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Authors: Sager-Fradkin, Kimberly A., Jenkins, Kurt J., Happe, Patricia J., Beecham, John J., Wright, R. Gerald, et al.

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**Kimberly A. Sager-Fradkin**[1,2], U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Olympic Field Station, 600 East Park Avenue, Port Angeles, Washington 98362

**Kurt J. Jenkins,** U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Olympic Field Station, 600 East Park Avenue, Port Angeles, Washington 98362

**Patricia J. Happe**, National Park Service, Olympic National Park, 600 East Park Avenue, Port Angeles, Washington 98362

**John J. Beecham**, Beringia South, 2723 North Lakeharbor Lane, Boise, Idaho 83703

**R. Gerald Wright**, University of Idaho, Department of Fish and Wildlife Resources, Moscow, Idaho 83843

and

**Roger A. Hoffman**, National Park Service, Olympic National Park, 600 East Park Avenue, Port Angeles, Washington 98362

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## Abstract

Dam removal and subsequent restoration of salmon to the Elwha River is expected to cause a shift in nutrient dynamics within the watershed. To document how this influx of nutrients and energy may affect black bear (*Ursus americanus*) ecology, we used radio-telemetry to record movements of 11 male and two female black bears in the Elwha Valley from 2002-06. Our objective was to collect baseline data on bear movements prior to dam removal. We calculated annual home ranges, described seasonal timing of den entry and emergence, and described seasonal patterns of distribution and habitat use. Adaptive kernel home ranges were larger for males (mean = 151.1 km$^2$, SE = 21.4) than females (mean = 38.8 km$^2$, SE = 13.0). Males ranged widely and frequently left the watershed during late summer. Further, they exhibited predictable and synchronous patterns of elevation change throughout each year. Bears entered their winter dens between 8 October and 15 December and emerged from dens between 10 March and 9 May. Male bears used low-elevation conifer and hardwood forests along the Elwha floodplain during spring, mid- to high-elevation forests and meadows during early summer, high-elevation forests, meadows and shrubs during late summer, and mid-elevation forests, shrubs and meadows during fall. Data acquired during this study provide important baseline information for comparison after dam removal, when bears may alter their late summer and fall movement and denning patterns to take advantage of energy-rich spawning salmon.

## Introduction

Strong ecological interactions between salmon (*Oncorhynchus* spp.) and brown (*U. arctos*) and black bears influence both bear populations and riparian ecosystems in western Canada and southern Alaska (Barnes 1989, Hilderbrand et al. 1999a,b, Reimchen 2000). Bears concentrate along fish-bearing streams to consume salmon and benefit from the influx of energy and nutrients transported to the system by spawning salmon (Miller et al. 1997, Hilderbrand 1999b). Salmon are a lipid-rich food source for bears, particularly in the fall when intense feeding is necessary for fat deposition prior to hibernation (Hilderbrand et al. 1999b, 2000). In turn, bears are important vectors of nutrient transport from marine to terrestrial systems by feeding on salmon and depositing feces and salmon carcasses on land (Hilderbrand et al. 1999a, Gende et al. 2004, Helfield and Naiman 2006). For example, bears on Chichagof Island, Alaska, removed nearly 50% of the pink (*O. gorbuscha*) and chum (*O. keta*) salmon from the stream and transported them to riparian terrestrial communities nearby (Gende et al. 2004). On the Kenai Peninsula, Alaska, 83-84% of the salmon-derived nitrogen found in white spruce (*Picea glauca*) needles within 500 m of a salmon-bearing stream was distributed by bears (Hilderbrand et al. 1999a), and in the Bristol Bay region of southwest Alaska bear activity accounted for up to 24% of riparian

[1]Author to whom correspondence should be addressed. Email: kim.sager@elwha.nsn.us

[2]Current Address: Lower Elwha Klallam Tribe, 51 Hatchery Road, Port Angeles, Washington 98363

nitrogen during periods of salmon abundance (Helfield and Naiman 2006).

By contrast, ecological relationships between salmon and black bears in western Oregon and Washington are ambiguous. Historical, often anecdotal, reports describe strong interactions between black bears and salmon in western Washington. For example, 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). More recently, however, reports of salmon in the diets of black bears in Oregon or Washington have been reported infrequently (Poelker and Hartwell 1973, Cederholm et al. 2000). This may reflect low availability of salmon due to declining stocks, or the fact that most spawning salmon are available during late summer through fall when bears traditionally feed on huckleberries (*Vaccinium* spp.) at high elevations and begin entering their winter dens (Cederholm et al. 2000). In a review of wildlife-salmon relationships in Oregon and Washington, Cederholm et al. (2000) concluded that "salmon populations do not represent a predictable food supply to bears in Washington and Oregon….", but they hypothesized 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." That hypothesis is supported by observations that hand-planted carcasses of salmon were consumed frequently by black bears in selected areas of Olympic National Park (ONP) when carcasses were made available prior to den entry (Cederholm et al. 1989).

Resource selection patterns of black bears have been studied in the Cascades Range of Oregon and Washington (Vander Heyden and Meslow 1999, Lyons et al. 2003, Gaines et al. 2005), and on Long Island, Washington (Lindzey and Meslow 1977). Previous studies indicated that bears use a variety of open-canopied foraging areas (Vander Heyden and Meslow 1999), avoid roads (Vander Heyden and Meslow 1999, Gaines et al. 2005), select riparian habitats seasonally (Vander Heyden and Meslow 1999, Lyons et al. 2003, Gaines et al. 2005), and frequent areas of high huckleberry production during late summer (Vander Hayden and Meslow 1999). These previous studies, however, provide no evidence of salmon influencing seasonal distribution patterns of black bears. Black bears on the Humptulips River on the southern Olympic Peninsula had access to relatively small hatchery runs of Chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon but did not concentrate activities around them during the fall (Gary W.Koehler, Washington Department of Fish and Wildlife, personal communication; also reviewed in Cederholm et al. 2000).

The planned removal of two dams from the Elwha River provides an unprecedented long-term research opportunity to study the influence of salmon restoration on black bear distribution and to evaluate Cederholm et al.'s (2000) hypothesis that bears in Washington could establish traditional use areas around salmon. Habitats above the two dams on the Elwha River are protected within ONP and should—barring modifications that could result from changing climate or fire regimes—provide a stable background for studying bear distributional responses to salmon restoration. Fisheries biologists hypothesize that six species of salmon and trout, including Chinook, coho, steelhead (*O. mykiss*), pink, chum, and sockeye (*O. nerka*) may establish self-sustaining populations following dam removal (Pess et al. 2008). We speculate that restoration of salmon will provide a significant nutrient subsidy to the Elwha River that could affect black bear ecology, including seasonal distribution and habitat selection patterns, timing of den entry, food habits, and population characteristics.

Our goals were to describe space and habitat use patterns of black bears prior to dam removal and to establish baseline information for assessing the long-term effects of salmon restoration on distribution patterns of bears in the Elwha Valley. We estimated home range size, seasonal timing of den entry and emergence, and seasonal patterns of elevation use and habitat selection. Changes in any of these measures over time may signal a response of bears to salmon restoration. Although our intent was to provide comparable information for both male and female black bears, we encountered difficulties capturing females and necessarily focused on males.

## Study Area

The Elwha Valley, the largest watershed in Olympic National Park, comprises approximately 832 $km^2$ on the north-central Olympic Peninsula. Key ecological features of the watershed, including characteristic climate, geomorphology, and

vegetation patterns have been described previously (Duda et al. 2008). We focused studies of black bears in the 'middle' and 'upper' river segments (defined by Duda et al. 2008) within ONP. There are approximately 18 kilometers of secondary roads and two, 30-40 unit front-country campgrounds within low elevations of the middle river. Further, dispersed backcountry recreation occurs throughout the watershed and backcountry camping is permitted >1.6 km from roads. Since the late 1990's ONP has promoted strict food storage regulations both in front country campgrounds and in the backcountry. We saw no evidence during this study that black bear distribution or behavior was influenced by human activities or habituation to human foods.

## Methods

### Animal Capture

We captured black bears between April and August, 2002-2005 using Aldrich-style foot snares (Johnson and Pelton 1980) or by free-range darting from the ground. We focused capture efforts at low elevations along the Elwha River during late April-June and at higher elevations along Hurricane Ridge on the northeastern divide of the Elwha Valley during July and August. Bears were anesthetized with a mixture of ketamine hydrochloride (HCL; 4.4 mg/kg) and xylazine HCL (2.2 mg/kg) or with tiletamine HCl and zolazepam HCl (Telazol, Fort Dodge Laboratories, Fort Dodge, Iowa; 7.0 mg/kg, Kreeger 1997) administered with a syringe pole or $CO_2$ darting rifle. We determined gender of each bear and estimated ages by examining tooth wear or extracting the first upper premolar (LeCount 1986). We also marked each bear with numbered and color-coded ear tags and microchips (AVID Microchip Identification Systems, Folsom, Louisiana). All capture and handling protocols were reviewed and accepted by the Institutional Animal Care and Use Committee at Oregon State University.

We fitted each immobilized adult bear with a 950-g GPS (Global Positioning System) radiocollar (GPS Simplex or Tellus Basic, Televilt TVP Positioning AB, Lindesberg, Sweden) coded with a unique color combination for easy visual identification of marked animals in the field. Each collar contained a 12-channel GPS receiver, a very high frequency (VHF) radio transmitter, mortality and activity sensors, and a drop-off mechanism. We programmed each GPS receiver to obtain a location either four (2002 and 2003), three (2004), or six (2005-2006) times daily from spring to fall (1 April-30 October) and once daily during the denning period (1 November-31 March). We programmed collars to obtain locations every four to eight hours, resulting in bear locations during day, night, and crepuscular hours. At each programmed time, GPS receivers aboard the collars searched for satellites for up to four minutes. If a collar contacted at least three satellites the following data about the bear's location were stored: date, time, latitude, longitude, dilution of position (DOP), and whether the GPS location was 2-dimensional (three satellites used to obtain location) or 3-dimensional (≥ four satellites used to obtain location). We downloaded stored data from each collar three or four times annually using a RX-900 Receiver (Televilt TVP Positioning AB) from a fixed-wing aircraft. We released collars via a remote drop-off mechanism and, when possible, retrieved collars after their release.

### Home Range Analysis

We estimated black bear annual home ranges using 100% minimum convex polygons (MCP) and a 95% adaptive kernel method with likelihood cross-validation for choosing kernel width (Horne and Garton 2006a). We calculated MCP's to allow for comparison with historical studies in Washington and to provide an unambiguous measure for future comparisons. We chose adaptive kernel over fixed kernel estimators following the approach described in Horne and Garton (2006b). We found that adaptive kernel estimators with smoothing parameters chosen by likelihood cross-validation outperformed fixed kernel estimators for all bear home ranges.

We used the software program Animal Space Use (Horne and Garton 2007) to calculate adaptive kernel home ranges. We limited home range analyses to bears with >160 locations obtained over >16 weeks, based on preliminary analyses indicating that additional sampling had little influence on home range estimates (unpublished data). Home ranges included the pooled locations from all seasons and years for an individual bear.

### Timing of Denning

We determined dates of den entry and emergence by examining GPS data for each bear and each

year of the study. Because we were unable to acquire GPS locations from inside of bear dens, we assumed that the final GPS location of the fall for each bear approximated the date of den entry, and that the first recorded location of spring approximated the date of den emergence. We also determined means and ranges of elevations of the final GPS locations recorded for all bears prior to den entry and the first GPS locations recorded after den emergence.

### Analysis of Seasonal Distribution

Because GPS telemetry data are biased in favor of areas with optimum GPS reception, we weighted locations to reduce biases associated with topographic and vegetative obstruction of GPS reception (Sager-Fradkin et al. 2007). We used sample weighting methods in both our analysis of seasonal distribution and our analysis of habitat selection by black bears. Sager-Fradkin et al. (2007) used test GPS collars to model the effects of overstory vegetation, topography, and elevation on the probability ($P$) of a collar successfully acquiring a GPS location in the Elwha Valley. We applied that model to GPS locations of radio-collared bears by computing the probabilities associated with acquiring each GPS location and subsequently weighting each bear location by the inverse of its modeled probability of detection (i.e., $1/P$). For example, if a successful GPS telemetry location had an estimated $P = 0.5$, we weighted that location by a factor of two because it is expected that only half of the locations of bears under similar environmental conditions were successfully stored.

We examined seasonal distribution patterns of male black bears graphically by plotting the weekly mean elevation of radio-collared bears and by plotting the weekly mean proportion of bear locations on floodplain-associated habitats. We chose these metrics because they are straightforward for future comparisons after fish restoration. We used ArcMap 9.2 (ESRI, Redlands, California) to assign an elevation to each bear coordinate. We defined floodplain-associated habitats as areas less than 10 degrees in slope, below 650 m in elevation, and within 1,000 m of the Elwha River or its tributaries. Initially we intended to estimate bear use of "true" floodplain habitat but inspection of the data revealed considerable seasonal use by bears of low-elevation areas adjacent to floodplains. We computed the mean elevation of locations compiled for individual collared bears each week and then graphed the weekly means from individual bears. Similarly, we determined the weekly proportion of locations in floodplain-associated habitats and graphed weekly means.

### Analysis of Habitat Selection

We examined seasonal habitat selection patterns of GPS radio-collared black bears by comparing cover types used by individual bears seasonally to cover types available within the study area (i.e., second-order selection; Johnson 1980). We defined the study area as the 100% MCP that included the aggregate of all collared bear locations (Thomas and Taylor 1990, Manly et al. 1993). We examined graphs of weekly elevation distributions of bears to determine biologically meaningful seasons for the analysis of habitat selection. We defined four seasons based on homogeneity of use by bears, seasonal plant phenology, timing of snowmelt, and the breeding season of bears. Seasons were defined as spring (den emergence–31 May), early summer (1 June–15 July), late summer (16 July–30 September), and fall (1 October–den entry).

We used compositional analysis to compare the seasonal use of habitats by male black bears to the proportion of habitats available within the study area and to develop a ranking of cover type preferences (Aebischer et al. 1993). Compositional analysis uses Wilk's lambda scores for determining random use of the available habitat, in which a significant value of this test statistic indicates overall departure from random use (Aebischer et al. 1993). We conducted compositional analyses of habitat selection using Resource Selection for Windows software (Leban 1999). Compositional analysis uses the animal, rather than the individual GPS location, as the sampling unit (Aebischer et al. 1993). Aebischer et al. (1993) suggested an absolute minimum of six animals for compositional analysis, though preferably 10. Depending on season, we included 7-11 male bears in each seasonal analysis.

We defined use as the proportion of cover type classes within 180-m error radii of the estimated bear locations (Table 1). We chose a 180-m radius buffer for two reasons. First, Rettie and McLoughlin (1999) demonstrated that placing buffers around individual animal locations reduced inaccuracies and biases inherent in many

TABLE 1. Cover type classes used in compositional analysis of habitat selection by black bears, Olympic National Park.

| Class | Code | Proportion in study area |
|---|---|---|
| Water, rock, snow | Rock/snow | 0.145 |
| Meadows, heather | Mead/heath | 0.054 |
| Shrub | Shrub | 0.043 |
| Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) | PSME/TSHE | 0.454 |
| Mountain hemlock (*Tsuga mertensiana*), subalpine fir (*Abies lasiocarpa*) | TSME/ABLA | 0.232 |
| Pacific silver fir (*Abies amabilis*), Alaska yellow cedar (*Chamaecyparis nootkatensis*) | ABAM/CHNO | 0.067 |
| Hardwood mix, big leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*) | Hardwoods | 0.004 |

telemetry-based habitat selection studies, and revealed the importance of habitat mosaics in resource selection by wildlife. Secondly, 180 m accounted for 95% of the GPS telemetry error reported for our study area (Sager-Fradkin et al. 2007). This approach was also taken by Lyons et al. (2003) for their study area in the North Cascades, Washington. As previously described, we weighted each GPS location by the inverse of its estimated detection probability to reduce biases associated with missed GPS locations.

We classified the vegetation composition of habitats within the study area and within error buffers around individual location points using the Pacific Meridian Resources (PMR) GIS coverage for ONP (Pacific Meridian Resources 1996). To improve interpretability and power of the analysis, we reduced the original 25 cover type classes to seven cover type classes for the spring analysis and six cover type classes for the early summer, late summer, and fall analyses based on similarity in plant community composition and structure (Table 1). Species classification maps were 89.8% accurate across all cover classes in ONP (Pacific Meridian Resources 1996). During early summer, late summer, and fall we combined hardwoods with the Douglas fir (*Pseudotsuga menziesii*)—western hemlock (*Tsuga heterophylla*) class because several bears did not use hardwoods during these periods. This would have required us to substitute the zero values with an arbitrarily small value (i.e., 0.01 or 0.001), thus increasing the chance of a misclassification error in compositional analysis (Bingham et al. 2007).

## Results

### Bear Capture

We captured 18 individual bears between 2002 and 2005, including 16 males and two females. Of 18 bears caught, we equipped two females and 14 males with GPS radio-collars and released one large male and one subadult male with eartags only. We recaptured and collared six bears at least twice, including the two females, for a total deployment of 23 GPS collars. Because we acquired data from only two females, we have described their respective home ranges but excluded them from other analyses due to low sample size. Of the 23 GPS collars deployed, several were either shed or failed prematurely. We collected data on movements of 14 different bears, although only 10 male and two female bears provided sufficient data for home range analyses (Table 2; Range: 161-973 locations/animal).

### Home Ranges

Bears in the Elwha watershed—particularly males—ranged widely, and the collective movements of GPS collared bears encompassed most of the Elwha watershed (Figure 1). Several bears moved to adjacent watersheds, primarily during the early summer breeding and late summer huckleberry foraging seasons. These bears used subalpine areas in the upper Queets, Hoh, Quinault, Sol Duc and Dosewallips Valleys. However, all bears returned to the Elwha to over-winter.

TABLE 2. Black bears captured in the Elwha Valley, Olympic National Park, 2002-2005.

| Bear No. | Date of first capture | Gender | Estimated age. at capture (yrs) | No locations recorded | Dates of data collected |
|---|---|---|---|---|---|
| 2002-02 | 5/16/2002 | M | 14[1] | 637 | 5/21/2002-7/19/2002; 5/12/2004-5/30/2004; 5/14/2005-10/24/2005 |
| 2002-05 | 6/3/2002 | M | 8-15[2] | 399 | 6/4/2002-5/22/2003 |
| 2002-06 | 6/17/2002 | M | 4-7[2] | 507 | 6/18/2002-9/7/2003 |
| 2002-08 | 7/18/2002 | F | 8-15[2] | 370 | 7/19/2002-7/29/2003; 6/2/2004-9/16/2004 |
| 2002-10 | 8/7/2002 | F | 11[1] | 442 | 8/7/2002-8/1/2003; 6/7/2004-5/31/2006 |
| 2003-01 | 5/9/2003 | M | 8[1] | 393 | 5/10/2003-7/29/2004 |
| 2003-02 | 5/28/2003 | M | 14[1] | 161 | 5/29/2003-8/22/2003; 7/9/2004-7/31/2004 |
| 2003-03 | 6/3/2003 | M | 8-15[2] | 265 | 6/4/2003-9/24/2003 |
| 2003-04 | 7/16/2003 | M | 8-15[2] | 195 | 7/16/2003-5/10/2004 |
| 2004-04 | 5/18/2004 | M | 11[1] | 973 | 4/28/2005-5/9/2006 |
| 2005-01 | 5/19/2005 | M | 2-3[2] | 333 | 5/19/2005-10/24/2005 |
| 2005-02 | 6/28/2005 | M | 8-15[2] | 313 | 6/30/2005-10/23/2005 |

[1]Age estimated from cementum annuli of extracted premolar
[2]Age estimated from tooth wear patterns (LeCount 1989)

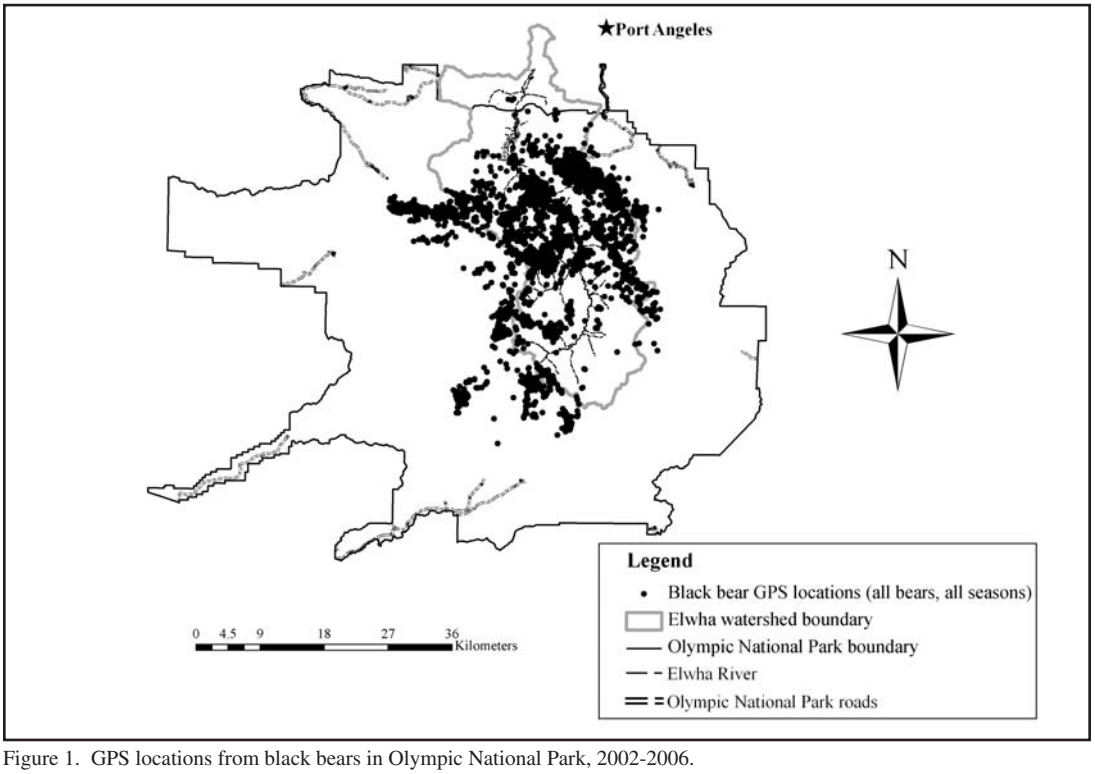


Figure 1. GPS locations from black bears in Olympic National Park, 2002-2006.

TABLE 3. Home range sizes of black bears equipped with GPS radio-collars in the Elwha Valley, Olympic National Park, 2002-2006.

| Home Range Measure | n | Mean | SE | Range |
|---|---|---|---|---|
| 95% Adaptive kernel ($km^2$) | | | | |
| Male | 10 | 151.1 | 21.4 | 62.8 - 276.9 |
| Female | 2 | 38.8 | 13.0 | 25.9 - 51.8 |
| 100% Minimum Convex Polygon ($km^2$) | | | | |
| Male | 10 | 305.8 | 37.1 | 120.3 - 467.3 |
| Female | 2 | 60.9 | 27.9 | 33.0 - 88.8 |

Home range sizes of male bears were highly variable. Annual 95% adaptive kernel home ranges for males ranged in size from 62.8 to 276.9 $km^2$ (mean = 151.1, SE = 21.4; Table 3). Female bears had smaller home ranges than males. One female had a home range of 51.8 $km^2$ and the other had a home range of 25.9 $km^2$ (mean = 38.8, SE = 13.0; Table 3). MCP home ranges were larger than adaptive kernel home ranges. Male 100% MCP home ranges averaged 305.8 $km^2$ (SE = 37.1) and female MCP home ranges averaged 60.9 $km^2$ (SE = 27.9; Table 3).

## Denning

We acquired at least one year of over-winter data for 7 different collared black bears in ONP (five males, two females). Male bears entered their winter dens between 8 October and 15 December (mean = 18 November) and emerged from dens between 10 March and 31 March (mean = 25 March; Table 4). Female bears entered their winter dens between 28 October and 8 December (mean = 16 November) and emerged from dens between 19 April and 9 May (mean = 28 April; Table 4).

## Seasonal Distribution

The seasonal elevation distribution of male bears in ONP followed a predictable pattern that was largely synchronous among five years of the study. Male bears used low elevations in the early spring (mean = 722.6 m, SE = 19.7; Figure 2a) and higher elevations during the transition from late spring to early summer that encompassed the breeding season (mean = 1,265.5 m, SE = 11.9; Figure 2a). Males consistently used high elevations during late summer (mean = 1,394.3 m, SE = 5.5; Figure 2a) and lower elevations prior to den entry during fall (1,111.4 m, SE = 14.7; Figure 2a).

Seasonal elevation patterns were less variable for the two female bears that we captured at high elevations. Females remained at relatively high elevations from den emergence in the spring to den entry in the fall. Mean weekly locations of female bears averaged 1,414.6 m (SE = 19.8) during spring, 1,446.4 m (SE = 11.5) during early summer, 1,421.6 m (SE = 29.7) during late summer, and 1,186.8 m (SE = 62.4) during fall.

Coincident with their use of low elevations during spring, male bears used floodplain-associated habitats primarily during spring (Figure 2b). Weekly mean proportions of bear locations recorded in floodplain-associated habitats averaged 16.0% (SE = 4.1) during spring, 1.5% (SE = 0.6) during early summer, 0.8% (SE = 0.4) during late summer, and 1.4% (SE = 0.8) during fall.

TABLE 4. Denning dates and elevations for seven bears in the Elwha Valley, Olympic National Park, 2002-2006.

| | No. bears | No. winters | Range | Mean | SE |
|---|---|---|---|---|---|
| Male denning dates | | | | | |
| Den entry dates (month/day) | 5 | 5 | 10/8 - 12/15 | 11/18 | 11.4 days |
| Den emergence dates (month/day) | 5 | 5 | 3/10 - 3/31 | 3/25 | 3.9 days |
| Female denning dates | | | | | |
| Den entry dates (month/day) | 2 | 4 | 10/28 - 12/8 | 11/16 | 10.9 days |
| Den emergence dates (month/day) | 2 | 4 | 4/19 - 5/9 | 4/28 | 4.1 days |
| Male denning elevations | | | | | |
| Den entry elevation (m) | 5 | 5 | 955 - 1580 | 1189 | 114.4 |
| Den emergence elevation (m) | 5 | 5 | 397 - 898 | 596 | 90.3 |
| Female denning elevations | | | | | |
| Den entry elevation (m) | 2 | 4 | 1185 - 1707 | 1428 | 107.7 |
| Den emergence elevation (m) | 2 | 4 | 1346 - 1647 | 1467 | 65.5 |

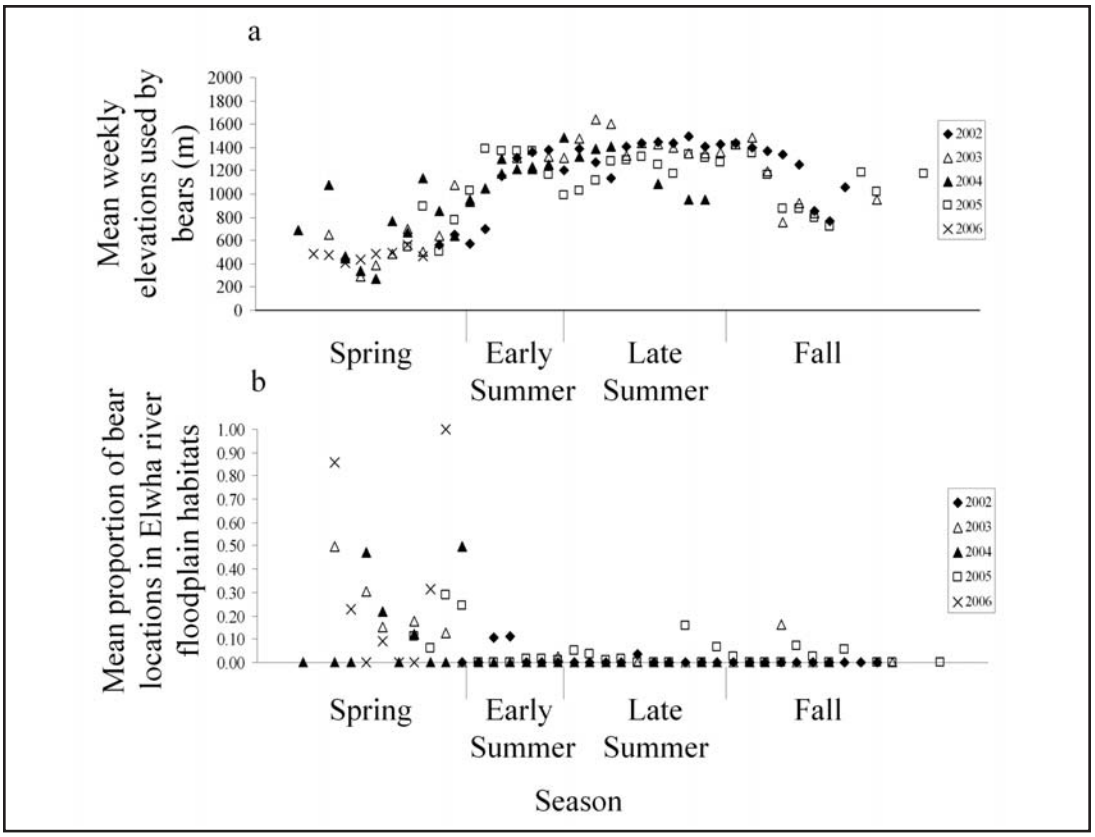


Figure 2. Seasonal use by male bears of the Elwha Valley, Olympic National Park, 2002-2006. Weekly mean elevations (a) across four seasons and five years and weekly mean proportion (b) of bear locations in Elwha floodplain-associated habitats. Seasons were defined as spring (den emergence–31 May), early summer (1 June–15 July), late summer (16 July–30 September), and fall (1 October–den entry).

### Habitat Selection Analysis

Male bear use of vegetation cover types was disproportional to availability within the study area during each season. Compositional analysis of second-order selection resulted in ranking matrices that ordered habitats from most to least use during each of four seasons (Table 5). During spring, male bears used hardwood and low- to mid-elevation forests (Douglas fir, western hemlock) more than other available cover types ($\lambda = 0.0681$, df = 6, $P < 0.05$, $n = 7$; Table 5, Figure 3). During early summer, bears used meadows and higher-elevation forest types (Mountain hemlock [*Tsuga mertensiana*] and subalpine fir [*Abies lasiocarpa*]) more than other cover types ($\lambda = 0.0782$, df = 5, $P < 0.001$, $n = 10$), whereas during late summer they used meadows and shrubs ($\lambda = 0.0429$, df = 5, $P < 0.0001$, $n = 11$; Table 5, Figure 3). During fall the greatest use was in shrub habitats, meadows, and low- to mid-elevation forests (Douglas fir, western hemlock; $\lambda = 0.0702$, df = 5, $P < 0.05$, $n = 7$; Table 5, Figure 3). The rock and snow cover class and the Pacific silver fir (*Abies amabilis*) and Alaska yellow cedar (*Chamaecyparis nootkatensis*) cover class were both used less than available across all seasons, whereas meadows and heather were used more than they were available across all seasons (Figure 3).

## Discussion

Throughout the mountain west, movements of black bears are driven largely by mating behavior, energetic demands, and seasonally changing availability of foods (Amstrup and Beecham 1976, Unsworth et al. 1989, Beecham and Rohlman

TABLE 5. Ranking matrices from analysis of habitat selection for male black bears in Olympic National Park, 2002-2006. Habitat type descriptions and codes given in Table 1.

| Season | n[1] | Matrix of resource rankings[2] | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Spring | | | | | | | | | |
| | 7 | | Hardwood | PSME/TSHE | Shrub | Mead/Heath | TSME/ABLA | ABAM/CHNO | Rock/Snow | Rank |
| | | Hardwood | | +++ | +++ | +++ | +++ | +++ | +++ | 6 |
| | | PSME/TSHE | --- | | +++ | + | +++ | +++ | +++ | 5 |
| | | Shrub | --- | --- | | + | + | +++ | +++ | 4 |
| | | Mead/Heath | --- | - | - | | + | + | + | 3 |
| | | TSME/ABLA | --- | --- | - | - | | + | + | 2 |
| | | ABAM/CHNO | --- | --- | --- | - | - | | + | 1 |
| | | Rock/Snow | --- | --- | --- | - | - | - | | 0 |
| Early Summer | | | | | | | | | |
| | 10 | | Mead/Heath | TSME/ABLA | Shrub | PSME/TSHE | ABAM/CHNO | Rock/Snow | | Rank |
| | | Mead/Heath | | + | +++ | +++ | +++ | +++ | | 5 |
| | | TSME/ABLA | - | | +++ | +++ | +++ | +++ | | 4 |
| | | Shrub | --- | --- | | +++ | +++ | +++ | | 3 |
| | | PSME/TSHE | --- | --- | --- | | + | + | | 2 |
| | | ABAM/CHNO | --- | --- | --- | - | | + | | 1 |
| | | Rock/Snow | --- | --- | --- | - | - | | | 0 |
| Late Summer | | | | | | | | | |
| | 11 | | Mead/Heath | Shrub | TSME/ABLA | Rock/Snow | ABAM/CHNO | PSME/TSHE | | Rank |
| | | Mead/Heath | | +++ | +++ | +++ | +++ | +++ | | 5 |
| | | Shrub | --- | | + | +++ | +++ | +++ | | 4 |
| | | TSME/ABLA | --- | - | | +++ | +++ | +++ | | 3 |
| | | Rock/Snow | --- | --- | --- | | + | +++ | | 2 |
| | | ABAM/CHNO | --- | --- | --- | - | | +++ | | 1 |
| | | PSME/TSHE | --- | --- | --- | --- | --- | | | 0 |
| Fall | | | | | | | | | |
| | 7 | | Shrub | Mead/Heath | PSME/TSHE | TSME/ABLA | ABAM/CHNO | Rock/Snow | | Rank |
| | | Shrub | | +++ | + | +++ | +++ | +++ | | 5 |
| | | Mead/Heath | --- | | + | + | +++ | +++ | | 4 |
| | | PSME/TSHE | - | - | | + | + | + | | 3 |
| | | TSME/ABLA | --- | - | - | | + | +++ | | 2 |
| | | ABAM/CHNO | --- | --- | - | - | | + | | 1 |
| | | Rock/Snow | --- | --- | - | --- | - | | | 0 |

[1]Number of male bears used in the analysis

[2]The signs signify whether the habitat category represented in the row was used more (+) or less (-) than the habitat category in the corresponding column. Triple signs (+++ or ---) indicate a significant difference ($P < 0.05$) between the two habitat categories. Single signs (+ or -) indicate a non-significant difference. Habitat categories were ranked in order of use from 0 (least used) to 5 or 6 (most used).

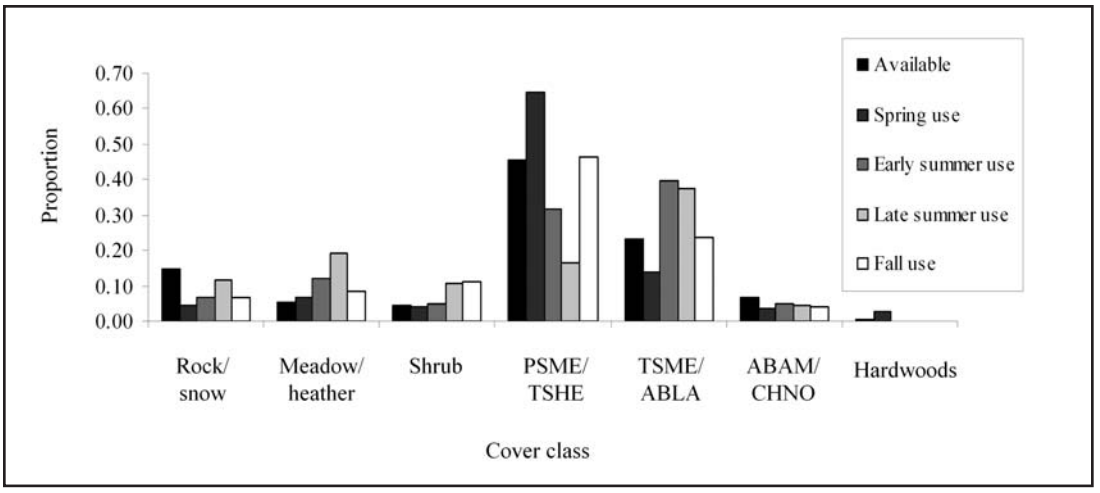


Figure 3. Seasonal availability of seven cover types and proportional use of those cover types by black bears in Olympic National Park, 2002-2006.

1994). Male black bears in the Elwha Valley were highly opportunistic in exploiting their seasonally variable environment. They moved widely in a year, but exhibited predictable inter-annual patterns of distribution and habitat use that suggest seasonal differences in behavior and food availability.

Home range sizes of bears in ONP (mean = 39 km$^2$ for females and 151 km$^2$ for males) were similar to those in lowlands of the western Olympic Peninsula (mean = 28 km$^2$ for females and 126 km$^2$ for males; Koehler and Pierce 2003) and study areas in the North Cascades Range (mean = 18-37 km$^2$ for females and 74–290 km$^2$ for males; Koehler and Pierce 2003, Lyons et al. 2003). Annual home ranges of two females in ONP were considerably smaller than those of males. Although this inference is drawn from a limited sample, corroborative evidence of gender differences in home range size has been reported throughout the range of black bears (Beecham and Rohlman 1994, Powell et al. 1997, Lyons et al. 2003).

Our use of GPS telemetry permitted a more fine-grained temporal analysis of seasonal distribution and habitat selection patterns of black bears in Washington mountain ranges than has been possible previously using VHF telemetry (Koehler and Pierce 2003, Lyons et al. 2003, Gaines et al. 2005). GPS telemetry, however, is susceptible to biases resulting from poor GPS reception in habitats with dense vegetation or topographic obstruction (Sager-Fradkin et al. 2007). Although we used sample weighting methods to account for missing bear locations, application of weights allowed us to recoup only 6% of lost locations (Sager-Fradkin et al. 2007). Because GPS reception is affected most strongly by canopy cover and topography, it is likely that we underestimated use of low-elevation coniferous forest habitats as well as seasonal variation in use of those habitats by black bears. If actual use of low-elevation forested habitats by bears was greater than we found, this would only serve to accentuate the patterns of seasonal distribution we observed.

Male bears exhibited pronounced seasonal shifts in their use of the Elwha Valley on an annual basis, favoring low elevations, floodplain-associated habitats, forests and hardwood stands during early spring and high-elevation meadows, shrubs and forest stands as the seasons progressed from early to late summer. The strongly synchronous pattern of elevation shifts exhibited by male bears across five years provides a stable pattern for future comparison.

Male bears focused activity during spring in low elevations along the Elwha River where they selected a mosaic of hardwoods and Douglas fir and western hemlock forests. Bears lose both lean body mass and lipid stores during winter fasting (Hilderbrand et al. 2000), and will use plant protein to regain lean body mass in spring following den emergence (Noyce and Garshelis 1998). Hardwood stands along the Elwha provided bears with easy access to foraging opportunities on

succulent grasses and forbs. Herbaceous vegetation is rich in protein during spring; however, it is low in fats and carbohydrates and many adult males (≥ 6 years old) that feed exclusively on vegetation during spring tend to lose weight (Jonkel and Cowan 1971, Beecham and Rohlman 1994, Noyce and Garshelis 1998). Meat is an important addition to spring bear diets and carrion plays an especially vital role in contributing to lean body mass gains when bears emerge from their winter dens (Hilderbrand et al. 1999c). We observed several male bears foraging on elk carcasses in the Elwha floodplain during spring, providing anecdotal support for the importance of carrion to bear diets where it is available. Bears in the North Cascades of Washington also selected low- to moderate-elevation forests during the early season (Gaines et al. 2005) and annual home ranges with a hardwood component, as reflected in the high resource selection ranking of a deciduous forest type with a riparian deciduous component (Lyons et al. 2003).

The early summer breeding season of black bears is a transitional period during which males frequently move great distances, presumably in search of females (Amstrup and Beecham 1976, Rogers 1987, Kovach and Powell 2003). Adult males may lose weight during this season (Noyce and Garshelis 1998), reflecting trade-offs between forage intake and increased energy expenditures associated with mating. We found black bears at both low and high elevations during early summer but the trend was for increased use of high elevations and diminished use of low-elevation floodplains. Selection of meadows and subalpine forests during early summer suggests that male bears followed the receding snow as plant phenology developed at higher elevations, a pattern also seen in Idaho (Amstrup and Beecham 1976).

Black bears forage on grasses and herbaceous vegetation in spring, but switch to hard and soft masts as they become available during summer and fall (MacHutchon 1989, Unsworth et al. 1989, Holcraft and Herrero 1991). In ONP during late summer, from mid-July through September, male black bears remained at high elevations selecting subalpine meadows, shrubs, and fir forests. Huckleberries are an important late summer staple for black bears throughout the Pacific Northwest (Jonkel and Cowan 1971, Poelker and Hartwell 1973, Amstrup and Beecham 1976), providing a vital source of energy and nutrients for bears to regain mass in the form of lipids following breeding and prior to denning during fall. During years of huckleberry abundance, black bears with body masses between 80 and 100 kg—typical of black bears in Olympic National Park—are capable of harvesting enough huckleberries to gain mass at their physiological maximum (Welch et al. 1997).

During autumn, male black bears in the Elwha Valley continued using high elevations but also increased use of mid elevations prior to denning. Male bears favored shrub habitats to a greater degree than subalpine meadows during fall, presumably because of the continued presence of moist forbs and berries (e.g., mountain ash [*Sorbus* spp.], huckleberries) in protected avalanche chutes at lower elevations than the subalpine zone. These shrub habitats likely provided a final nutrient subsidy for male bears prior to entering their winter dens at mid elevations between October-December. In Idaho, shrubfield habitats were also important sources of huckleberries during fall (Young and Beecham 1986, Unsworth et al. 1989).

Although we found clearly repeatable seasonal shifts in elevation and habitat use by males, we could not assess those patterns in females due to our small and potentially biased sample of females. The two radio-collared females focused their activities at high elevations from late spring through fall and displayed considerably less altitudinal movements than did males. This high-elevation focus by females was likely a combined result of their smaller home ranges and the fact that they were captured at higher elevations, and may not adequately represent females throughout the watershed.

Despite our considerable efforts at trapping bears along the Elwha River, we were unsuccessful at capturing females at low elevations. Trapping and snaring frequently results in a male-biased sample of black bears, but male capture bias in the Elwha Valley (9 males:1 female) was substantially greater than has been reported previously in Washington (1.4 males:1 female, Partridge et al. 2001; 2.4 males:1 female, Lyons et al. 2003; 1.9 males:1 female, Koehler and Pierce 2005). We rarely observed females with cubs on the floodplain during spring and we suspect that the preponderance of males in our sample reflected both a greater wariness of females (Beecham and Rohlman 1994) and the prevalence of adult males using floodplain-associated habitats during spring.

Studies have shown that adult male bears will deter females from using optimum habitats and that females will change their spatial distribution in response to removal of adult males (Sargeant and Ruff 2001). Previous studies also suggest that foraging decisions made by females may reflect trade-offs between nutrient intake and the risk of infanticide, and that females with young may avoid areas frequented by males (Ben-David et al. 2004). Within ONP, the older age structure of the bear population relative to the population of bears outside the park (Gary M. Koehler, Washington Department of Fish and Wildlife, personal communication) and elsewhere in western Washington (Partridge et al. 2001) suggests that frequent use of the floodplain by dominant males may contribute to female avoidance of floodplain-associated habitats during spring.

The current distribution of bears in the Elwha indicates there was little or no influence of anadromous fish on black bears captured within the park. There are presently no anadromous fish in the Elwha River within the boundaries of the park (i.e., above the dams), and we observed no movement by radio-collared bears to areas below the dams during late summer and fall when fish spawn in the lower river. Adjoining watersheds on the Olympic Peninsula do support spawning salmon, and although we observed bears using high-elevation habitats in the Queets, Quinault, and Hoh Valleys during late summer, we saw no evidence of radio-collared bears concentrating activities along these salmon-bearing rivers. Instead, bears focused activity at high elevations during late summer through fall, corroborating evidence that bears form traditional use areas around huckleberries in mountain ecosystems of the Pacific Northwest (Gary M. Koehler, Washington Department of Fish and Wildlife, personal communication; Vander Hayden and Meslow 1999).

Fisheries biologists have speculated on the spatial extent, timing, and numbers of salmon that are expected to return to the Elwha after dam removal (DOI 1996, Pess et al. 2008). Of the six species of wild salmon and trout projected to recolonize above the dams, coho, Chinook, and steelhead are expected to recolonize to the greatest spatial extent due to their current population status, strong swimming abilities that enable them to negotiate natural barriers, and the abundance of favorable alluvial spawning habitat upriver (Pess et al. 2008). Of these three species, the timing of coho and Chinook runs will overlap considerably with the period that bears are currently foraging in the fall prior to entering their winter dens. The projected recovery and distribution of pink, chum, and sockeye salmon is less certain due to their current low populations below the dams, and the fact that they will be less able to negotiate difficult barriers (Pess et al. 2008). Historically, pink salmon were the most plentiful of the salmonids in the Elwha River, but their numbers are currently low (DOI 1996, Pess et al. 2008). If pink salmon recover they could become the most abundant fish to spawn in the Elwha, though they will spawn only every other year (DOI 1996). The spawning season of pink salmon will also overlap with the fall period of bear activity. Ultimately, coho, Chinook, and pink salmon may provide the most important nutrient and energy subsidies for black bears in the Elwha River watershed.

We can only speculate whether black bears will change annual distribution patterns in the Elwha Valley to capitalize on locally abundant fish, but we raise several possibilities: 1) movements of both male and female black bears will increase along the floodplain during late fall when coho, Chinook, and pink runs return upriver; 2) bears may respond to increased food availability by entering winter dens later than they do when feeding exclusively on huckleberries; 3) the bear population may increase in density and productivity; and 4) bears, as a result of feeding on salmon, may facilitate nutrient transport from the Elwha River and its tributaries to surrounding riparian and upland habitats.

Patterns documented in other bear populations lend support to these predictions. On Admiralty and Chichagof Islands, Alaska, several radio-collared male brown bears remained active along a river channel through November and much of December, apparently to feed on late salmon runs (Schoen et al. 1987). Females have also been documented using salmon streams in fall, though females with cubs may avoid salmon streams altogether, may consume less salmon than their female counterparts without young, or may forage in areas or at times with lower probabilities of encountering other bears (Barnes 1989, Reimchen 1998, Ben-David et al. 2004). Population size and structure may also be affected by availability of salmon. Brown bears that feed on a diet of wild salmon are larger in size, have larger litters, and are found at higher densities than bears without access to salmon

(Miller et al. 1997, Hilderbrand et al. 1999b). Across Alaska, brown bear population densities were 6-80 times greater in salmon-rich coastal zones than in areas where salmon were absent or less abundant (Miller et al. 1997). Although black bear populations did not exhibit similar patterns, black bears did not use salmon resources to the same extent as brown bears, likely a result of competitive exclusion by brown bears (Miller et al. 1997, Jacoby et al. 1999). Miller et al. (1997) surmise that black bear densities are likely greater where brown bears are rare or absent and salmon are readily available. Further, black bears on the Kenai Peninsula of Alaska had diets that comprised primarily of salmon (53 ± 28%) when brown bears were rare (Jacoby et al. 1999).

Monitoring future trends in use of the Elwha watershed by black bears would contribute to an understanding of black bear relationships to salmon in the coastal Pacific Northwest. Samples of bear hairs and associated DNA collected from baited barbed-wire stations provide a cost-effective means to monitor trends in bear distribution, population structure, and relative density (Woods et al. 1999, Mowat and Strobeck 2000, Boulanger et al. 2004), as well as changes in ratios of marine-derived stable isotopes of carbon and nitrogen in the diet (Hilderbrand et al. 1996, 1999a; Jacoby et al. 1999). We have established hair/DNA collection sites throughout the low-elevation riparian zone of the Elwha River for operation during late spring, the current time of year that male bears focus activity on or near the Elwha floodplain, and during late summer and fall to coincide with the projected increase in anadromous fish following dam removal. Maintenance of these sites will allow us to document changes in bear population size and structure, as well as relative use of the Elwha River by bears subsequent to dam removal and salmon restoration. Additional long-term studies of bear distribution, population dynamics and nutrient status would be very useful to maximize understanding of the complex relationships between anadromous fish and bear populations in the Pacific Northwest.

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