DISCUSSION

The black bear population in Olympic NP appears to be structured by older-aged, sexually mature animals, a finding that may be explained by its protected status. Sixteen out of 18 bears captured were greater than 8 years old, and excluding one yearling, all were sexually mature. This is in stark contrast to the age-structure of bears captured outside of the park in the mid-1990s. Koehler (1998, 1999) captured 39 bears on the Olympic Peninsula, of which 29 were marked outside the park boundary and 10 were captured within Olympic NP. Median age of captured bears outside of Olympic NP was 3 years for both males and females, while within the park boundary, median ages were 11 years for males and 8.5 years for females. This discrepancy in age-structure between bear populations within and outside of Olympic NP is explained most easily by differences in protection status. Bears outside the park are hunted by sportsmen and may be trapped and killed on commercial tree farms to reduce tree damage. Within Olympic NP, hunting is illegal. Koehler (1998, 1999) documented one natural mortality of a black bear in Olympic NP. On the contrary, across 3 harvested populations in Washington, he documented that at least 22% of tagged bears were killed during the hunting season, with a total mortality of 36% if depredation hunts and hunter wounding losses were taken into account (Koehler, Personal Communication).

The older age-structure of Olympic's bear population may be indicative of a healthy population. A population in Idaho with an age-structure weighted heavily towards non-breeding bears and with few adult males was experiencing heavy hunting pressure (Beecham 1983). In contrast, populations of black bears that are dominated by older bears, as indicated by higher median ages and lower proportion of breeding bears, are generally considered to be healthy (Beecham and Rohlman 1994).

Though our capture records suggest that Olympic NP's bear population contains a preponderance of males, with a male:female ratio of 8:1, I suspect this is an artifact of differential capture success. Females, particularly those accompanied by cubs, were extremely difficult to capture, usually avoiding our traps even when placed in areas known to be occupied by females. In addition to their apparent wariness of trap locations, females may have been challenging to capture due to their exclusion by large males. Several of our trap sites, particularly in early spring, were located in or near meadows containing high-quality forage. Dominance of these sites by large males may have resulted in avoidance by females.

Other studies report differential capture success between males and females, but not to the extent of this study. In the northeastern Cascade Mountains of Washington, researchers captured 26 males and 11 females, for a male:female ratio of 2.4:1 (Lyons et al. 2003). Researchers in the Bow Valley of Banff National Park captured 14 males and 11 females in Aldrich snares, resulting in a male:female ratio of 1.3:1 (Hebblewhite et al. 2003). Koehler (1998, 1999) caught 25 males and 14 females on his Olympic study site, for a ratio of 1.8 males to every female. Within the park, he captured 6 males and 4 females for a male:female ratio of 1.5:1. Bears captured in the park were darted from helicopters, which I suspect reduces sex-specific bias and more accurately represents the 'true' ratio of males to females in Olympic NP. Nonetheless, males may still have a greater likelihood of being captured by any means due to their propensity towards traveling greater distances, having larger home ranges, and using more open habitats than females (Koehler and Pierce 2003, Lyons et al. 2003, Pelton 2003, Powell et al. 1997).

Though GPS collars provided considerably more data than was possible with VHF collars, several GPS radio-collars placed on black bears in Olympic NP failed to perform as expected. Multiple collar failures during the study resulted in a substantial loss of data on individual bears. Unfortunately, this was a consequence of using newly developed technologies, and this study was not the first to suffer data loss. In western and northern Canada, out of 71 Televilt GPS-Simplex collars deployed on grizzly bears, only 38 (53%) performed as expected. Twenty collars (28%) experienced some degree of failure, and another 13 (18%) failed completely (Gau et al. 2004). Of 12 GPS radio-collars deployed on mule deer in British Columbia, 5 malfunctioned and provided unusable data (D’Eon 2003). Johnson et al. (2002) assessed GPS collar performance on free-ranging caribou in British Columbia and found that collar reliability was highly variable. Several collars failed prematurely, while very few (18%) performed as expected (Johnson et al. 2002). The authors discussed the trade-offs between reliability concerns in terms of lost time and money and the potentially large amount of data acquisition possible with this technology, and they admonished field researchers to carefully consider project objectives and budget constraints before pursuing the use of GPS technology (Johnson et al. 2002).

Fix-success rates of GPS collars placed on bears (mean = 39%; range 30-59%; Table 2.6) in Olympic NP were substantially lower than fix-success rates of experimental collars tested in the field (mean of means at test sites = 71%; range 38-94%; Table 1.3). However, they were similar to success rates reported for several other studies that examined use of GPS collar technology on free-ranging wildlife (D’Eon 2003: 27-63%, mean = 50%; Obbard et al. 1998: 32-65%; Schwartz and Arthur 1999: 50-74%). A rich literature is developing on the effect of animal behavior on the likelihood of a collar acquiring a fix, and several researchers have suggested that animal behavior contributes to lower GPS collar success rates on free-ranging wildlife (Bowman et al. 2000, D'Eon 2003, Obbard et al. 1998, Schwartz and Arthur 1999, T. Graves 2004 Personal Communication, D. Heard 2004 Personal Communication). On the Kenai Peninsula, Alaska, Schwartz and Arthur (1999) found that collars placed on bears had lower fix-success rates than stationary collars used for testing, and suggested this discrepancy may have resulted from terrain, individual differences between bears, and animal movement (Schwartz and Arthur 1999). Collars tested on bears in northern Ontario had a 46% fix acquisition rate, while a stationary test collar received fixes at a rate of 99%; the authors suggested this incongruity may have been due to animal movement or bedding behavior (Obbard et al. 1998).

Female composite home ranges (25.1 km$^2$) in Olympic NP were considerably smaller than male home ranges (68.7 km$^2$), a finding consistent with previous reports (Koehler and Pierce 2003, Lyons et al. 2003, Pelton 2003, Powell et al. 1997). In the northeast Cascades of Washington, female home ranges calculated as 95% adaptive kernels measured from 21.6 to 58.9 km$^2$ (mean = 37.1 km$^2$) while male home ranges varied in size from 57.9 to 1076 km$^2$ (mean = 289.7 km$^2$; Lyons et al. 2003). Across 3 study sites in Washington, Koehler and Pierce (2003) calculated 95% fixed kernel home ranges of black bears; mean male home ranges varied from 73.5 km$^2$ to 125.5 km$^2$ while mean female home range sizes were between 18.0 km$^2$ and 28.3 km$^2$.

The largest home ranges reported by Koehler and Pierce (2003) were those calculated for black bears on the Olympic study site, and the authors speculated that this may have been a response to diminished habitat quality and productivity. They conjectured that high annual rainfall on the Olympic Peninsula may affect plant chemistry and nutrient retention or cause reduced photosynthesis, thereby diminishing forage quality. However, my findings fail to lend support to this idea. Home ranges calculated for bears in Olympic NP during this study were most similar to those calculated for the Okanagon study site of Koehler and Pierce (2003), which was the most arid site examined in their study. The disparity in home range sizes between our studies may reflect annual variation, differences in habitat quality, or dissimilarity in the programs used to calculate 95% fixed kernel home ranges. I suspect that substantial differences occurred in the distribution of food resources between the lower-elevation, privately-managed forests of the Olympic Peninsula study area (Koehler and Pierce 2003) and the productive high-elevation areas frequented by bears in Olympic NP.

With few exceptions, seasonal home ranges of bears in Olympic NP were smaller than composite home ranges, with differences between spring and fall seasons corresponding with shifts in behavior patterns and seasonal differences in food availability. Black bears generally forage on graminoids and herbaceous vegetation in spring and use hard and soft mass during fall (Holcraft and Herroro 1991, Landers et al. 1979, MacHutchon 1989, Unsworth et al. 1989). Locality of these food types, combined with season-specific behaviors such as breeding, likely determined how bears in Olympic NP traversed their home ranges during a year.

Spring home ranges in Olympic NP appear to be a function of forage availability and breeding behavior. Black bears emerge from winter dens in the spring and experience a prolonged and localized ‘waking-up’ process before regaining their full faculty (as reviewed in Pelton 2003, Poelker and Hartwell 1973). During this period they often forage on graminoids and other persistent foods, but continue to lose energy (Jonkel and Cowan 1971, MacHutchon 1989). An examination of early spring data for bears in Olympic NP confirms that several bears exhibited this behavior; many of the first GPS points acquired after den emergence were confined to a small area. With the emergence of herbaceous vegetation in spring, bears in Olympic NP foraged heavily in valley bottom meadows, as has been reported elsewhere (Hatler 1972, Holcraft and Herrero 1991, MacHutchon 1989). At the onset of the breeding season (~June; Pelton 2003) male bears in Olympic NP began to travel large distances in search of females. A peak of activity in June has been documented by other researchers (Amstrup and Beecham 1976, Garshelis and Pelton 1980). These long-distance movements were apparent in the larger spring home ranges calculated for males in Olympic NP (mean = 60.49 km$^2$) compared to fall home ranges (mean = 50.91 km$^2$). With few exceptions, all male bears in Olympic NP had larger spring home ranges than fall home ranges, with the largest spring home range measured as 119.71 km$^2$. Female bears in Olympic NP exhibited an opposite pattern, with spring home ranges (5.76 km$^2$) that were nearly a third the size of fall home ranges (16.45 km$^2$). I speculate this difference was a result of each female being accompanied by cubs during at least one spring of the study.

Smaller fall than spring home ranges calculated for male bears in Olympic NP likely resulted from their use of higher-elevation, clumped food resources during fall. Huckleberries are an important fall food for bears in Olympic NP and elsewhere (Amstrup and Beecham 1976, Bull et al. 2001, Poelker and Hartwell 1973). During good berry years, black bears with body masses between 80 and 100 kg, such as those found in Olympic NP, are capable of harvesting enough huckleberries to gain mass at their physiological maximum (Welch et al. 1997). This supports the assertion that concentrated fall locations exhibited by bears in Olympic NP were driven by huckleberry availability. Bears in other areas have been reported to congregate on huckleberries during the fall period of hyperphagia and fat deposition (Jonkel and Cowan 1971).

Patterns manifested in black bear home ranges were also evident in the cyclical use of elevations by bears in Olympic NP. During spring in each year of the study, mean elevations of bears reflected their use of forbs in valley bottom meadows. During late May and June, bears followed the receding snow line into higher elevations. Presumably they continued to forage on grasses, and as reported for July bear diets in Oregon and Washington (Bull et al. 2001, Poelker and Hartwell 1973), may have consumed fungus, salal (*Gaultheria shallon*), evergreen needles, tree cambium, insects, or small birds and mammals. Bears in Olympic reached their maximum annual elevations in July and August. They remained in these subalpine areas until September and October when they returned to lower elevations to den. Patterns of elevation shift described here were also documented by Amstrup and Beecham (1976) for black bears in west-central Idaho.

As evident in both home range analysis and analysis of elevation shifts, black bears in Olympic NP moved further away from the Elwha River and its tributaries as summer progressed. These shifts away from the Elwha drainage bottom were reflective of changing forage availability, and provide baseline data for comparison after the effects of anadromous fish restoration become evident. Bears were located furthest from the Elwha River during the period between August and September, a period when fall chinook, coho, pink, chum, and sockeye salmon, cutthroat trout, and native char are anticipated to spawn in the Elwha (NPS 1996). Park fisheries biologists expect pink salmon to recover to an estimated 274,000 fish within 16 to 20 years of dam removal, a considerably larger run than any other expected for the Elwha (NPS 1996). Pink salmon will spawn in July, August, and September, and will spawn every other year (NPS 1996). These months coincide with months that Olympic bears are farther from the river, and whether bears learn to stay nearer the river after salmon have been restored is an important question that warrants future research.

Resource selection analyses established that black bears in Olympic NP selected a mosaic of habitats that were similar at both the scale of the study area and the scale of individual home ranges, with some minor differences. At both orders of selection, high rankings for meadows reflected the importance of both riparian and subalpine meadows. The analysis also revealed selection for hardwoods in the spring and subalpine vegetation during fall. The relatively high ranking of subalpine trees (TSME/ABLA) in spring may have been driven by two females and their use of subalpine areas year-around, and was therefore likely an overestimate of spring use of this habitat type by males.

Despite the scarcity of hardwoods within the study area, selection of this habitat type reflected bear use of hardwood and meadow mosaics along the Elwha River during spring. In addition to providing areas for foraging on grasses and forbs, riparian areas also provide critical resources such as shade, cover, and connectivity between forest types (Kellyhouse 1980, Lyons et al. 2003). Other researchers have documented the importance of low-elevation meadows and riparian vegetation during spring. In Trinity County, California, bear sign in wet meadows accounted for 55% of sign documented in

May, though this habitat type comprised only 1% of the study area (Kellyhouse 1980). Wet meadow types were also used significantly more than expected during spring in the Tahoe National Forest of California (Grenfell and Brody 1986). Bears in the north Cascades of Washington selected home ranges with a hardwood component, as reflected in the high-ranking of riparian and deciduous forest-types; the authors suggested that riparian areas were the most important habitat types for bears in their study area (Lyons et al. 2003). Hardwood forest types were also used more than expected in the Ozark Mountains of Arkansas (Clark et al. 1993), and riparian areas and mesic aspen stands were used by foraging black bears in Idaho (Unsworth et al. 1989).

During the fall season, compositional analysis at both scales of resource selection provided high ranks to meadows, subalpine trees (TSME/ABLA), and heather/shrub habitat types. Other researchers have stated the importance of subalpine areas during fall. In the northeastern Cascades, meadows and subalpine fir forest were ranked 4th and 5th (out of 14), respectively (Lyons et al. 2003), and black bears in northwestern Montana congregated in meadow areas above 6,000 feet during September when there was an abundance of huckleberries (Jonkel and Cowan 1971). In Idaho, shrubfield habitats were important sources of huckleberries during fall (Unsworth et al. 1989).

Douglas-fir and pine (PSME/PICO), western hemlock, spruce, and red cedar (TSHE/PISI/THPL), and Pacific silver fir and Alaska yellow cedar (ABAM/CHNO) were ranked comparatively lower than meadows, hardwoods, and subalpine vegetation for each season and at each order of resource selection. This result suggests either that bear use of these habitat types equaled or was less than availability, or that some telemetry bias still existed.

Weighting factors applied to each location prior to analysis of resource selection reduced bias rather than eliminated it completely. Therefore, habitat types with low canopy cover, high satellite view, and at higher elevations (i.e. meadows, subalpine vegetation) may have been overrepresented in analysis of resource selection, despite the application of correction factors. On the contrary, habitat types with heavy canopy cover and low satellite availability may have been underrepresented, particularly if animal behavior contributed to reduced GPS collar fix-acquisition success. Black bear preference for bedding in forests has been documented in Idaho (Unsworth et al. 1989) and observed in Olympic NP (Personal Observation). The reduced likelihood of a collar acquiring a fix if placed to mimic a bear bed (Chapter 1) in conjunction with the likelihood that GPS antennas on bedded bears do not point directly at the sky (T. Graves, Personal Communication) suggests that habitats used for bedding were likely underrepresented in this study.

Because GPS radio-collars are a relatively new technology for wildlife research and biases associated with their use have recently been documented, several researchers have concurrently begun to examine ways to correct for these biases. In a study of resource selection, D’Eon (2003) applied correction factors to animal location data from GPS collars and then compared results from the use of both uncorrected and corrected GPS data. He determined that conclusions from resource selection analyses were unchanged when biases were corrected, and suggested that his failure to find a difference in habitat use patterns between corrected and uncorrected data may have been attributable to unaccounted data loss, such as those occurring due the effects of animal behavior (D’Eon 2003). Though his specific techniques for weighting individual points were different from those used in this study, his conclusions may have implications for this study. It is plausible that I failed to account for all data loss, particularly those lost due to animal behavior. However, Frair et al. (2004) also employed correction factors in a study of resource selection, and their results show promise. They examined two methods (sample weighting and iterative simulation) to reduce bias in a resource selection study given a 30% data loss resulting from the use of GPS collars. They documented that use of sample weighting ($1/P_{success}$) reduced type II errors for certain habitat features and eliminated bias from closed conifer forest coefficients (Frair et al. 2004). Therefore, though it is impossible to determine how much bias resulting from systematic data loss was accounted for in my study, the application of weighting factors was an important step in an ongoing process to reduce bias in resource selection and home range studies.

## MANAGEMENT IMPLICATIONS

Seasonal distribution patterns of black bears have important implications for future management and monitoring of the park's black bear population. For example, bear use of low elevation habitats with a meadow and hardwood component has important implications for managing human-bear interactions. Because low elevation meadow areas are popular spring destinations for backpackers as well as activity centers for black bears, park managers can use descriptive information from this study to more convincingly and effectively communicate food-storage recommendations and requirements to park visitors. Data from this study may help park managers interpret the seasonality of bear-human conflicts during spring and develop appropriate management strategies.

Information on use of high-elevation habitats by bears has implications for the park's long-term monitoring program. These data provide basic information on seasonality of use, and will allow researchers and managers to assess the reliability of an aerial monitoring program. In conjunction with monitoring of huckleberry availability, which the park already conducts, aerial surveys may be a viable option for counting bears during fall.

These data also provide valuable baseline information by which to assess the future effects of dam removal and salmon restoration, and sets the stage for future monitoring programs along the Elwha River. Not only will home range and resource selection data provide important baseline information for comparison after dam removal, but data from this study will also be used to establish a bear hair-snagging study prior to removal of the

Elwha dams. Results from this study indicate early spring (mid April-Mid June) as the optimum season to collect hair samples from black bears for future studies of DNA and analysis of stable isotope composition in bear diets. Several contemporary grizzly and black bear research projects have taken advantage of advances in DNA-analysis technology to gather information on bear distribution patterns, population structure, and population size through the use of hair samples (Woods et al. 1999, Mowat and Strobeck 2000, Bouglanger et al. 2002). DNA extracted from the roots of hair can be used for individual identification and confirmation of animal sex. Furthermore, stable isotope analysis of hair provides information on ratios of carbon and nitrogen in the diet, thereby providing information on diet composition (Hilderbrand et al. 1996, Hilderbrand et al. 1999, Jacoby et al. 1999). Barbed-wire enclosure hair traps have been identified as the most effective method of collecting hair from bears (Woods et al. 1999). In 2006, Olympic NP biologists will use information gathered during this study to establish barbed-wire hair traps along the Elwha River corridor to collect bear hair for stable isotope and DNA analysis.

Finally, I have provided a realistic and viable option for applying weighting factors to animal location data from GPS radio-collars. Though animal behavior may have contributed to data loss that I could not quantify, I was still able to reduce bias in analysis of home range and resource selection of bears in Olympic NP. The continued use of GPS collar technology into the foreseeable future warrants that current researchers examine all possibilities for reducing bias.

## LITERATURE CITED

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Amstrup, S.C. and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. Journal of Wildlife Management 40:341-348.

Auger, J., S.E. Meyer, H.L. Black. 2002. Are American black bears legitimate seed dispersers of fleshy-fruited shrubs? American Midland Naturalist 147:352-367.

Ballard, W.B. 1992. Bear predation on moose: a review of recent North American studies and their management implications. Alces Supplement 1:162-176.

Barnes, V.G. Jr. 1989. The influence of salmon availability on movements and range of brown bears on southwest Kodiak Island. International Conference on Bear Research and Management 8:305-313.

Beecham, J.J. 1983. Population characteristics of black bears in west central Idaho. Journal of Wildlife Management 47:405-412.

Beecham, J.J. and J. Rohlman. 1994. A Shadow in the Forest: Idaho's Black Bear. University of Idaho Press, Moscow, ID. 245 pp.

Ben-David, M., T.A. Hanley, and D.M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos 83:47-55.

Bilby, R.E., B.R. Fransen, and P.A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53:164-173.

Boulanger, J., G.C. White, B.N. McLellan, J. Woods, M. Proctor, and S. Himmer. 2002. A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia, Canada. Ursus 13:137-152.

Bowman, J.L., C.O. Kochanny, S. Demarais, and B.D. Leopold. 2000. Evaluation of a GPS collar for white-tailed deer. Wildlife Society Bulletin 28:141-145.

Bull E.L., T.R. Torgersen, and T.L. Wertz. 2001. The importance of vegetation, insects, and neonate ungulates in black bear diet in northeastern Oregon. Northwest Science 75:244-253.

Burnham, K.P. and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, NY. 488 pp.

Cederholm, C.J., D.B. Houston, D.L. Cole, and W.J. Scarlett. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. Canadian Journal of Fisheries and Aquatic Sciences 46:1347-1355.

Cederholm, C.J., D.H. Johnson, R.E. Bilby, L.G. Dominguez, A.M. Garrett, W.H. Graeber, E.L. Greda, M.D. Kunze, B.G. Marcot, J.F. Palmisano, R.W. Plotnikoff, W.G. Pearcy, C.A. Simenstad, and P.C. Trotter. 2000. Pacific Salmon and Wildlife- Ecological Contexts, Relationships, and Implications for Management. Special Edition Technical Report, Prepared for D.H. Johnson and T.A. O'Neil (Manage. Dirs.), Wildlife-Habitat Relationships in Oregon and Washington. Washington Department of Fish and Wildlife, Olympia.

Cook, J.G., T.W. Stutzman, C.W. Bowers, K.A. Brenner, and L.L. Irwin. 1995. Spherical densiometers produce biased estimates of forest canopy cover. Wildlife Society Bulletin 23:711-717.

D’Eon, R.G., R. Serrouya, G. Smith, and C.O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30:430-439.

D’Eon, R.G. 2003. Effects of stationary GPS fix-rate bias on habitat-selection analyses. Journal of Wildlife Management 67:858-863.

Di Orio, A.P., R. Callas, and R.J. Schaefer. 2003. Performance of two GPS telemetry collars under different habitat conditions. Wildlife Society Bulletin 31:372-379.

Dussault, C., R. Courtois, J. P. Ouellet, and J. Huot. 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. Wildlife Society Bulletin 27:965-972.

Edenius, L. 1997. Field test of a GPS location system for moose, *Alces alces*, under Scandinavian boreal conditions. Wildlife Biology 3:39-43.

Elowe, K.D., and W.E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962-968.

Frair, J.L., S.E. Nielsen, E.H. Merrill, S.R. Lele, M.S. Boyce, R.H.M. Munro, G.B. Stenhouse, and H.L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41:201-212.

Frame, G.W. 1974. Black bear predation on salmon at Olsen Creek, Alaska. Z. Tierpsychol. 35:23-38.

Garshelis, D.L. and M.R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. Journal of Mammalogy 61:8-19.

Gau, R.J., R. Mulders, L.M. Ciarniello, D.C. Heard, C.B. Chetkiewicz, M. Boyce, R. Munro, G. Stenhouse, B. Chruszcz, M.L. Gibeau, B. Milakovic, and K.L. Parker. 2004. Uncontrolled field performance of Televilt GPS-Simplex collars on grizzly bears in western and northern Canada. Wildlife Society Bulletin 32:693-701.

Gende, S.M., T.P. Quinn, and M.F. Willson. 2001. Consumption choice by bears feeding on salmon. Oecologia 127:372-382.

Gende, S.M., T.P. Quinn, M.F. Willson, R. Heintz, and T.M. Scott. 2004. Magnitude and fate of salmon-derived nutrients and energy in a coastal stream ecosystem. Journal of Freshwater Ecology 19:149-160.

Girard, I., J.P. Ouellet, R. Courtois, C. Dussault, and L. Breton. 2002. Effects of sampling effort based on GPS telemetry on home-range size estimations. Journal of Wildlife Management 66: 1290-1300.

Hatler, D.F. 1972. Food habits of black bears in interior Alaska. The Canadian Field-Naturalist 86:17-31.

Hebblewhite, M., M. Percy, R. Serrouya. 2003. Black bear survival and demography in the Bow Valley of Banff National Park, Alberta. Biolgoical Conservation 112:415-425.

Hilderbrand G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus, and C. Servheen. 1996. Use of stable isotopes to determine diets of living and extinct bears. Canadian Journal of Zoology 74:2080-2088.

Hilderbrand, G.V., C.C. Schwartz, C.T. Robbins, M.E. Jacoby, T.A. Hanley, S.M. Arthur, and C. Servheen. 1999*a*. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77:132-138.

Hilderbrand, G.V., T.A. Hanley, C.T. Robbins, C.C. Schwartz. 1999*b*. Role of brown bears in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121:546-550.

Hilderbrand, G.V., C.C. Schwartz, C.T. Robbins, and T.A. Hanly. 2000. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. Journal of Wildlife Management 64:178-183.

Hilderbrand, G.V., S.D. Farley, C.C. Schwartz, and C.T. Robbins. 2004. Importance of salmon to wildlife: implications for integrated management. Ursus 15:1-9.

Holcraft, A.C. and S. Herrero. 1991. Black bear, *Ursus americanus,* food habits in southwestern Alberta. The Canadian Field-Naturalist 105:335-345.

Hooge, P.N. and B. Eichenlaub. 1997. Animal Movement Extension to ArcView, Version 2.0. Alaska Science Center- Biological Science Office, USGS, Anchorage, AK.

Hosmer, D.W. and S. Lemeshow. 2000. Applied Logistic Regression. John Wiley and Sons, New York, NY. 375 pp.

Jacoby, M.E., G.V. Hilderbrand, C. Servheen, C.C. Schwartz, S.M. Arthur, T.A. Hanley, C.T. Robbins, and R. Michener. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management 63:921-929.

Janeau, G., C. Adrados, J. Joachim, and D. Pepin. 2001. GPS performance in a temperate forest environment. Pages 69-72 *in* Tracking animals with GPS: An international conference held at the Macaulay Land Use Research Institute. Aberdeen, Scotland, March 2001. 113 pp.

Johnson, C.J. 2002. Expectations and realities of GPS animal location collars: results of three years in the field. Wildlife Biology 8:153-159.

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

Johnson, K. J., and M. R. Pelton. 1980. Prebaiting and snaring techniques for black bears. Wildlife Society Bulletin 8:46-54.

Jonkel, C.J. and I. Mct. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27:1-57.

Kellyhouse, D. G. 1975. Habitat utilization by black bears in northern California. International Conference on Bear Research and Management 4:221-227.

Kline, T.C. Jr., J.J. Goering, O.A. Mathisen, P.H. Poe, and P.L. Parker. 1990. Recycling of elements transported upstream by runs of Pacific Salmon: l. $\delta^{15}$N and $\delta^{13}$C evidence in Sashin Creek, southeastern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:136-144.

Koehler, G. 1998. Progress report: federal aid in wildlife restoration, black bear (*Ursus americanus*) research in Washington. Dec. 1998. Washington Department of Fish and Wildlife, Olympia, WA. Unpublished report. 12 pp.

Koehler, G. 1999. Progress report: federal aid in wildlife restoration, black bear (*Ursus americanus*) research in Washington. Dec. 1999. Washington Department of Fish and Wildlife, Olympia, WA. Unpublished report. 15 pp.

Koehler, G.M. and D.J. Pierce. 2003. Black bear home-range sizes in Washington: climatic, vegetative, and social influences. Journal of Mammalogy 84:81-91.

Kreeger, T. J. 1997. Handbook of Wildlife Chemical Immobilization. International Wildlife Veterinary Services, Inc., Laramie, WY. 342 pp.

Kunkel, K.E. and L.D. Mech. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Canadian Journal of Zoology 72:1557-1565.

Landers, J.L., R.J. Hamilton, A.S. Johnson, R.L. Marchinton. 1979. Foods and habitat of black bears in southeastern North Carolina. Journal of Wildlife Management 43:143-153.

LeCount, A.L. 1986. Black bear field guide. Arizona Game and Fish Department, Special Report, number 16. Phoenix, AZ. 130pp.

Licoppe, A.M. and J. Lievens. 2001. The first radio-tracking results from a female free-ranging red deer (*Cervus elaphus L.*) fitted with a GPS collar in Ardenne, Belgium. Pages 25-27 *in* Tracking animals with GPS: An international conference held at the Macaulay Land Use Research Institute. Aberdeen, Scotland, March 2001. 113 pp.

Lyons, A.L., W.L. Gaines, C. Servheen. 2003. Black bear resource selection in the northeast Cascades, Washington. Biological Conservation 113:55-62.

Manly, B., L. McDonald, and D. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London. 177 pp.

Moen, R., J. Pastor, Y. Cohen, and C. C. Schwartz. 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60:659-668.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61:530-539.

Moen, R., J. Pastor, and Y. Cohen. 2001. Effects of animal activity on GPS telemetry location attempts. Alces 37:207-216.

Mowat, G. and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. Journal of Wildlife Management 64:183-193.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, NY. 547 pp.

NPS (National Park Service). 1996. Elwha River Ecosystem Restoration Implementation, Final Environmental Impact Statement. National Park Service, Olympic National Park, Port Angeles, Washington.

NPS (National Park Service). 2001. NPS Management Policies, Chapter 4.4: Biological Resource Management. National Park Service, Washington, D.C.

Obbard, M.E., B.A. Pond, and A. Perera. 1998. Preliminary evaluation of GPS collars for analysis of habitat use and activity patterns of black bears. Ursus 10:209-217.

Partridge, S.T., D.L. Nolte, G.J. Ziegltrum, and C.T. Robbins. 2001. Impacts of supplemental feeding on the nutritional ecology of black bears. Journal of Wildlife Management 65:191-199.

Pelton, M.R. 2003. Black bear. Pages 547-555 *in* Wild Mammals of North America: Biology, Management, and Conservation, 2nd Edition. Edited by G.A. Feldhamer, B.C. Thompson, and J.A. Chapman. The Johns Hopkins University Press, Baltimore, MD. 1216 pp.

Poelker, R. J., and H. D. Hartwell. 1973. Black bear of Washington. Washington State Game Department. Biological Bulletin No. 14. Olympia, WA. 180 pp.

Powell, R.A., J.W. Zimmerman, and D.E. Seaman. 1997. Ecology and behaviour of North American black bears. Chapman and Hall, London, U.K. 203 pp.

Quinn, T.P. and M.T. Kinnison. 1999. Size selective and sex selective predation by brown bears on sockeye salmon. Oecologia 121:273-282.

Quinn, T.P. and G.B. Buck. 2000. Scavenging by brown bears, *Ursus arctos*, and glaucous-winged gulls, *Larus glaucescens*, on adult sockeye salmon, *Oncorhynchus nerka*. Canadian Field-Naturalist 114:217-223.

Quinn, T.P. and G.B. Buck. 2001. Size and sex selective mortality of adult sockeye salmon: bears, gulls, and fish out of water. Transactions of the American Fisheries Society 130:995-1005.

Quinn, T.P., L. Wetzel, S. Bishop, K. Overberg, and D.E. Rogers. 2001. Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. Canadian Journal of Zoology 79:1782-1793.

Quinn, T.P., S.M. Gende, G.T. Ruggerone, and D.E. Rogers. 2003. Density-dependent predation by brown bears on sockeye salmon. Canadian Journal of Fisheries and Aquatic Sciences 60:553-562.

Reimchen, T.E. 2000. Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. Canadian Journal of Zoology 78:448-457.

Rempel, R.S., A.R. Rodgers, and K.F. Abraham. 1995. Performance of a GPS animal location system under boreal forest canopy. Journal of Wildlife Management 59:543-551.

Rempel, R.S. and A.R. Rodgers. 1997. Effects of differential correction on accuracy of a GPS animal location system. Journal of Wildlife Management 61:525-530.

Rodgers, A.R. 2001. Tracking animals with GPS: The first 10 years. Pages 1-10 *in* Tracking animals with GPS: An international conference held at the Macaulay Land Use Research Institute. Aberdeen, Scotland, March 2001. 113 pp.

Ruggerone, G.T., R. Hanson, and D.E. Rogers. 2000. Selective predation by brown bears foraging on spawning sockeye salmon. Canadian Journal of Zoology 78:974-981.

Samson, C., and J.Huot. 1995. Reproductive biology of female black bears in relation to body mass in early winter. Journal of Mammalogy 76:68-77.

Samuel, M.D., 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.

Schwartz, C.C. and S.M. Arthur. 1999. Radiotracking large wilderness mammals: integration of GPS and Argos technology. Ursus 11:261-274.

Seaman, D.E. and R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Seaman, D.E., B. Griffith, and R.A. Powell. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95-100.

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

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman & Hall. London, England.

Simberloff, D. Biodiversity and bears – a conservation paradigm shift. Ursus 11:21-28.

Taylor, S.D. 2002. Addressing observation bias within a GPS-telemetry study of coastal mountain goats. M.S. Thesis, University of British Columbia.

Thomas, D.L. and E.J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322-330.

Unsworth, J.W., J.J. Beecham, and L.R. Irby. 1989. Female black bear habitat use in west-central Idaho. Journal of Wildlife Management 53:668-673.

Waller, J.S. and R.D. Mace. 1997. Grizzly bear habitat selection in the Swan Mountains, Montana. Journal of Wildlife Management 61:1032-1039.

Welch, C.A., J. Keay, K.C. Kendall, and C.T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78:1105-1119.

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

Willson, M.F. and K.C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology 9:489-497.

Willson, M.F., S.M. Gende, and B.H. Marston. 1998. Fishes and the forest: Expanding perspectives on fish-wildlife interactions. BioScience 48:455-462.

Winter, B. D., R. Reisenbichler, and E. Schreiner. 2001. The importance of marine-derived nutrients for ecosystem health and productive fisheries. U.S. Department of Interior, National Park Service, Olympic National Park, Elwha Restoration Project Office. 32 pp.

Woods, J.G., D. Paetkau, D. Lewis, B.N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616-627.

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

Worton, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794-800.

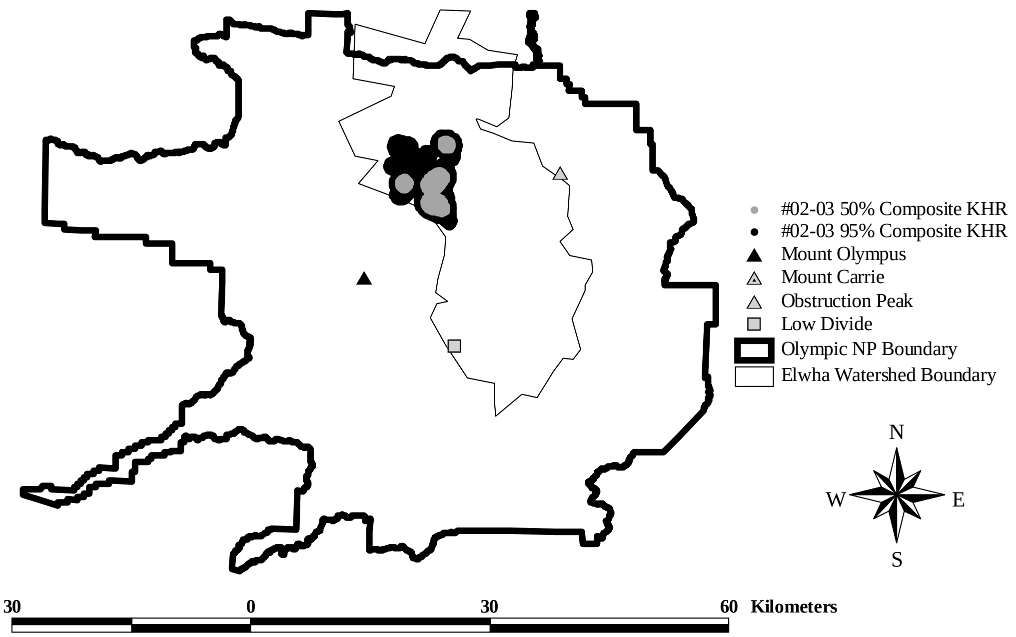
Wright, R.G. 1992. Wildlife research and management in the National Parks. University of Illinois Press, Chicago. 224 pp.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 pp.

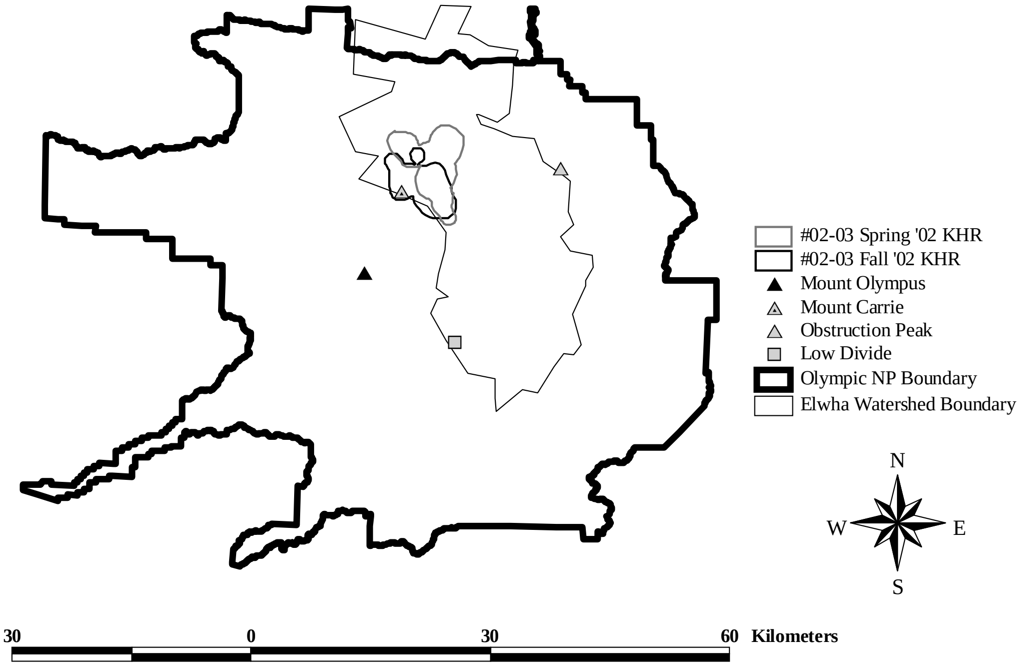
Ziegltrum , G.J. 2004. Efficacy of black bear supplemental feeding to reduce conifer damage in western Washington. Journal of Wildlife Management 68:470-474.

Appendix 1. Ninety-five and fifty percent composite (A) and 95% seasonal (B) fixed-kernel home ranges of 10 GPS radio-collared black bears in Olympic NP, 2002-2004.

**A. Bear #2002-03**

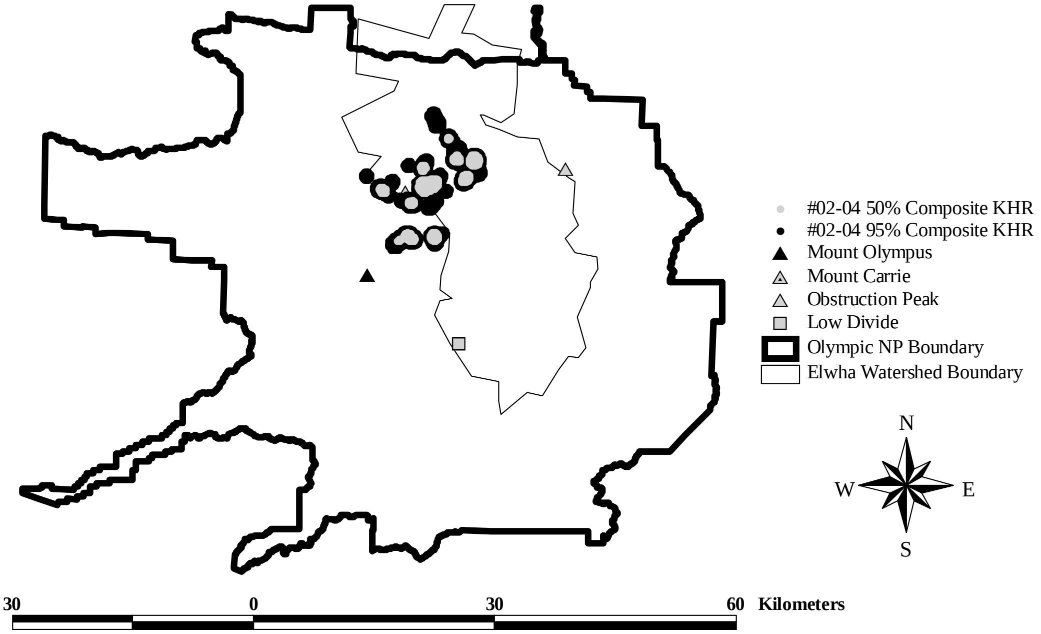


**B. Bear #2002-03**

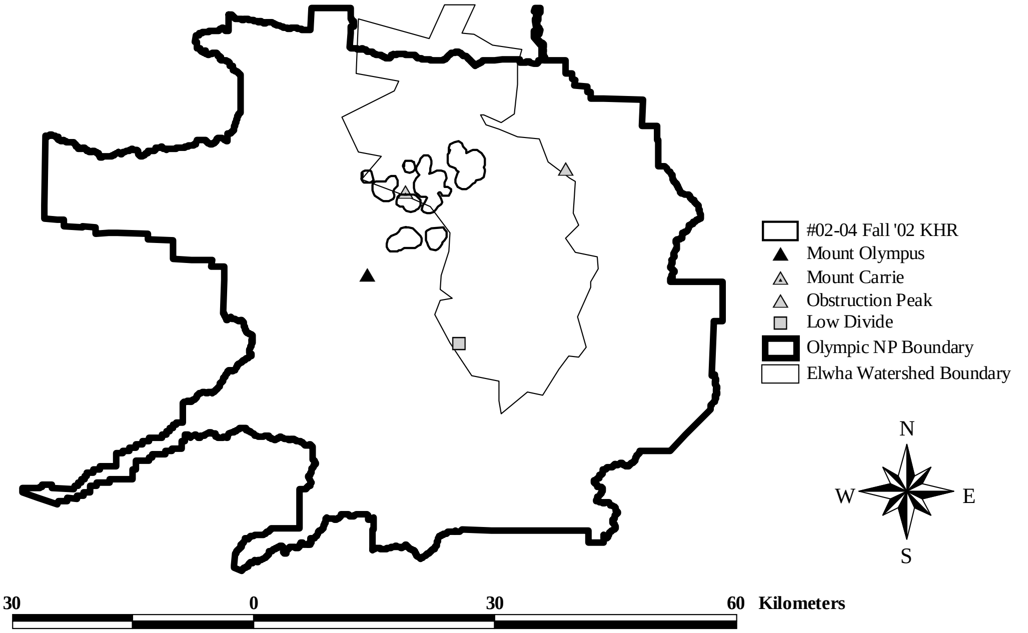


Appendix 1. Continued.

## A. Bear #2002-04

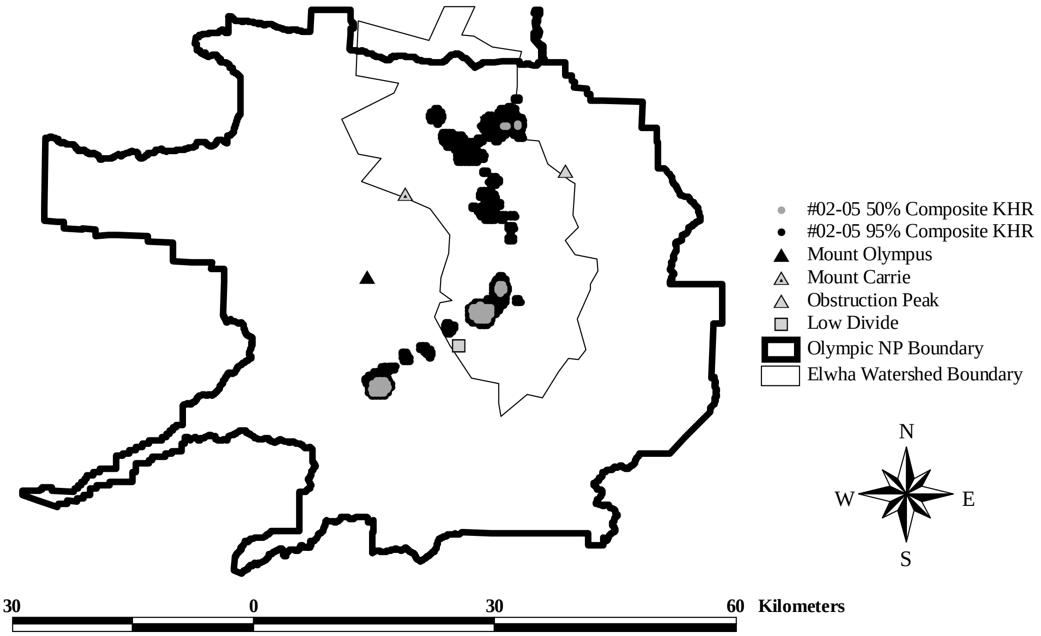


## B. Bear #2002-04

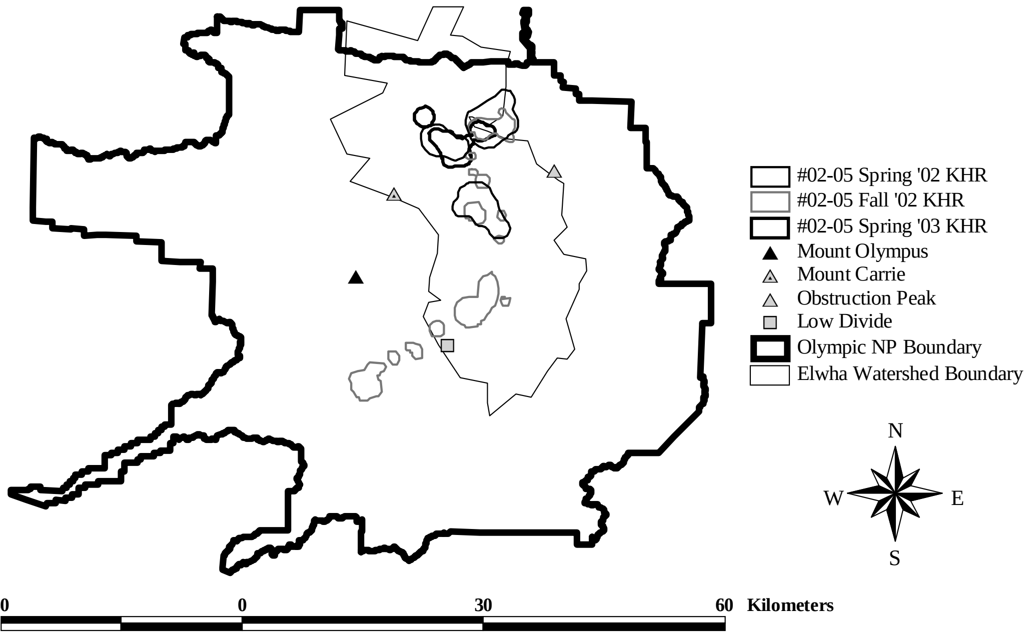


Appendix 1. Continued.

### A. Bear #2002-05

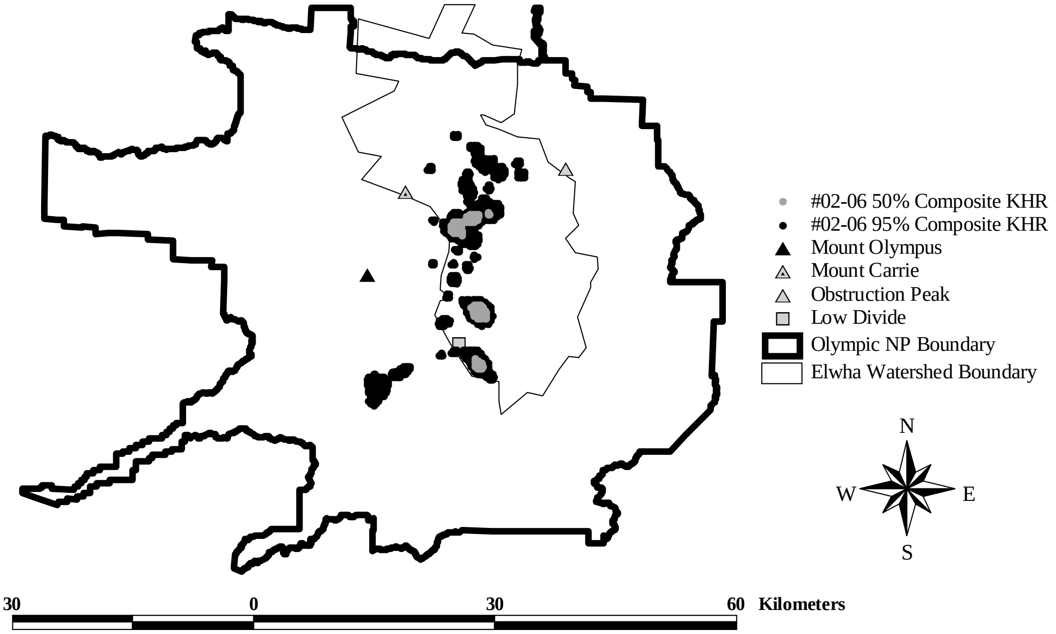


### B. Bear #2002-05

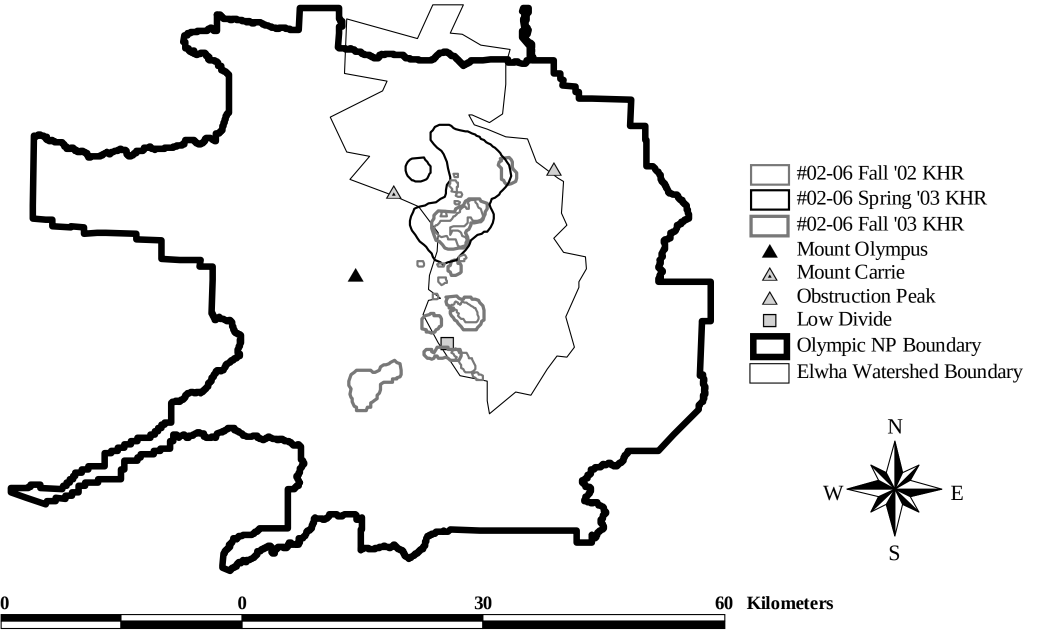


Appendix 1. Continued.

## A. Bear #2002-06

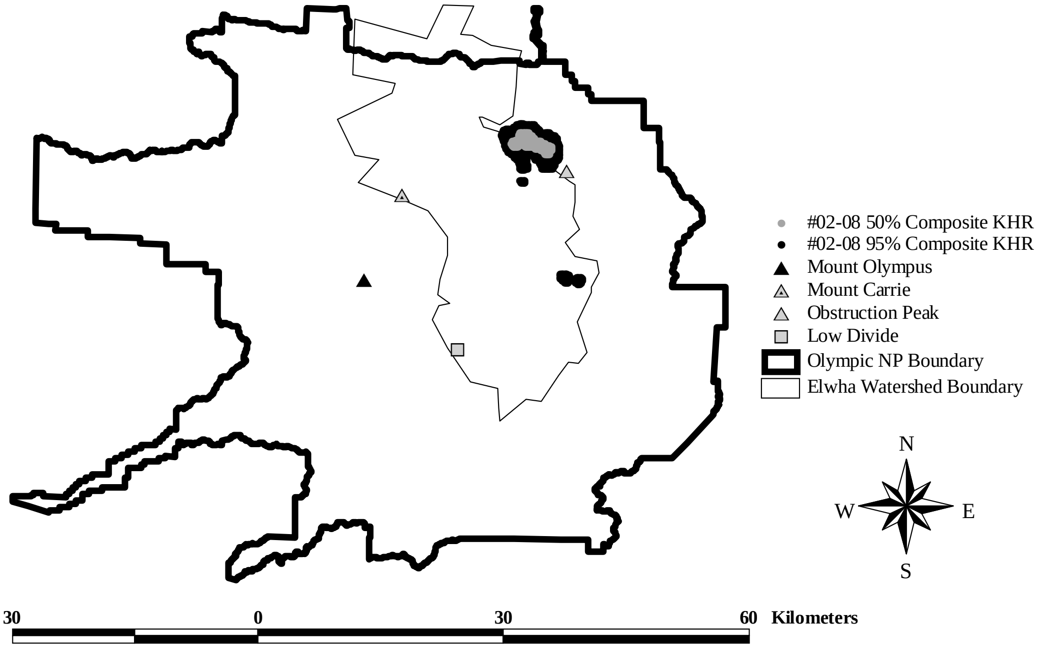


## B. Bear #2002-06

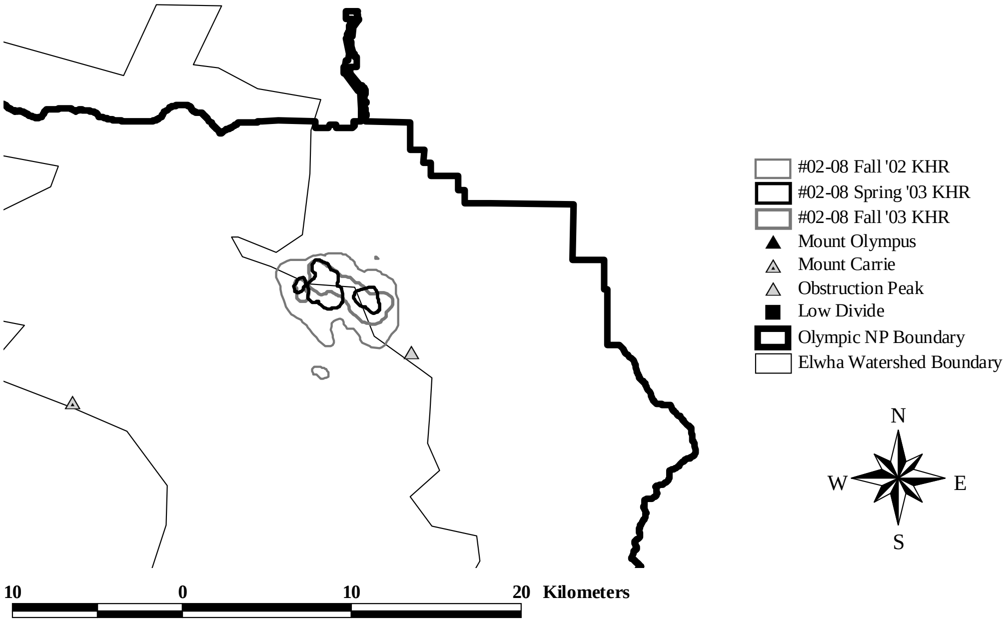


Appendix 1. Continued.

## A. Bear #2002-08

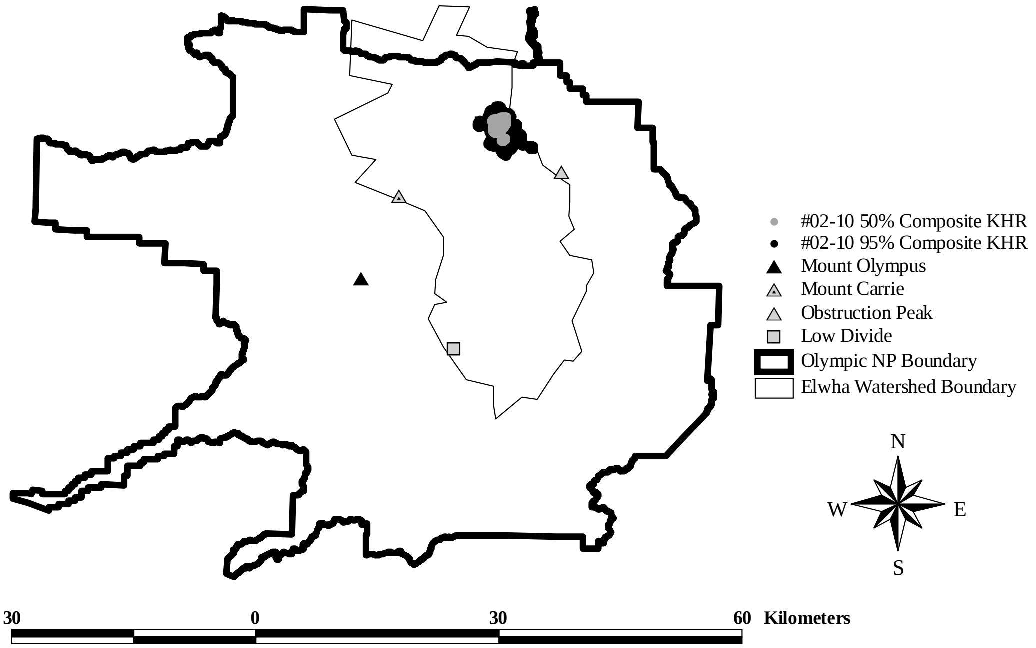


## B. Bear #2002-08

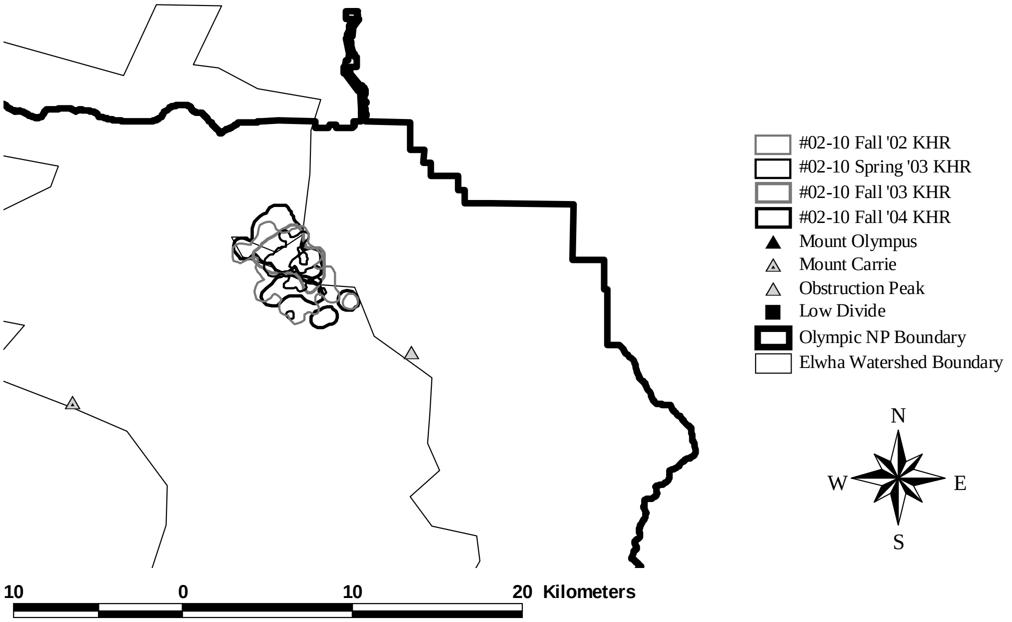


Appendix 1. Continued.

### A. Bear #2002-10

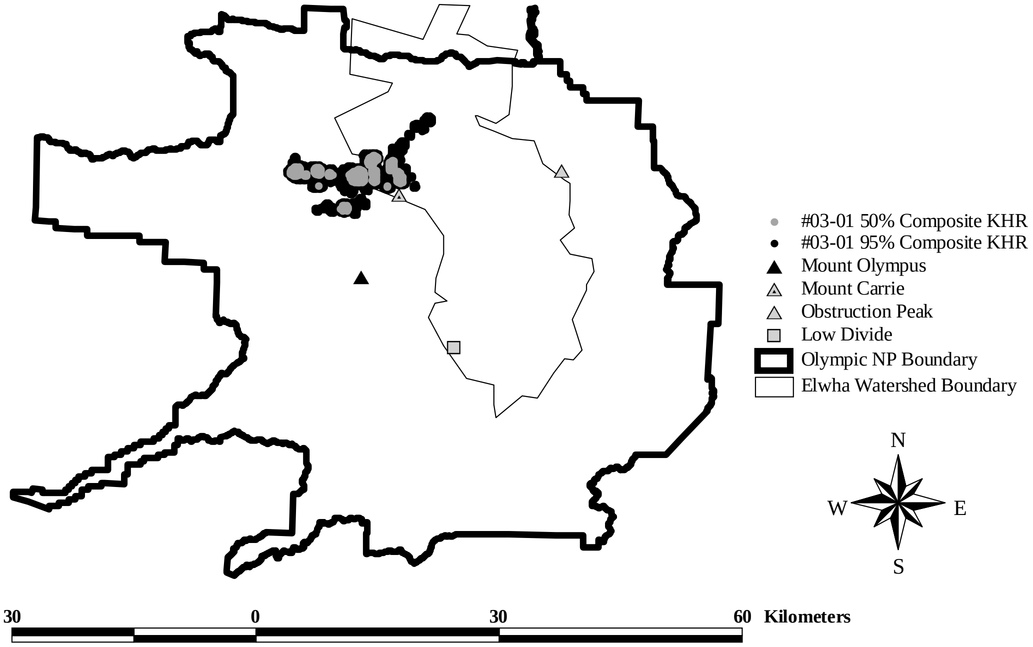


### B. Bear #2002-10

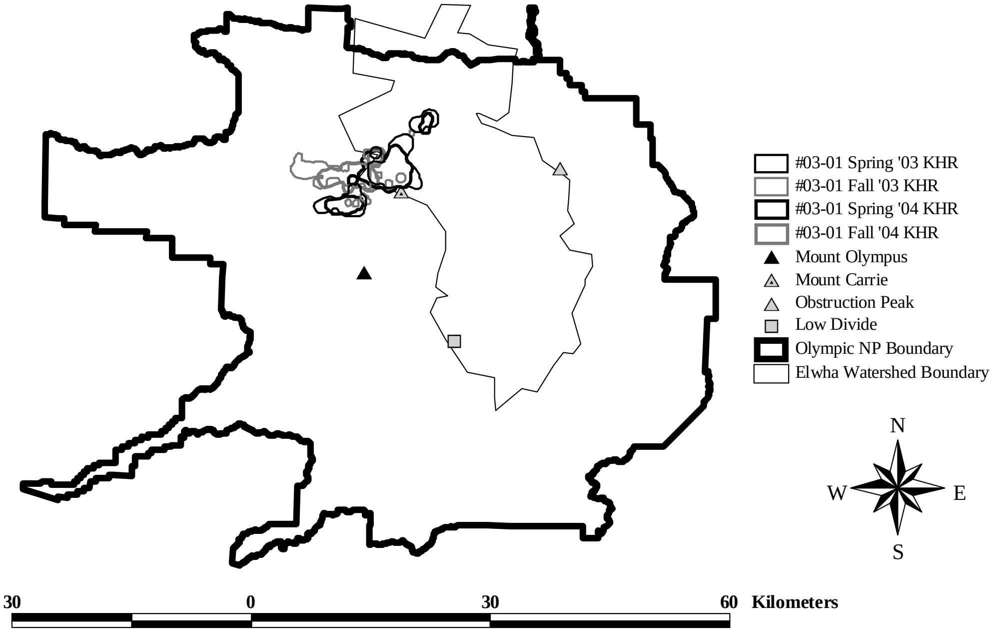


Appendix 1. Continued.

**A. Bear #2003-01**

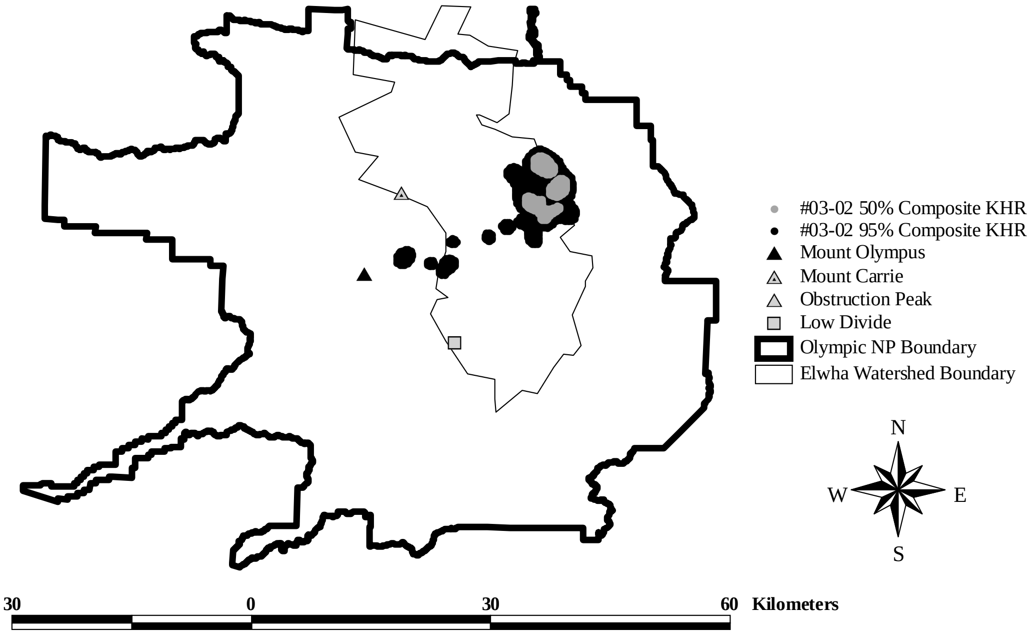


**B. Bear #2003-01**

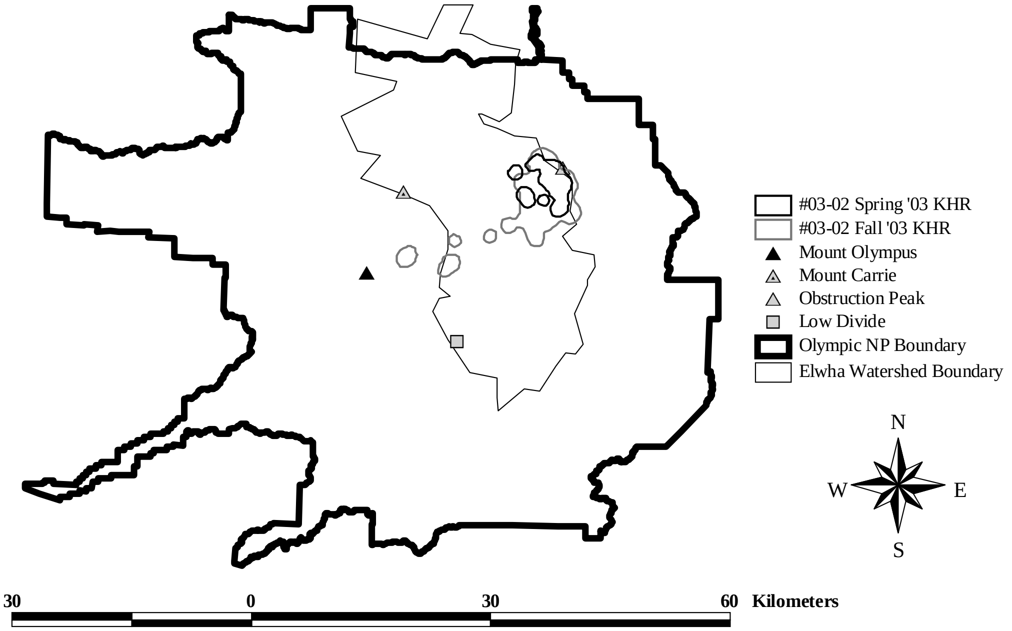


Appendix 1. Continued.

## A. Bear #2003-02

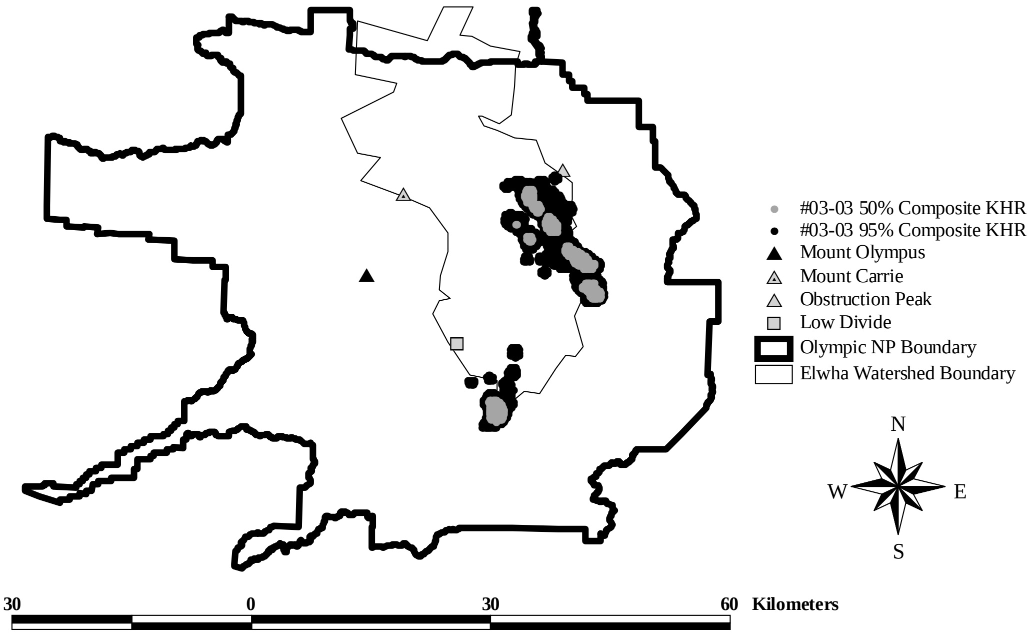


## B. Bear #2003-02

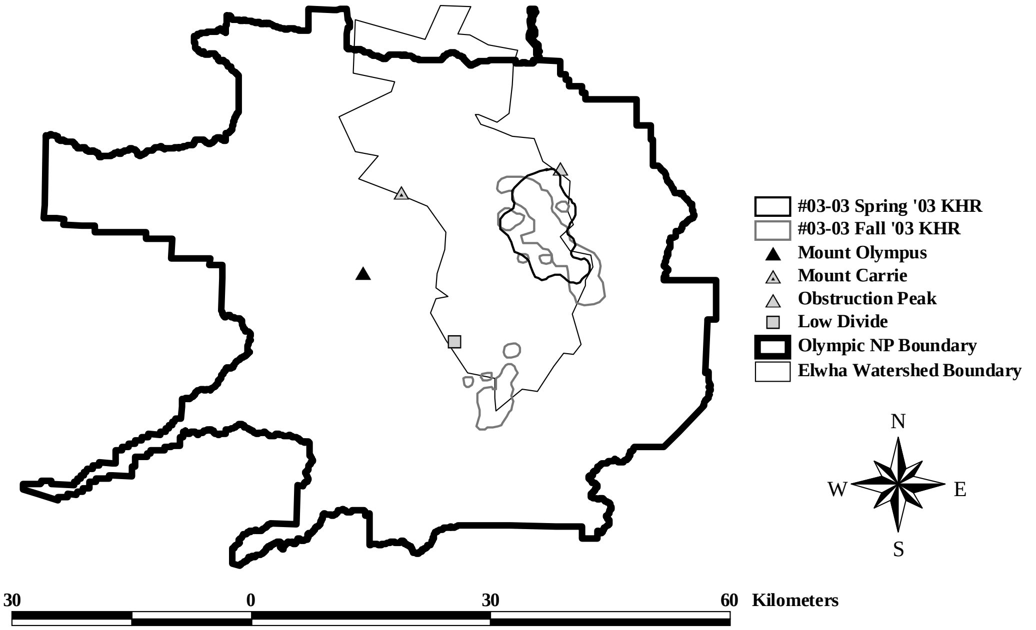


Appendix 1. Continued.

## A. Bear #2003-03

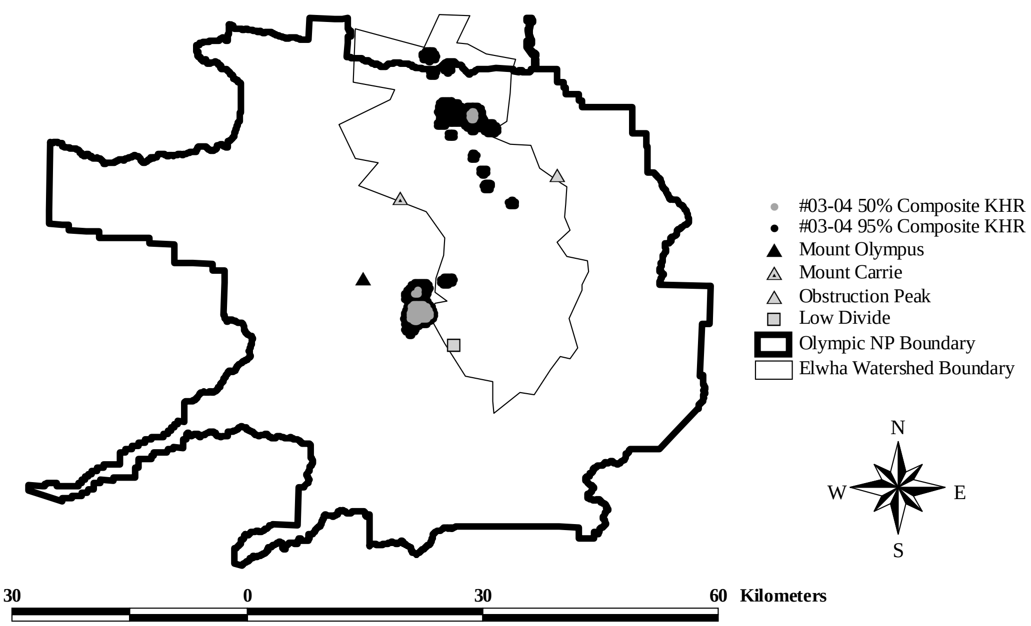


## B. Bear #2003-03



Appendix 1. Continued.

### A. Bear #2003-04



### B. Bear #2003-04