Influence of phenology on site selection by female American black bears in coastal British Columbia

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Abstract: We examined factors that affect site selection by female American black bears (*Ursus americanus*) in coastal British Columbia, Canada, 1992–95. We monitored 9 radiocollared females and compared sites that were selected within their home ranges to those that were not selected using 1-1 matched logistic regression procedures. We used information-theoretic inference to assess the effect of 19 habitat, temporal, and spatial variables in 27 candidate models to explain selection of sites within home ranges. The model that best explained site selection was 50 times more likely to be the best model, given the data, than the second-best model. The best model suggested that the probability that a site would be used by female black bears increased with increasing values of phenologically adjusted berry value interacting with light levels, phenologically adjusted succulent forage value, and forest harvesting. Probability of use decreased with increasing distance from streams dependent upon salmon (*Oncorhynchus* spp.) availability and increasing distance from low-traffic roads. Although the best model included horizontal visibility and distance to high-traffic roads as variables, these factors had undetermined effects on the probability of use (95% confidence interval of odds ratio encompassed 1). Including phenological adjustments for abundance of berries and succulent foods greatly increased the support for the models by the data, compared to models based on cover of food plants alone. These results confirm that bears are cognizant of both temporal and spatial differences in food availability and that they modify their selection of sites based on these differences. Our results imply that site selection by female black bears involved a complex set of decisions about not only food availability, but also disturbance by humans. To increase the compatibility of timber production with conservation of black bear habitat, managers need to consider the spatial and temporal effects of the creation of food-rich openings and different types of roads on the suitability and effectiveness of habitats to support black bears.

Key words: 1-1 matched logistic regression, Akaike's information criterion, American black bear, British Columbia, disturbance, forage, forest management, habitat, phenology, site selection, *Ursus americanus*

From the dry pine forests of Arizona to wet temperate rainforests of western North America, American black bears (*Ursus americanus*) exploit a wide variety of habitats to acquire the resources needed to survive and reproduce. Wet meadows (California; Kelleyhouse 1980), conifer stands and clearcuts (Washington State; Lindzey and Meslow 1977, Barber 1983), forests that produce hard mast (Powell et al. 1997), and aspen stands (Pelchat and Ruff 1986) are all habitats that black bears use successfully throughout their range. Regardless of the habitats that are used, black bear populations will not thrive without adequate resources, which directly affect reproductive output (Garshelis 1994).

Site selection, the process by which bears choose a point in space at which to acquire resources, is affected by many factors, which can be either habitat or non-habitat related. Habitat factors are typically resources, such as forage, that influence site selection through their distribution and abundance. Non-habitat factors affect the ability of an individual to exploit the resource.

Non-habitat factors can play a key role in determining habitat effectiveness, that is, habitat "usability" after

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accounting for human influences (Hood and Parker 2001). A variety of human activities can displace bears in their normal day-to-day activities (McLellan and Shackleton 1988). Although much of the selection of habitats by black bears has been linked to food productivity (Powell et al. 1997), other features are required, particularly by some segments of the population, for habitats to be effective. For example, female and subordinate individuals are susceptible to attack from other animals, including male bears (Davis and Harestad 1996), and must temper their selection for food resources with requirements for security cover. Lindzey and Meslow (1977) demonstrated that female black bears in Washington State used areas with less food productivity because these habitats were more secure.

In the coastal forests of British Columbia, forest harvesting has significantly modified the distribution and abundance of food and security resources needed by female black bears. Historically, most coastal temperate forests were typically comprised of canopy gaps (Lertzman et al. 1996) that produced small patches of foods adjacent to dense forest structure. The conversion of these forests into relatively large, food-rich openings may have little added value for female black bears because these openings, although potentially rich in food resources, may have relatively low security value. In addition, such openings may only serve as potential forage areas for a relatively short time (10–15 years of an 80–100 year commercial forest rotation).

The objective of our study was to identify the habitat and non-habitat characteristics that affected site selection by female black bears during the non-denning period at the within-home range spatial scale in coastal British Columbia. Information on the influence of habitat change on females is required by forest managers to ensure that habitat changes are not detrimental to the health and fitness of black bear populations.

Study area

The 540-km^2 study area was approximately 40 km south of Port McNeill on northern Vancouver Island, British Columbia, Canada. Elevations ranged from 10 m to >1500 m. Winters were cool and wet, as was typical in coastal temperate forests. Annual precipitation at Woss (southeast end of the study area) ranged from 1,600 to 2,610 mm during the study (Ministry of Forests, Victoria, British Columbia, Canada, unpublished data). Seventy-seven percent of the mean annual precipitation fell between October and March with approximately 15% falling as snow (Rochelle 1980).

Mean maximum daily temperature for July was 19.8°C and for December was 3.2°C (Ministry of Forests, Victoria, British Columbia, Canada, unpublished data).

In the climax state, vegetation in the study area was dominated by western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), mountain hemlock (*Tsuga mertensiana*), yellow-cedar (*Chamaecyparis nootkatensis*), and Pacific silver fir (*Abies amabilis*). Red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), and black cottonwood (*Populus trichocarpa*) occurred as minor deciduous species in successional areas or forest gaps. None of the deciduous species produced hard mast crops suitable as food for black bears.

Shrubs and herbaceous vegetation that produced food for bears were abundant in old forests and in a variety of successional and non-forested habitats. Berry-producing shrubs included *Vaccinium* species, salal (*Gaultheria shallon*), red elderberry (*Sambucus racemosa*), *Ribes* species, and thimbleberry (*Rubus parviflorus*). Succulent herbaceous vegetation included young growth or flowers of plants such as horsetails (*Equisetum* spp.), sedges (*Carex* spp.), clovers (*Trifolium* spp.), graminoids and some non-native plant species (wall lettuce, *Lactuca muralis*; hairy cat's-ear, *Hypochaeris radicata*). Some species, such as salmonberry (*Rubus spectabilis*), produced both succulent vegetation (shoots) and berries.

Prior to extensive timber harvesting, stand-initiating events within forests of the study area were rare or infrequent. As a consequence, the forests were historically dominated by late-successional (mature and old forest) structural stages with canopy gaps. A variety of pathogens and natural disturbances, such as geomorphic disturbances, wind, floods, and fire, affect forest structure and composition at generally small spatial scales and variable time intervals (Wong et al. 2003). Forest harvesting, primarily using clearcut methods, began in the study area in 1923 and resulted in large tracts of even-aged stands with dense canopies surrounded by either remnants of old forest or regenerating clearcuts. Approximately 45% of the forests in the study area were exposed to disturbance (primarily forest harvesting) between 1923 and 1995 (Green 2000), with most forest harvesting having occurred in the bottom of the Nimpkish River valley.

Harvested areas initially regenerated with productive herbs and berry plants, especially salal and *Vaccinium* species. Regenerating conifers often form a continuous canopy within 50 years of stand initiation that leads to an understory with few plants that provide forage for black bears (Barber 1983). Tree species that are found in

late-successional forests become dominant in the canopy after approximately 80 years, but forests do not reach old-forest conditions with productive understories for approximately 200 years (British Columbia Ministry of Forests and British Columbia Ministry of Environment, Lands and Parks 1995).

Human activity other than that associated with the forest industry was limited. The North Island Highway ran through the northeast portion of the study area. A minor railway paralleled the highway, which was used only by the forest company for transporting logs. Access to the study area was extensive on active and inactive log-hauling roads. The road density was highest in the valley bottom. Bear hunting occurred in the study area April 1 to June 15 and September to mid-December of each year. Hunters were not allowed to bait bears, but could use hounds. Most bears killed during the study were on or near the extensive road network.

Methods

We used Aldrich foot snares and modified culvert traps to capture bears between May 1992 and August 1994. We affixed radiocollars to female bears that we captured. Live-trapping and radiocollaring protocols were approved by the Animal Care committee of Simon Fraser University as being in accordance with the principles and guidelines of the Canadian Council on Animal Care. Based on observed breeding behavior, we considered female bears to be adults at ≥4 years of age.

Radiotracking

We collected point locations of radiocollared black bears from May 1992 to June 1995. We attempted to locate radiotagged bears twice weekly during the non-denning period using standard telemetry procedures (White and Garrott 1990:42) whenever possible. We primarily obtained radiolocations from the ground, but occasionally conducted aerial tracking surveys when bears could not be found for extended times. We estimated the linear error associated with each radio-location on the basis of visual or auditory detection of the tagged bear, signal attenuation, or error triangles of bearings collected during ground telemetry. From this error measurement, we examined each radiolocation to ensure that it was sufficiently precise to be attributed to only 1 stand (i.e., error polygon was limited to a single stand polygon; only those radiolocations for which the observer confidently determined the stand in which the location occurred were used for the analysis of selection within home ranges). We excluded radiolocations that

were not temporally independent by determining the time required for each bear to cross its home range at its maximum observed movement rate (generally <16 hours) or were repeated observations at or near winter dens.

Within home range selection

We estimated multi-annual home ranges for female black bears to determine areas that were available to each bear. We used the 95% fixed kernel method with the smoothing parameter generated by least-squares cross validation (animal movement extension to Arc-View 3.1, Environmental Systems Research Institute, Inc., Redlands, California, USA; Hooge and Eichenlaub 1999) to estimate the utilization distribution (UD; Worton 1989) for each black bear for the entire period that it was monitored. We employed a minimum of 30 radio-locations for each estimate (Seaman et al. 1999). For the estimation of home ranges, we used all radiolocations that were estimated to be accurate within 500 m (a different criteria than above).

For each radiolocation, we also generated a simultaneously unused point that was randomly located within each animal's home range. This paired point represented a site that could be potentially used by an individual, but was not used at the time of the radiolocation. This stratified approach linked an unused site to a radio-location because it was unused at the exact moment that the radiolocation was collected (a temporally linked unused paired point). That is, because we knew where an individual was at the exact moment of its radio-location, we could also identify an unused point within its home range for comparison.

We used spatial data to determine the values of the habitat and non-habitat variables associated with each radiolocation and paired point. We used a 1:15,000 ecosystem map of the study area (Green 2000) to identify the stands in which each radiolocation and paired point occurred, using the combination of ecosystem and structural stage information as the basic mapped unit. Ecosystem polygons were delineated on the basis of relatively homogenous moisture and nutrient regimes, structural stages, site modifiers, terrain and soil components, and site attributes (British Columbia Ministry of Environment, Lands and Parks and British Columbia Ministry of Forests 1998). These polygons were assigned 1 of 6 structural stages: sparsely vegetated (generally <5 years old), herb–shrub (5–20 years), pole–sapling (20–40 years), young forest (40–80 years), mature forest (80–250 years), and old forest (>250 years). Polygons varied from 1 to 55 ha. The successional

stages were prorated to 1994, the midpoint of our study, to account for forest harvesting that occurred after our study but before the map was produced. We also determined the proximity to escape trees, which we defined as stands with trees suitable for climbing (i.e., young forest or older structural stages with trees >10 m tall), for each radiolocation and paired point from the ecosystem map. We used digital topographical data to determine the elevation, proximity to water, and proximity to streams bearing salmon (as determined from field observations) of each radiolocation and paired point. We also used digital road data to determine proximity to various transportation corridors for each radio-location and paired point. Transportation corridors were classified into 2 types that reflected different levels and types of expected vehicle traffic. We considered high-way and main logging roads as high-traffic roads, and spur logging roads and the railway corridor as low-traffic roads.

Habitat measurements

We also collected on-the-ground habitat information to provide structural and vegetation descriptions of each combination of ecosystem and structural stage within the study area (stand description plots). We conducted habitat assessments at random geocoordinates within the study area. At these plots ($n = 278$, $\bar{x} = 7$ plots/ stand type, $SD = 8$), we measured the values of a 400-m^2 patch that reflected the average values for each combination of ecosystem and structural stage. At each plot, we recorded biogeoclimatic variant and site series (Green and Klinka 1994), slope, aspect, elevation, and the percent cover of vegetation (ocular estimates for trees, shrubs, herbs, and mosses) in a square 400-m^2 plot around a central point. We assessed horizontal visibility cover by measuring the average distance from plot center at which a 1-m tall bear would be obscured by vegetation, debris, or topography in the 4 cardinal directions. Mean values for each habitat variable were calculated for each combination of ecosystem and structural stage. These stand-scale habitat values were then assigned to each radiolocation and paired point on the basis of ecosystem and structural stage combination.

To assess plant food productivity, we identified 66 genera or species in the study area that could provide forage for black bears, based on the feeding ecology of black bears in similar coastal forests (Barber 1983, A.G. MacHutchon, wildlife consultant, Comox, British Columbia, Canada, unpublished data). Food plants were classified as either succulent (young growth, forbs, shoots, flowers, graminoids) or berry-producing. We

created a species-specific value score for each food ranging between 0 and 1 depending on its relative ability to produce soft mast (berries, fruit) or succulent vegetation (Appendix, available at www.ursusjournal.com/volumes/ursus-17.htm). Because the production of edible parts changes over time, we also derived phenology curves for each food plant (Fig. 1). These curves predicted the date-specific relative abundance value of forage associated with each species of plant and ranged between 0 (no food value) and 1 (peak food value). These phenology curves were based on published reports (e.g., Barber 1983) and field observations of the start, peak, and end of berry and succulent abundance in typical sites throughout the year. We assigned each food to 1 of 10 generalized phenology curves (Appendix, www.ursusjournal.com/volumes/ursus-17.htm) on the basis of field observations during site investigations and habitat sampling. We also monitored the presence of spawning salmon during field work and developed an abundance curve for salmon based on these observations. These curves allowed us to estimate the relative abundance of food for each species on a daily basis throughout the year.

We assessed the date-specific productivity of each plant food encountered at the stand description plots by deriving both a phenologically adjusted berry and succulent value. This value was the product of the species-specific value score, date-specific phenology value, and percent cover of each species of food plant. Phenologically adjusted berry and succulent values ranged between 0 and 100. For example, a plot with 15% cover of red huckleberry was given a score of 1.0 for producing berries because it is a prolific berry-producer and known bear food. On 23 July (the peak phenology for this species; see Appendices A and B), the berry value of this plant was 15 (15 [% cover] x 1 [value score] x 1 [phenology value]). The phenologically adjusted berry value for red huckleberry at the same plot on 28 August was approximately 6.5 because its phenology score had dropped to 0.43. Some species provided both berry and succulent forage (for example, salmonberry), so these plants had both phenologically adjusted berry and phenologically adjusted succulent values. We summed the phenologically adjusted berry value of each food plant for each stand description plot to derive a total phenologically adjusted berry value of that plot. This process was repeated for the phenologically adjusted succulent cover. Because the amount of light that reaches berry-producing plants affects the productivity of berries (Martin 1983), we also estimated light levels in each stand by calculating the inverse of the percent
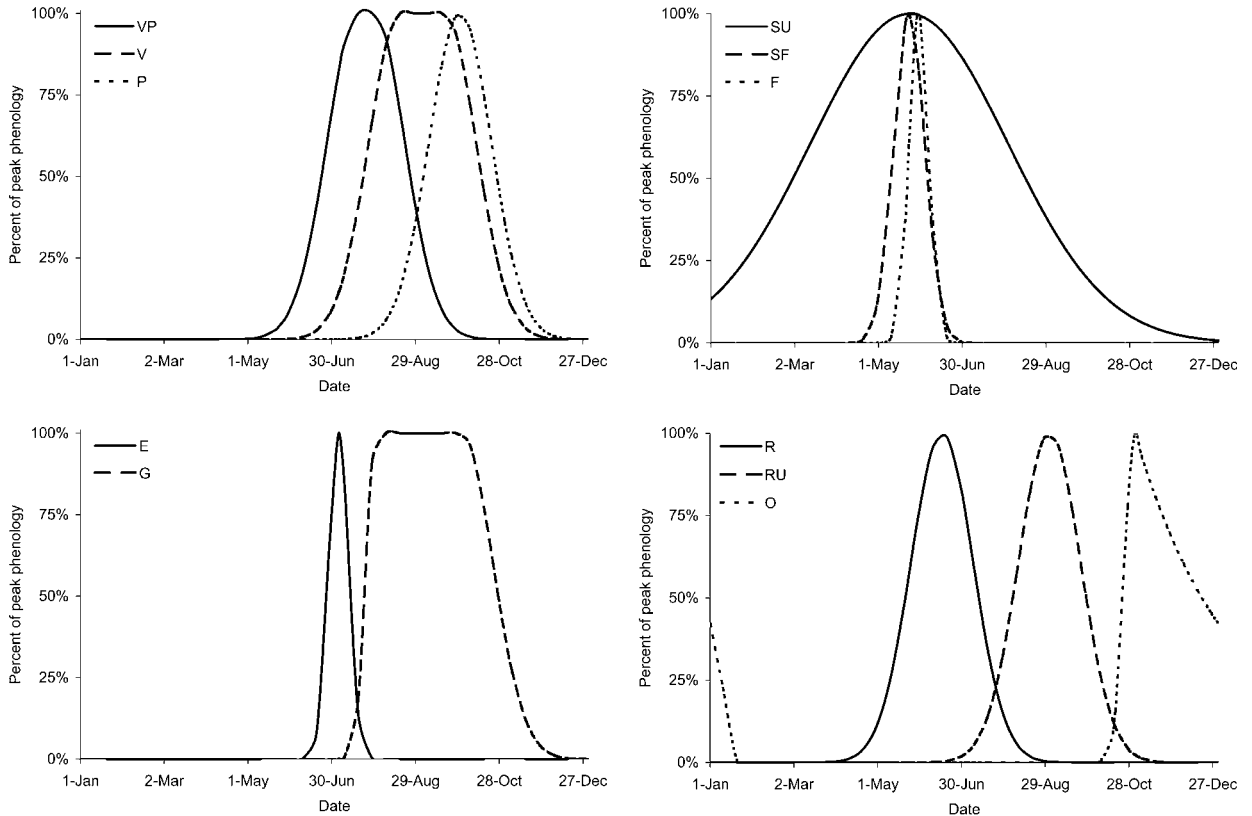
Fig. 1. Phenology curves used to predict date-specific abundance of 66 food types for female American black bears in coastal British Columbia, Canada, 1992–95. Each curve corresponds to predicted date-specific abundance of forage for each type of food. VP = red huckleberry (*Vaccinium parvifolium*); V = other *Vaccinium* species, black raspberry (*Rubus leucodermis*), and thimbleberry; P = Pacific crabapple (*Malus fusca*), cherries (*Prunus* spp.), devil's club (*Oplopanax horridus*), gooseberries and currants (*Ribes* spp.); SU = succulent herbs; SF = salmonberry flowers, fireweed (*Epilobium angustifolium*), and chocolate lily (*Fritillaria affinis*); F = wild strawberry (*Fragaria* spp.); E = elderberry fruit; G = salal berries; RU = trailing blackberry (*Rubus ursinus*); R = other *Rubus* species; O = spawning *Oncorhynchus* species and rosehips (*Rosa* spp.). Full list of food species and their associated scores and phenology curves at www.ursusjournal.com/volumes/ursus-17.htm.

tree canopy cover plus 1 (to allow for calculation of a value in stands with no tree canopy cover).

Data analysis

We used an information-theoretic approach (Burnham and Anderson 1998) to assess the factors that affected selection of sites within home ranges by female black bears. First, we developed a set of *a priori* candidate models to explain selection based on literature and suspected ecological relationships. Second, we assessed multicolinearity among variables in each model with ordinary least squares regression. In cases of correlation between variables, we excluded one set of the correlated variables from that model on the basis of *a priori* understanding. We then determined which model was

best supported by the data. Finally, we used multi-model inference to generate an 'average' model to predict site selection by female black bears.

Our set of candidate models (Appendix, www.ursus journal.com/volumes/ursus-17.htm) represented combinations of variables that were expected to affect site selection by black bears. These models were based on published results from studies conducted in other areas as well as on hypothesised relationships specific to our study area. Each of these models included combinations of variables that were expected to influence the quality of a site for its food, security, or both. When we included interaction terms in our models, we excluded main effects.

Model parameterization

We employed maximum likelihood estimation using 1-1 matched logistic regression methods (Hosmer and Lemeshow 2000:226) to parameterize each candidate model. Model parameterization involved the 1-1 comparison of a site used by a radiocollared bear to a simultaneously unused site randomly located within its home range. This 1-1 matched approach compared a used site to a simultaneously unused site and allowed us to consider the effects of phenological changes in food abundance over time on site selection. Following this design, each radiolocation and simultaneously unused paired point were considered a stratum. As identified by Keating and Cherry (2004), the resulting model does not adequately estimate the probability of use because stratum-specific effects are not included in the model. However, with a 1-1 matched study, the interpretation of odds ratios for identified parameters remains the same as other logistic regression analyses (Hosmer and Lemeshow 2000:242). Thus, although we could not predict overall probability of use (i.e., a resource selection probability function), we used the odds ratios to interpret the effect of each parameter on the probability of use by female bears.

To eliminate the effects of pseudoreplication, we weighted each radiolocation so that its relative contribution to the data set was consistent among bears (that is, sampling weights). We weighted each radiolocation by 84 (mode sample size) divided by the total number of radiolocations for that bear.

Model selection and averaging

We calculated Akaike's information criterion (AIC) score (Burnham and Anderson 2001) for every model and ranked the relative support for each by comparing scores among models. For each model in the candidate set, we calculated the log likelihood (log L), number of estimated parameters (K), AIC (Burnham and Anderson 1998), difference between AIC score and the minimum AIC score for the candidate set (Δ_{AIC}), and Akaike weight (strength of evidence, w_i; Burnham and Anderson 1998). We identified the best model from the candidate set by selecting the model with the lowest AIC score. We used Akaike weights (w_i) to quantify strength of evidence about model-selection uncertainty among the candidate set of models. We constructed 95% confidence interval sets of the candidate models based on the Akaike weights. We used multi-model inference (Burnham and Anderson 1998) to estimate model-averaged parameters and unconditional 95% confidence intervals in the production of a best predictive model.

Results

We radiocollared 9 female bears (7 adults, 2 juveniles) during 3 summers of live-trapping, accumulating 1,141 radiolocations during the non-denning period between 24 May 1992 and 8 June 1995. Of these radiolocations, 983 met our precision criterion for use in the habitat analysis. We collected between 27 and 172 radiolocations that were suitable for inclusion in the habitat analyses for each radiocollared female ($\bar{x} = 109$, SD = 43, $n = 9$). Five of the 9 females had dependent young at some point during monitoring. The average size of the home ranges was 7.83 km^2 (SD = 4.66, $n = 9$).

The 95% confidence interval set of models for factors affecting selection of sites within the home ranges of the radiocollared female American black bears included only one model. This model included the variables phenologically adjusted berry value dependent on light level, phenologically adjusted succulent value, proximity to fish dependent on availability of salmon, horizontal cover, proximity to high-traffic roads, proximity to low-traffic roads, and the presence of logging. Although the best model was not definitive (next-best model with $\Delta_{AIC} < 10$, Burnham and Anderson 1998:128), both top and second-best models included similar variables (www.ursusjournal.com/volumes/ursus-17.htm). This second best model excluded the 2 variables proximity to salmon-bearing streams dependent on the presence of salmon and presence of logging, (but did include the presence of escape trees dependent on reliant young) and had an Δ_{AIC} of 7.844.

There was very little support for any of the remaining 25 models ($w_i \leq 0.007$). The models that performed most poorly were those that used the traditional approach of predicting use based on structural stage or canopy closure, for which the data provided essentially no support.

The multi-model parameterization of the best model indicated that several factors strongly affected site selection by female black bears within their home ranges (Table 1). The probability of use of a site increased with phenologically adjusted berry value interacting with light and phenologically adjusted succulent value. Bears also chose sites closer to salmon-bearing streams when salmon were spawning. The presence of recent forest harvesting (<15 years) positively affected the likelihood that female bears used the site, and bears were more likely to use sites that were closer to low-traffic roads. Although the best model included horizontal visibility and distance to high-traffic roads as

Table 1. Model-averaged parameter estimates for best-fit model to predict values of variables at sites selected within the home ranges of radiocollared female American black bears monitored in coastal British Columbia, Canada, 1992–95. Horizontal visibility is the average distance that a 1-m tall bear could be seen in 4 cardinal directions.

Variable	$w_+(j)$	Model-averaged parameter estimate	Unconditional SE	Odds ratio	95% CI	Relationship with probability of use
Scored and phenologically adjusted berry value dependent on light	1	0.1260	0.0182	1.847[a]	1.698–2.056	positive
Scored and phenologically adjusted succulent value	1	0.0422	0.0127	1.235[a]	1.110–1.360	positive
Horizontal visibility	1	−0.0003	0.0033	0.994[b]	0.830–1.157	not predictable
Presence of forest harvesting	0.973	0.3515	0.1402	1.421	1.146–1.696	positive
Distance to salmon-bearing stream dependent on salmon availability	0.974	−0.0009	0.0004	0.979[b]	0.960–0.998	negative
Distance to high-traffic road	1	0.0001	0.0002	1.003[b]	0.992–1.014	not predictable
Distance to low-traffic road	1	−0.0021	0.0006	0.949[b]	0.920–0.978	negative

[a]Change in probability of use with 5-unit increase in value.
[b]Change in probability of use with 25-m increase in value.

variables, these 2 factors had ambiguous effects on the probability of use (95% confidence interval of odds ratio encompassed 1).

Discussion

Selection of sites by female American black bears in coastal British Columbia during the non-denning period was strongly linked to resources that provided food. Site selection was also related to distance from and type of transportation corridor. We noted that the probability of use increased with increasing food, the presence of recent forest harvesting, and proximity to low-use transportation corridors. This implies that site selection by female black bears involved a complex set of decisions about not only food availability, but also the effects of human disturbance.

Food

The strongest relationships we documented between habitat variables and site selection were those involving food resources. We observed that temporally adjusted availability of foods, both in the forms of plant products (berry and succulent tissue) and fish, most strongly and consistently affected the use of sites within home ranges. These results suggest that female black bears made decisions on site selection based not only on the cover of food-producing plants, but also on the phenological development of these food plants or the availability of spawning salmon. It appears that bears were cognizant of both temporal and spatial variation in food availability and that they modified their selection of sites based on these variations.

Berry-producing shrubs clearly played an important role in the selection of sites by females, and many other studies have observed that black bears modify their selection of sites based on food (Lindzey and Meslow 1977, Powell et al. 1997). However, little research has examined the temporal effect of plant phenology on site selection other than to examine relative selection of sites with regards to gross seasonal categories (Young and Beecham 1986, Boileau et al. 1994). Our results suggest that, given similar light conditions, a 5% increase in cover of a highly ranked berry species at its peak phenology was associated with an 88% increase in probability of use by female bears. The positive relationship between use and the presence of recent forest harvesting may be due to the increased productivity of plants in open, regenerating cutblocks and the relative abundance of insects associated with dead and down debris found in these areas.

The abundance and value of succulent vegetation also appeared to have a substantial effect on site selection throughout the year. This may be because bears need to maintain a diet comprised of a variety of plant foods for the effective assimilation of energy. Rode and Robbins (2000) suggested that black bears consume succulent vegetation even during periods of peak berry abundance to meet protein and other nutrient requirements. Scat analyses from other studies of black bears also documented this trend (Barber 1983, Boileau et al. 1994). Our observations that succulent vegetation continued to be a factor in site selection even during periods of peak berry abundance were consistent with this hypothesis. We observed that a 5-unit increase in succulent value increased the probability of a site being used by female black bears by 23%. The increased probability of use

associated with proximity to low-traffic roads may be the result of the relatively high potential cover of succulents in these areas, resulting from exposed mineral soils and direct seeding to control erosion. The influence of succulents in site selection at the within-home range spatial scale suggests that female bears preferred to incorporate succulent vegetation in their diets despite the increased availability of berries.

Spawning salmon are also an important component of diets of black bears in coastal British Columbia (Reimchen 1998). The seasonal availability of salmon affected the selection of sites by radiotagged bears, and we documented females occasionally feeding on washed-up fish carcasses. Interestingly, bears adjusted their proximity to spawning streams only when fish were present. For example, our model predicted that with each 25 m in distance away from spawning streams during the peak spawning period, the probability of use declined by 2%. Again, this suggests that bears are cognizant of the temporal changes in availability of food resources within their home ranges.

Our analysis was unique in that we included measures of date-specific food abundance to explain site selection, rather than basing models solely on plant cover. Nutrition, digestibility, palatability, and availability all play critical roles in the relative importance of specific plants in the diets of black bears (Powell et al. 1997). Inclusion of these phenological changes in our models greatly increased the support for these models over models based on food-plant cover alone (see also Nielson et al. 2003). Our model, which included a phenological adjustment for productivity of edible plant parts, was significantly more likely, given the data, than the model that was nearly identical, except for the lack of phenological adjustments.

Effect of site selection on mortality risk

Early successional, berry-rich regenerating clearcuts were among the highest quality foraging habitats for female black bears in our study area. As part of the forest harvesting activities that created these openings, log-hauling and spur roads were common in these clearcuts. Access provided by these roads likely exposes bears to higher levels of mortality risk than unroaded areas (Nielson et al. 2004).

The association of roads with productive habitats for bears may introduce several forms of human-caused mortality to the population. Bears are occasionally killed in collisions with vehicles, and we documented several deaths of bears in our study from this factor. Roads may also facilitate hunting mortality (Brody and Pelton 1989)

because they provide easier access for hunters to areas of dense food resources for bears. For example, during our fieldwork, we documented at least 3 adult females and 1 adult male that were legally shot by hunters or poached from spur roads. Other researchers have noted that roads tend to increase access to hunters and poachers, and thus can lead to increased mortality risk (McLellan and Shackleton 1988, Nielson et al. 2004).

The concentration of food-rich sites in human-modified areas, in concert with the positive relationship between site selection and the proximity to low-use railroads and spur roads, likely exposes bears to higher levels of mortality risk than unroaded areas. The net effect of this relationship may be that, by having food concentrated in highly accessible areas, forest-harvesting activities increased the vulnerability of bears to mortality from hunting. This may have population implications because none of the best models suggested that female black bears modified their selection of sites during hunting season.

Although included in the best model within the candidate set, the effects of horizontal cover and proximity to high-traffic roads at the within-home range spatial scale were unclear. This may be because female bears select for horizontal cover at a finer spatial scale, such as patches within stands. Alternatively, these factors may have had differential effects on site selection, depending on different behaviors (such as sleeping compared to foraging). Additional data is needed to help determine the effects of these factors.

Model selection

Incorporating date-specific phenology factors into our models allowed us to assess the dynamic effects of changing food abundance resulting from annual plant phenology on site selection by bears, which has not been fully captured in previous assessments of habitat selection by bears. Critical to our approach was the use of the 1-1 paired design that allowed for temporal stratification of our samples so we could compare the abundance of food at used and unused sites as these values changed over time.

Several models widely used by researchers to quantify habitat selection by black bears performed very poorly in our analysis. These models were typified by general variables based on site groups and structural stages (old-style "habitat" models). As identified by Morrison (2001), these models likely performed poorly because they did not reflect the true underlying resources that affect selection. This highlights the dangers of using

categories of 'homogenous' habitats that may not be viewed as homogenous by the animal. This result suggests that our perceptions of habitat categories often do not reflect the actual distribution of resources that are perceived by the animal (see also Nielson et al. 2003). Future models could also perhaps be improved by including "home range supply" or like indices of overall habitat availability.

The predictive capacity of our best model remains untested. Verification of this model by independent data would be extremely valuable for widespread application of these results and to assess model fit. Conducting *k*-fold cross validation (Boyce et al. 2002) would allow for further evaluation of model fit.

Management implications

Mature and late-successional forests historically dominated much of the coastal temperate rainforests of British Columbia. These forests were characterized by multi-storied canopy layers with up to 30% of the forest area in canopy gaps arising from edaphic and topographic features (Lertzman et al. 1996). Fruit-bearing shrubs such as salal, salmonberry, and devil's club, all of which are important forage species for bears, have been shown to have consistently greater cover in these canopy gaps (Inselberg 1993). This distribution of patchy, abundant food sources with low horizontal visibility was likely an ideal configuration for female black bears because food resources were distributed in small patches with relatively high security values.

Forest harvesting, however, changes these habitats from their historic patterns by creating comparatively large openings with high concentrations of plants that provide food for bears, especially berry-producing shrubs such as salal and *Vaccinium* species. However, creation of these food-rich forest openings can have negative consequences for female black bears. Increased vehicular access afforded to these concentrations of food may expose the population to focused hunting or illegal poaching mortality.

Forest managers have several options available to enhance or maintain habitats for female black bears. Silvicultural practices that attempt to emulate the natural disturbance regime of coastal temperate rainforest likely provide the best balance between food productivity and security for females. Although operationally and economically difficult under certain conditions, small gaps resulting from the extraction of 3–10 trees in an otherwise continuous forest matrix (Lertzman et al. 1996) would better mimic historical natural conditions for

female black bears than found under past management practices. This approach would have the net result of enhancing forage potential while maintaining the large trees and dense shrub layers needed for security cover by female black bears in coastal British Columbia. Larger retention patches, such as those found in many variable retention systems currently in use by some forest companies, may also achieve similar results. However, access roads for both of these harvesting systems would need to be deactivated following harvesting to ensure that road-related mortality risk in these areas was not increased.

Various post-harvesting stand tending techniques can also increase or decrease the utility of habitats to provide forage for bears. Stand-tending prescriptions that affect the amount of light reaching the shrub layer of forests will affect forage production. Reduced stocking standards, pruning, juvenile spacing of trees, planting trees in clusters (Wood 2001), prescribed burning (Martin 1983), and seeding with grasses following road deactivation can enhance forage production for bears in regenerating coastal forests.

The effects of maintaining road access into food-rich clearcuts may have negative consequence on populations of black bears in coastal forests. By creating food-rich openings with high accessibility, forest development activities may increase the vulnerability of bears to hunting mortality. Thus, forest management that eliminates or limits motorized access following forest harvesting, especially to stands that have high value for both food and security cover that are most likely to be used by females, would clearly benefit populations of coastal black bears.

Whereas the importance of food and security requirements were the focus of this analysis, black bears in coastal British Columbia need other resources that can only be supplied by forested habitats. Specifically, a sufficient supply of winter dens is likely critical to maintain stable bear populations. Relative to other areas within the range of black bears, climatic conditions in coastal temperate rainforests are substantially wetter than other areas. These cool, wet conditions constrain the types of dens that bears can use for denning. Large tree-related structures (large standing trees, logs, root boles, and stumps) were the only features suitable for keeping bears warm, dry, and secure during the wet, cool winters (Davis 1996). Trees that produce these structures develop only in late-successional forests and are rare (and declining) in intensively managed second-growth forests. Prudent management of black bear habitat must consider the long-term supply of these

elements, along with the supply of foraging and security habitats.

Acknowledgments

Literature cited

BARBER, K.R. 1983. Use of clearcut habitats by black bears in the Pacific northwest. Thesis, Utah State University, Logan, Utah, USA.

BOILEAU, F., M. CRETE, AND J. HUOT. 1994. Food habits of the black bear, *Ursus americanus*, and habitat use in Gaspesie Park, eastern Quebec. Canadian Field-Naturalist 108: 162–169.

BOYCE, M.S., P.R. VERNIER, S.E. NIELSON, AND F.K.A. SCHMIEGELOW. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

BRITISH COLUMBIA MINISTRY OF ENVIRONMENT, LANDS AND PARKS AND BRITISH COLUMBIA MINISTRY OF FORESTS. 1998. Field manual for describing terrestrial ecosystems. Government of British Columbia. Land management handbook 25. Victoria, British Columbia, Canada.

BRITISH COLUMBIA MINISTRY OF FORESTS AND BRITISH COLUMBIA MINISTRY OF ENVIRONMENT, LANDS AND PARKS. 1995. Biodiversity guidebook. Province of British Columbia. Victoria, British Columbia, Canada.

BRODY, A.J., AND M.R. PELTON. 1989. Effects of roads on black bear movements in western North Carolina. Wildlife Society Bulletin 17:5–10.

BURNHAM, K.P., AND D.R. ANDERSON. 1998. Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

———, AND ———. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research 28:111–119.

DAVIS, H. 1996. Characteristics and selection of winter dens by black bears in coastal British Columbia. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

———, AND A.S. HARESTAD. 1996. Cannibalism by black bears in the Nimpkish Valley, British Columbia. Northwest Science 70:88–92.

GARSHELIS, D.L. 1994. Density-dependent population regulation of black bears. Pages 3–14 *in* M.K. Taylor, editor. Density-dependent population regulation of black, brown, and polar bears. International Conference of Bear Research and Management Monograph Series 3.

GREEN, R.N., AND K. KLINKA. 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. British Columbia Ministry of Forests. Land management handbook 28. Victoria, British Columbia, Canada.

———. 2000. Terrestrial ecosystem mapping of Canadian Forest Products' Tree Farm License 37. Canadian Forest Products Limited, Woss, British Columbia, Canada.

HOOD, G.A., AND K.L. PARKER. 2001. Impact of human activities on grizzly bear habitat in Jasper National Park. Wildlife Society Bulletin 29:624–638.

HOOGE, P.N., AND B. EICHENLAUB. 1999. Animal movement extension to ArcView, version 2.04. Alaska Biological Sciences Center, US Geological Survey, Anchorage, Alaska, USA.

HOSMER, D.W., AND S. LEMESHOW. 2000. Applied logistic regression. Second edition. John Wiley & Sons, New York, New York, USA.

INSELBERG, A.E. 1993. A survey of the composition and structure of forest ecosystems in the Tofino Creek watershed on Vancouver Island. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.

KEATING, K.A., AND S. CHERRY. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68:774–789.

KELLEYHOUSE, D.G. 1980. Habitat utilization by black bears in northern California. International Conference on Bear Research and Management 4:221–227.

LERTZMAN, K.P., G.D. SUTHERLAND, A. INSELBERG, AND S.C. SAUNDERS. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology 77:1254–1270.

LINDZEY, F.G., AND E.C. MESLOW. 1977. Home range and habitat use by black bears in southwestern Washington. Journal of Wildlife Management 41:413–425.

MARTIN, P. 1983. Factors influencing globe huckleberry fruit production in northwestern Montana. International Conference on Bear Research and Management 5:159–165.

MCLELLAN, B.N., AND D.M. SHACKLETON. 1988. Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. Journal of Applied Ecology 25:451–460.

MORRISON, M.L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management 65:613–23.

NIELSON, S.E., S. HERRERO, M.S. BOYCE, AND R.H.M. MUNRO. 2003. Development and testing of phenologically driven grizzly habitat models. Ecoscience 10:1–10.

———, ———, ———, R.D. MACE, B. BENN, M.L. GIBEAU, AND S. JEVONS. 2004. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biological Conservation 120:101–113.

PELCHAT, B.O., AND R.L. RUFF. 1986. Habitat and spatial relationships of black bears in boreal mixedwood forest of Alberta. International Conference on Bear Research and Management 6:81–92.

POWELL, R.A., J.W. ZIMMERMAN, AND D.E. SEAMAN. 1997. Ecology and behaviour of North American black bears: home ranges, habitat and social organization. Chapman and Hall, London, UK.

REIMCHEN, T.E. 1998. Nocturnal foraging behaviour of black bears, *Ursus americanus*, on Moresby Island, British Columbia. Canadian Field-Naturalist 112:446–450.

ROCHELLE, J.A. 1980. Mature forests, litterfall and patterns of forage quality as factors in the nutrition of black-tailed deer on northern Vancouver Island. Dissertation, University of British Columbia, Vancouver, British Columbia, Canada.

RODE, K.D., AND C.T. ROBBINS. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78:1640–1645.

SEAMAN, D.E., J.J. MILLSPAUGH, B.J. KERNOHAN, G.C. BRUNDIGE, K.J. RAEDEKE, AND R.A. GITZEN. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

WHITE, G.C., AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

WONG, C., H. SANDMANN, AND B. DORNER. 2003. Historical variability of natural disturbances in British Columbia: A literature review. FORREX–Forest Research Extension Partnership. FORREX Series 12. Kamloops, British Columbia, Canada.

WOOD, C. 2001. Grizzly bear habitat in managed forests: silviculture treatments to meet habitat and timber objectives. British Columbia Ministry of Forests, Research Branch, Extension Note EN45. Victoria, British Columbia, Canada.

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

YOUNG, D.D., AND J.J. BEECHAM. 1986. Black bear habitat use at Priest Lake, Idaho. International Conference on Bear Research and Management 6:73–80.