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Thermoregulation, Risk, And Den Stability Influence Grizzly Bear Den-Site Selection

Nathan Steven Libal

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THERMOREGULATION, RISK, AND DEN STABILITY INFLUENCE GRIZZLY

BEAR DEN-SITE SELECTION

By

Nathan Steven Libal

A Thesis
Submitted to the Faculty of
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BEAR DEN-SITE SELECTION

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　　　　　　　　INFLUENCE GRIZZLY BEAR DEN-SITE SELECTION

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Grizzly bear (*Ursus arctos*) den-site selection may be influenced by multiple factors at varying spatial extents. To test for hierarchical selection, I compared grizzly bear den sites ($n = 21$) to random locations in the Southern Lakes, Yukon at two scales: mesoscale (within 1 km of dens) and microscale (within 100 m of dens). I observed selection for den opening slope, pixel slope, soil content, and horizontal cover at the mesoscale. At the microscale, I observed selection for opening slope and horizontal cover. To further test the role of security and the sex hypothesis of sexual segregation, I compared adult female ($n = 142$), adult male ($n = 36$), and juvenile ($n = 35$) den locations in Denali National Park and Preserve, Alaska. Adult females spatially segregated from adult males, with dens characterized by higher elevations and steeper slopes than adult male den sites.

DEDICATION

I dedicate this research to my parents, Steve and Joyce Libal, and to my fiancée

Deb Martell. Thank you for always supporting and encouraging me.

ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION

Den selection and use is an important component of bear ecology. Bear

hibernation is generally attributed to limited food resources during winter (Nelson 1980),

when bears reduce energetic costs by reducing metabolic rates (Folk 1974). Den sites

may also provide thermal advantages and likely provide a secure location for parturition

(Nelson 1973, Harding 1976, Libal et al. 2011). At larger spatial scales, grizzly bears in

northern, mountainous environments appear to select den sites at higher elevations

(reported elevations vary, but are above minimum elevations within respective study

areas; Craighead and Craighead 1972, Pearson 1975, Vroom et al. 1980, Servheen and

Klaver 1983, Schoen et al. 1987, Ciarniello et al. 2005, Libal et al. 2011). Higher

elevations may be selected in part for increased snow cover, providing improved thermal

insulation (Vroom et al. 1980). Selection for elevation is not always uniform between

age or gender classes, however, with adult females denning at higher elevations than

adult males (Schoen et al. 1987, Haroldson et al. 2002, Libal et al. 2011). Where

available, steep terrain also is characteristic of northern grizzly bear denning habitat and

may be selected for isolation and security (Schoen et al. 1987). As with elevation,

differences between age/gender classes have been observed, with adult females selecting

steeper terrain than adult males (Schoen et al. 1987, Libal et al. 2011).

At smaller spatial scales, dens are frequently constructed in areas where tree roots, rocks, or other structures provide stability (Pearson 1975, Vroom et al. 1980, Schoen et al. 1987, Ciarniello et al. 2005). Dens are also constructed commonly on moderately steep slopes (20–40°), which may contribute to ease of excavation, den stability, and optimal thermal properties (Craighead and Craighead 1972, Pearson 1975, Harding 1976, Vroom et al. 1980, Servheen and Klaver 1983, Schoen et al. 1987, Ciarniello et al. 2005).

While empirical evidence is lacking, cover also may be an important characteristic of *Ursus* spp. den locations (Cicnjak 1991, Kusak and Huber 1998, Martorello and Pelton 2003). Cover may reduce predation/infanticide risk, which have been hypothesized to influence grizzly bear resource selection (Wielgus and Bunnell 1995, Dahle and Swenson 2003b, Rode et al. 2006, Libal et al. 2011).

Previous research has not examined hierarchical den-site selection in grizzly bears. Thus, I addressed spatial selection using den-site data from the Southern Lakes region, Yukon and Denali National Park and Preserve, Alaska. I further addressed possible spatial segregation between age/gender classes of bears.

CHAPTER II

HIERARCHICAL DEN-SITE SELECTION OF GRIZZLY BEARS IN THE

SOUTHWEST YUKON

Introduction

Habitat selection can occur at multiple spatial scales, where an animal first selects

a home range and then decides which habitats within the home range to use for different

purposes (e.g., foraging, mating, etc.) (Johnson 1980). At larger spatial scales, animals

may select habitats to reduce effects of factors most limiting individual fitness (Rettie and

Messier 2000, McLoughlin et al. 2004). Other, less important limiting factors may then

influence habitat selection decisions at smaller spatial scales (Rettie and Messier 2000,

McLoughlin et al. 2004).

Hierarchical habitat selection has been reported for grizzly bears, where selection

varied between study areas and within and among individual home ranges (McLoughlin

et al. 2002, Ciarniello et al. 2007). At large spatial extents grizzly bears appeared food-

limited, selecting habitats based on spatial and temporal food availability (McLoughlin et

al. 2002, Ciarniello et al. 2007). At smaller spatial scales security influenced selection

(McLoughlin et al. 2002, Ciarniello et al. 2007). Hierarchical selection of denning

habitat has been demonstrated in other carnivore species including striped skunk

(*Mephitis mephitis*) and Canada lynx (*Lynx canadensis*) (Hwang et al. 2007, Squires et al.

2008). Similar to grizzly bears, resource availability and security were important variables at large and small scales, respectively (Storm 1972, Koehler 1990, Larivière et al. 1999, Larivière and Messier 2000, Hwang et al. 2007, Squires et al. 2008).

To accurately describe resource selection and provide sound management decisions, biologists must account for scale dependence (Addicott et al. 1987, McLoughlin et al. 2002, Ciarniello et al. 2007). While hierarchical selection has been demonstrated with grizzly bears, hierarchical den-site selection has not been examined. To test if den-site selection varies at different spatial extents, I investigated denning habitat at meso- (within 1 km radius surrounding dens) and micro- (within 100 m radius surrounding dens) scales. At the mesoscale I predicted that den sites would be selected for thermal cover and security. Thus, I predicted that dens would be above 1,100 m (Pearson 1975), and on steeper terrain than surrounding areas. At the microscale I predicted selection for structural stability and security. I predicted that excavated material would be predominantly soil (sand and smaller), as these particles are more cohesive. To further provide structural stability, I predicted that dens would be located on steeper slopes, and that vegetation would be predominantly trees and shrubs as these vegetation types have greater rooting depth than herbaceous vegetation. To provide security, I predicted greater horizontal cover at the den than surrounding areas.

Study Area

The study area was defined using a minimum convex polygon around known den locations, and encompassed about 6,854 km² of the Southern Lakes, Yukon, Canada (60°23'00" N 134°03'00" W). Mean annual temperature is about –2° C, with mean

January and July temperatures of –23° and 13° C, respectively (Smith et al. 2004). Study

area elevations range from about 600–2,600 m. The region is in the Coast Mountains,

within the rain shadow of the St. Elias Range and receives 200–325 mm annual

precipitation, 50–75% as snow (Smith et al. 2004). White spruce (*Picea glauca*) and

lodgepole pine (*Pinus contorta*) are common tree species, with white spruce occurring

from valley bottoms to tree line on mesic slopes and lodgepole pine dominating flat, xeric

areas (Larsen and Markel 1989, Smith et al. 2004). Extensive trembling aspen (*Populus*

tremuloides) stands occur on southern slopes, whereas black spruce (*Picea mariana*),

balsam poplar (*Populus balsamifera*), and paper birch (*Betula papyrifera*) are distributed

patchily throughout the region. Forest canopies are open, with shrub species including

soapberry (*Shepherdia canadensis*), kinnikinnick (*Arctostaphylos uva-ursi*), prickly rose

(*Rosa acicularis*), and crowberry (*Empetrum nigrum*). Shrub birch (*Betula* spp.),

kinnikinnick, and lichens are common above tree line (Smith et al. 2004). Grizzly bear

population density is less than other areas of Yukon. In 1989 the population was

estimated at 82–139 bears (13–22 bears/1,000 km²; Larsen and Markel 1989).

Methods

Data collection

During April–May 2010 and 2011 I used fixed-wing aircraft to fly transects over

the study area and identify grizzly bear dens during den emergence. To locate additional

dens, I used data from radio-collared individuals in a concurrent grizzly bear study

conducted by Environment Yukon. I also conducted ground surveys during summer

2010 and 2011, and used public notices to encourage residents to report den sightings. In cases where potential den sites could not be attributed to grizzly bears through visual detection of bears, I used presence of grizzly bear hair and elevation (e.g., above tree line) to separate grizzly bear dens from black bear (*U. americanus*) dens. I based elevation criteria on differences between denning elevations of sympatric grizzly bears and black bears in mountainous regions (Miller 1990, Aune 1994).

I measured mesoscale characteristics at the den site and 3 random points located within one km of the den opening. At each location I recorded elevation and slope of the pixel (30 m^2) containing the den, percentage cover of trees and shrubs, percentage soil content, and horizontal cover to describe den sites. I also recorded slope at the den opening. Elevation and slope were obtained for the pixel containing each den site using a digital elevation model (Environment Yukon, 2007). Elevation of the pixel was classified to the nearest meter and slope was classified as 0–90°. I extracted pixel-scale data using ArcMap 9.3 (Environmental Systems Research Institute, Redlands, California, USA). To quantify percentage soil content, a 30x30x30 cm soil core was taken from the center of the excavation fan. From soil cores, percentage soil was estimated visually and recorded as percentage composition of particles <2 mm (Ministry of Environment, Lands, and Parks and Ministry of Forests 1998). I used a 0.5 × 1.0 m cover board (divided into 2 0.5-m^2 squares; Nudds 1977) to estimate horizontal cover. I recorded horizontal cover readings 11.2 m from den openings, establishing my first reading in a random direction (0–360°) and taking three subsequent readings 90° from the previous (Squires et al. 2008). I estimated tree/shrub cover visually as the percentage cover of all applicable species in an 11.2 m radius circle centered on the den opening. I excluded vegetation

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data for dens old enough that vegetation cover may have changed since den excavation

(e.g., dens with vegetative growth on excavated material). Slope at the den was estimated

for a 3 m line centered on the den opening.

I measured microscale characteristics at the den site and one random point within

100 m of the den opening. At each point I recorded percentage cover of trees and shrubs;

percentage soil content; horizontal cover; and slope at the den opening using the same

methodology as my mesoscale data collection.

Data analysis

I calculated mean distance between dens using mean distance between all

pairwise den combinations. I compared attributes of den sites to random points at each

scale using mixed model analysis of variance. To account for possible dependence

between dens and proximate random locations, I treated cluster (dens and associated

random locations at both the meso- and microscales were assigned the same cluster) as a

random effect. To account for inherent variability in the data, I set α = 0.10 *a priori*

(Grosbois et al. 2008). To meet method assumptions, variables with non-normal

distributions were transformed using square root and arcsin transformations prior to

analyses. All means and standard errors from analyses are reported in untransformed

units.

Results

I located 21 grizzly bear dens (20 excavated, 1 natural cave). I located eighteen dens from aircraft or by foot and three were located using coordinates from two GPS-collared adult female bears. Mean distance between dens was 57.5 km, $SD = 31.2$ km. At the mesoscale, pixel slope for dens was about 33% steeper ($F_{1,60} = 13.33$, $P < 0.001$) than for random locations (Table 2.1). Den opening slope was nearly twice as steep ($F_{1,60} = 30.73$, $P < 0.001$) as random locations. Bears selected for greater percentage soil content ($F_{1,59} = 9.24$, $P = 0.004$) with dens characterized by 38% more soil than random locations. Bears also selected for horizontal cover ($F_{1,51} = 20.44$, $P < 0.001$), with 77% greater cover at dens than random locations. Pixel elevation and tree/shrub cover were similar (elevation: $F_{1,60} = 0.13$, $P = 0.716$; tree/shrub cover: $F_{1,51} = 2.65$, $P = 0.110$) between dens and random locations.

At the microscale level, den opening slope was about 60% steeper ($F_{1,20} = 26.05$, $P < 0.001$) than at random locations (Table 2.1). Horizontal cover at the den was 36% greater ($F_{1,17} = 5.00$, $P = 0.039$) than random locations. Percentage soil content ($F_{1,19} = 1.26$, $P = 0.275$) and tree/shrub cover ($F_{1,17} = 0.68$, $P = 0.421$) were similar between dens and random locations.

Table 2.1 Habitat attributes of grizzly bear den locations, Southern Lakes, Yukon, Canada, 2010–2011.

Scale	Variable	Den				Random			
		n	Mean[a]	SE	Range	n	Mean[a]	SE	Range
Mesoscale (1,000 m)	Pixel elevation (m)	21	1,497.24A	14.52	1,351.00–1,615.00	61	1,501.61A	15.68	1,159.00–1,786.00
	Pixel slope (°)	21	19.10A	1.63	7.00–31.00	61	14.36B	1.06	3.00–44.00
	Opening slope (°)	21	30.86A	1.80	15.00–45.00	61	15.21B	1.44	0.00–41.00
	Soil content (%)	20	60.50A	3.16	35.00–80.00	61	43.85B	3.54	0.00–100.00
	Horizontal cover (%)	18	62.28A	5.63	18.00–100.00	52	35.27B	4.24	0.00–100.00
	Tree/shrub cover (%)	18	60.61A	5.72	16.00–90.00	52	48.46A	4.06	0.00–100.00
Microscale (100 m)	Opening slope (°)	21	30.86A	1.80	15.00–45.00	21	19.33B	2.30	2.00–40.00
	Soil content (%)	20	60.50A	3.16	35.00–80.00	21	53.81A	5.89	0.00–100.00
	Horizontal cover (%)	18	62.28A	5.63	18.00–100.00	18	45.78B	7.99	3.00–100.00
	Tree/shrub cover (%)	18	60.61A	5.72	16.00–90.00	18	65.44A	4.89	32.00–100.00

[a] Means not sharing a letter within rows differed ($P < 0.10$).

Discussion

Grizzly bears in this study exhibited hierarchical den-site selection. Under hierarchical selection, animals select habitat at the largest spatial extents based on factors most limiting individual fitness, selecting for less important limiting factors at smaller scales (Rettie and Messier 2000, McLoughlin et al. 2004). Grizzly bears appeared to select dens for thermal cover at a larger spatial scale than I examined. Den elevations were above 1,100 m, which supported my prediction; however, elevation was similar between dens and random locations, suggesting selection for thermal cover (e.g., areas with increased snow depth and duration) did not occur at meso- or microscales. Denning is energetically demanding, resulting in substantial body mass loss (Hilderbrand et al. 2000, Belant et al. 2006). Grizzly bears in mountainous regions typically den at higher elevation sites with deeper snow packs because deep snow provides greater insulation in the den, reducing energetic costs of thermal regulation during denning (Craighead and Craighead 1972, Pearson 1975, Vroom et al. 1980, Servheen and Klaver 1983, Schoen et al. 1987, Ciarnello et al. 2005, Libal et al. 2011). Thus, selection for thermal cover at large spatial scales was expected.

Den security was selected at both spatial extents examined, supporting my hypotheses. Selection for steeper terrain occurred at the mesoscale, and bears selected for horizontal cover at both meso- and microscales. Observed selection suggests that risk avoidance is important at small scales, similar to striped skunk and Canada lynx (Hwang et al. 2007, Squires et al. 2008). That both of these species selected for security at smaller spatial extents than I observed in grizzly bears may be due to scale effects. Body mass determines standard and maximum metabolic rates (Peters 1983, Ottaviani et al.

2006), with increased energetic requirements of larger species resulting in greater home range sizes (McNab 1963, Schoener 1968, Perry and Garland 2002). This is particularly true among species with scattered food resources (McNab 1963, Gittleman and Harvey 1982, Haskell et al. 2002, Ottaviani et al. 2006). The large body size of grizzly bears may increase the scale at which bears respond to their environment (Mech and Zollner 2002, Perry and Garland 2002, Gehring and Swihart 2004, Holland et al. 2005), resulting in selection for security at a scale larger than smaller-bodied carnivores. Because I constrained mesoscale to 1 km surrounding dens, I was unable to address whether security influenced selection at larger spatial extents.

Den stability was important at a larger spatial extent than predicted. Selection for steeper opening slopes occurred at both spatial extents examined. Mean den opening slope and range were similar to other studies (Craighead and Craighead 1972, Pearson 1975, Harding 1976, Vroom et al. 1980, Servheen and Klaver 1983, Schoen et al. 1982, Ciarniello et al. 2005), and likely represented the range of slopes providing stable conditions for an excavated den (Vroom et al. 1980). Selection for high percentage soil content was only evident at the mesoscale, suggesting that variation in soil stability in this landscape occurs at greater than 100 m radius patch sizes. That percentage tree/shrub cover did not differ from random at either spatial extent suggests it is not an accurate metric for stability at these scales. As with security, I was unable to address if stability influenced den-site selection at larger spatial extents.

My data did not allow partitioning of dens between different age or gender classes of bears. Adult female bears may spatially segregate from adult male bears while denning to reduce risk to their reproductive investment (Libal et al. 2011). The three

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dens for which I could attribute use by gender or age class were occupied by adult females. Two of these dens had maximum observed horizontal vegetation cover and pixel slope for all three were in the upper quartile. Though insufficient to draw conclusions, these data suggest that adult females in the Southern Lakes region may select for steeper terrain and greater cover than other age/gender classes, providing segregation from adult males. Future research should incorporate age/gender class data to investigate possible segregation.

Observed hierarchical selection underscores the importance of incorporating scale dependence in grizzly bear management. To address limiting factors and provide life requisites, managers must account for how decisions affect available habitat at various scales. With respect to grizzly bear den-site selection, large-scale management in my study area should emphasize ensuring availability of high elevation habitats. Management at smaller scales should ensure availability of horizontal cover on moderately steep slopes.

CHAPTER III

DESPOTISM AND RISK OF INFANTICIDE INFLUENCE GRIZZLY BEAR DEN-
SITE SELECTION

Introduction

Animal distribution theory has two pervasive models: the ideal free distribution
and ideal despotic distribution models. The ideal free distribution model applies to non-
territorial animals and states individuals are distributed proportionately to resources
available (Fretwell and Lucas 1970). Under this model individuals assess the quality of
available habitats, and move unhindered among habitat units to select those considered
best (Fretwell and Lucas 1970). The ideal despotic distribution model applies to
territorial animals, with dominant individuals displacing subordinates from higher quality
habitats (Fretwell 1972). Subordinates' selection of habitat is therefore constrained by
the distribution and behavior of dominant individuals (Fretwell 1972). This displacement
in part forms an animal's realized niche (Belant et al. 2010). Evidence for ideal despotic
distribution has been demonstrated across a broad range of taxa (Murray et al. 2007, Oro
2008, Purchase and Hutchings 2008, Smith et al. 2011).

Risk of predation and infanticide has long been hypothesized to influence
behavior and resource selection in animals (Festa-Bianchet 1988, Bergerud et al. 1990,
Gotceitas and Brown 1993, Dahle and Swenson 2003a, Rode et al. 2006). Though

studies of evolutionary responses to risk have largely focused on predator/prey systems, evidence of these responses to conspecifics has also been found (Myllymäki 1977, Hrdy 1979, Packer and Pusey 1983, Colley et al. 1989, Gotceitas and Brown 1993, Beier 1995, Coulon et al. 1995, Van Schaik and Kappeler 1997, Ebensperger 1998, Pierce et al. 2000, Dahle and Swenson 2003a, Ferreras et al. 2004, Rode et al. 2006, Keehner 2009). For example, dispersal in juvenile field voles (*Microtus agrestis*), cougars (*Puma concolor*), and Iberian lynx (*Lynx pardinus*) apparently serves in part to reduce risk from conspecifics (Myllymäki 1977, Beier 1995, Ferreras et al. 2004). Habitat selection by juvenile Atlantic cod (*Gadus morhua*) and seal salamanders (*Desmognathus monticola*) is also affected by risk from larger conspecifics (Colley et al. 1989, Gotceitas and Brown 1993). To reduce infanticide risk by unfamiliar males, many primate species have evolved permanent male-female associations (Van Schaik and Kappeler 1997). Sexual segregation is another method by which mammal species with male-biased size dimorphism appear to reduce risk from conspecifics (Hrdy 1979, Dahl and Swenson 2003a, Rode et al. 2006). In some cases, female African lions (*Panthera leo*) and their young abandon prides and become temporarily nomadic when a new male has taken over, thus avoiding infanticide by the new dominant male (Packer and Pusey 1983). Similarly, female alpine marmots (*Marmota marmota*) and their young may shift territories when new males encroach (Coulon et al. 1995). Resource partitioning between adult male and adult female cougars with young may also reduce risk of infanticide through sexual segregation (Pierce et al. 2000, Keehner 2009). Though empirical evidence for decreased infanticide events in segregating individuals is lacking, segregated female alpine marmots did successfully wean young (Coulon et al. 1995, Ebensperger 1998). Sexual segregation

by mature females to protect young from immigrant adult males is known as the sex hypothesis of sexual segregation (Hrdy 1979, Wielgus and Bunnell 1995).

Sexual size dimorphism is common in many species, including those with polygynous and promiscuous breeding strategies and has been demonstrated to result in sexual segregation (Wielgus and Bunnell 1995, Rode et al. 2006, Keehner 2009). In bear populations, adult males are physically larger and dominant over other gender/age classes (Rode et al. 2006). Increased body size in male bears is also positively associated with within-group dominance and increased breeding opportunities (Stonorov and Stokes 1972, Kovach and Powell 2003, Bellemain et al. 2006a). Consumption of abundant, highly digestible food increases grizzly bear size and condition (Hilderbrand et al. 1999, Belant et al. 2006). Thus, individuals with access to high quality food sources benefit from increased body size, and therefore improved fitness (Hilderbrand et al. 1999).

Intraspecific predation has been observed in bear populations, in which adult males have killed juveniles (independent, non-breeding individuals) and adult females (Pearson 1975, Taylor et al. 1985, Case and Buckland 1998, Swenson et al. 2001). Although mechanisms driving intraspecific predation in bears are not completely understood, intraspecific aggression and population regulation may be involved (Pearson 1975, Bunnell and Tait 1981, Taylor et al. 1985, Case and Buckland 1998). To reduce predation risk, juvenile grizzly bears may spatially and temporally segregate from dominant, non-kin adult males (Mattson et al. 1987, Gunther 1990, Mattson 1990). Sexual segregation has also been observed in grizzly bear populations, with mature females avoiding male-occupied habitats, potentially to reduce risk of infanticide (Wielgus and Bunnell 1995). Infanticide of unrelated young may provide a reproductive

advantage for the infanticidal male, as females without young may be brought into estrous earlier and bred by the infanticidal male (Swenson et al. 1997, Bellemain et al. 2006b). In Alaska, spatial distribution of bears near salmon (*Oncorhynchus* spp.) streams appears driven by adult male bear presence, with adult females with young avoiding streams frequented by adult males (Rode et al. 2006). Seasonal range size of adult females also appears influenced by risk of infanticide in Scandinavia, where oestrous females occupy a larger area during the mating season while females with cubs select small ranges to avoid males (Dahle and Swenson 2003a).

Energetic demands of hibernation result in substantial body mass loss (Hilderbrand et al. 2000, Belant et al. 2006); therefore, it would be advantageous for all bears to locate dens near areas where food is likely to be abundant shortly after den emergence in spring. However, spatial segregation between gender/age groups of bears has been reported (Schoen et al. 1987, Haroldson et al. 2002). Juveniles and adult females, particularly females with dependent young, may be more vulnerable to predation and infanticide by male bears during hibernation (Pearson 1975, Schoen et al. 1987). Consequently, risk from conspecifics may influence den-site selection in grizzly bears. To reduce predation risk, juveniles may spatially or temporally segregate from adult males during the denning season. As infanticide is maladaptive to adult female grizzly bears, they may also modify timing and location of den sites to avoid males, as suggested for polar bears (*U. maritimus*; Derocher and Stirling 1990).

To avoid detection by adult male grizzly bears, juveniles and adult females may den at higher elevations (Schoen et al. 1987, Haroldson et al. 2002), arrive at these sites earlier (Haroldson et al. 2002, McLoughlin et al. 2002b, Manchi and Swenson 2005) and

leave the denning area later (Haroldson et al. 2002, McLoughlin et al. 2002b, Manchi and

Swenson 2005), than adult male bears. My objective was to test if spatial distribution of

grizzly bear den sites supports the ideal despotic distribution model. I also tested whether

the sex hypothesis of sexual segregation (Hrdy 1979), under the umbrella of ideal

despotic distribution theory, further explains den-site selection of adult female grizzly

bears. I predicted to reduce risk of infanticide and predation, adult females and juveniles

spatially segregate from adult males by choosing den sites at higher elevations than adult

males. I further predicted that adult females segregate to a greater extent than juveniles

to protect their reproductive investment from potentially infanticidal males.

Study Area

The study area was defined using a minimum convex polygon around known den

locations and encompassed about 7,068 km^2 of Denali National Park and Preserve

(63°3$^'$24.63$^"$ N 150°49$^'$19.44$^"$ W). Temperatures vary depending on elevation and season;

reaching 32° C in summer and dropping to -47° C in winter (Mech et al. 1998). Study

area elevations range from 152–4,116 m. The region lies partially in the rain shadow of

Denali and receives less precipitation than areas south of the mountain. Still, winter

snow pack reaches depths of about 200 cm (Mech et al. 1998). White spruce (*Picea

glauca*), birch (*Betula* spp.), and aspen (*Populus* spp.) are common tree species from

valley bottoms to about 700 m. Willow (*Salix* spp.) and alder (*Alnus* spp.) are common

from about 500 m to treeline (500–1,300 m). Mountain avens (*Dryas* spp.) mats and

lichens are abundant in tundra (≥1,000 m). Several forms of disturbance are common in

the study area, including the Muldrow Glacier, ice action (erosion due to ice flows during

spring break up) along waterways, and wildfires at lower elevations (Mech et al. 1998).

Population trends for the resident grizzly bears were summarized previously (Owen and

Mace 2006) and are generally stable, with an estimated lambda = 0.9963, *SE* = 0.0166.

The estimated mean litter size for this population is 2.03 cubs/litter, and the estimated

annual reproductive rate = 0.35, *SE* = 0.04. Cub and yearling survival rates are relatively

low at about 0.34, *SE* = 0.04 and 0.60, *SE* = 0.07 respectively. Young generally stay with

the mother for 2 years before dispersing. Subadult and adult survival rates are high at

approximately 0.96, *SE* = 0.04 and 0.96, *SE* = 0.01, respectively. In addition to grizzly

bears, the area supports populations of black bears, wolves (*Canis lupus*), caribou

(*Rangifer tarandus*), and moose (*Alces alces*) (Sheldon 1930). Though there are few

human settlements in the park, Denali National Park and Preserve receives 350,000–

460,000 visitors annually (National Park Service 2010).

Methods

Data collection

Between 1990–1998, grizzly bears were captured by Denali National Park and

Preserve staff using aerial darting and fitted with very high frequency (VHF) radiocollars

(Taylor et al. 1989). Bear ages were estimated by counting cementum annuli from an

upper premolar (Matson's Laboratory, Milltown, Montana, USA) (Craighead et al. 1970).

Bears were classified as adult female (≥5 years old), adult male (≥5 years old), or

juvenile (≤4 years old). I used age four as the cut-off for juveniles based on later

reproduction for northern grizzly bears (Leland and Miller 1980, Belant et al. 2010). Den

sites were located between September and May each winter using aerial telemetry, plotted on United States Geological Survey (USGS) 7.5 minute topographic maps, and converted to Universal Transverse Mercator grid coordinates.

Four landscape variables were used to classify the exact den locations (single pixel): land cover, elevation, slope, and aspect. Land cover was the dominant vegetation community or other surface cover type as classified by the Earth Satellite Corporation and the National Park Service (DENA Land Cover Mapping Project, ~48 m^2 pixel size, 2001). Several land cover types were combined based on vegetative similarities: open woodland spruce with open woodland/stunted spruce, broadleaf with mixed forest, alder shrub with willow shrub, low shrub/birch/willow with low shrub/sedge, dwarf shrub with dwarf shrub/rock, wet herbaceous with aquatic herbaceous, sparse vegetation with bare ground, and silty water with clear water for 12 covertypes (Table 3.1). Elevation, slope, and aspect were obtained for the pixel containing each den site using a USGS digital elevation model (US GeoData – Alaska, ~48 m^2 pixel size, 2010). Elevation of each pixel was classified to the nearest meter and slope was classified as 0–90°. Aspect of each pixel was converted from degrees to a cardinal direction (north = 316–45°; east = 46–135°; south = 136–225°; west = 226–315°; or flat) (Baldwin and Bender 2008). All landscape data was extracted using ArcMap 9.3 (Environmental Systems Research Institute, Redlands, California, USA). From initial evaluations of habitat patch size, estimated maximum location error, and pixel resolution, accuracy of resource metrics extracted was appropriate for analyses (Montgomery et al. 2010, Montgomery et al. 2011).

Table 3.1   Covertypes used to classify adult female, adult male, and juvenile grizzly bear den sites, Denali National Park and Preserve, Alaska, USA, 1990–1998.

Covertype	Description
Dense conifer forest	Dense canopy forest dominated by spruce
Open woodland spruce	Open canopy forest dominated by spruce
Broadleaf/mixed forest	Open or dense canopy forest with multiple species
Alder/willow shrub	Shrub community dominated by alder and willow
Closed low birch shrub	Dense shrub community dominated by birch
Low shrub/birch/willow/sedge	Open or dense shrub community with multiple species
Dwarf shrub	Open or dense shrub community with smaller plants
Dry herbaceous	Open herbaceous community associated with drier sites
Wet herbaceous	Open herbaceous community associated with wet sites
Sparse vegetation	Characterized by mixture of bare soil, rock, and herbaceous plants
Snow/ice	Characterized by year-round ice or snow
Open water	Lakes and ponds

Data analysis

I tested for multicollinearity ($r > 0.7$) of den-site variables to justify inclusion in candidate models. I used mixed model analysis of variance to compare den site landscape characteristics among adult female, adult male, and juvenile bears for relationships with elevation and slope. I controlled for repeated measures of bears ($n \geq 1$ den per individual) and treated year as a random effect, with bear ID nested within year. I used Tukey's range test for multiple comparisons. I compared den site aspects using chi-square analysis. I set $\alpha = 0.10$ *a priori* for all analyses, as we expected our explanatory variables to vary greatly (Grosbois et al. 2008). Land cover of den sites was summarized for each gender/age class. I also summarized variables between juvenile males and juvenile females to account for possible bias between these classes.

I used maximum entropy to model probable denning habitat (Maxent 3.3.3a;

Phillips et al. 2006, Baldwin and Bender 2008). Maximum entropy is a machine learning

method for modeling species distributions from presence-only data, in which correlates at

known locations are compared to the same correlates at 10,000 random points in the

study area. Maximum entropy minimizes relative entropy between known location data

and random point data (Elith et al. 2011). Resulting models assign a 0 to 100 value (0 to

100% probability of occurrence) to all pixels, ranking them by relative suitability.

Because maximum entropy compares presence locations to random locations, absence

locations are not needed for analysis (Johnson and Pelton 1981, Oli et al. 1997).

I created separate models for adult female, adult male, and juvenile den sites

using all variable combinations and each model was evaluated using receiver operating

characteristic (ROC) plots. The ROC plots represent a model's ability to predict den

locations and availability by plotting sensitivity against 1 – specificity (Baldwin and

Bender 2008). I used the AUC statistic to select the most accurate model. Area under

curve values range from 0.5 to 1.0, with 0.5 indicating no greater fit than expected by

chance and 1.0 indicating perfect model fit (Baldwin and Bender 2008). I calculated

standard errors for resulting AUC values by specifying that Maxent randomly set aside

30% of the den sites as test data. Maxent then used the remaining 70% of den sites as

training data to fit a model, testing model fit using the test data. One problem with the

AUC approach is that AUC values may be greatest for models with many variables even

if some of those variables have negligible influence (Baldwin and Bender 2008). To

account for this, I used a critical ratio test (Pearce and Ferrier 2000) to compare global

models to the best 1–3 variable models for each gender/age class to see if improvement

from additional variables was significant at α = 0.10. I then calculated Spearman rank

correlation coefficients between competing models, and related the resulting coefficients

to the table by Hanley and McNeil (1983) to obtain adjusted correlation coefficients (r).

These adjusted correlation coefficients were included in a critical ratio test (Pearce and

Ferrier 2000):

$$Z = A_1 - A_2 / \sqrt{[(SE_{A1} + SE_{A2}) - (2r \times SE_{A1} \times SE_{A2})]}$$

(3-1)

where A_1 is the AUC value for the highest-ranked model, A_2 is the AUC value for

a lower-ranked model, and SE is the standard error for each respective model. I

developed thresholds for probability of use by maximizing sensitivity and minimizing

specificity and converted these results to a binary response of presence or absence

(Baldwin and Bender 2008). Using the most parsimonious models, I mapped denning

habitats of adult female, adult male, and juvenile grizzly bears.

Results

From 1990–1998, 142 adult female, 36 adult male, and 35 juvenile (20 male, 15

female) den sites were located. Den-site elevation and slope were similar between

juvenile males (elevation: mean = 1,309 m, SE = 102; slope: mean = 20.2°, SE = 2.2) and

juvenile females (elevation: mean = 1,332 m, SE = 109; slope: mean = 19.4°, SE = 3.6).

Den-site elevation varied by gender/age class ($F_{2,63}$ = 2.49, P = 0.091), with adult females

denning at higher elevations than adult males (T_{58} = 2.22, P = 0.075). Juveniles denned

at elevations similar to adult females (T_{66} = 1.02, P = 0.567) and adult males (T_{66} = 1.23,

P = 0.443). Den-site slope also varied by gender/age class ($F_{2,84}$ = 4.57, P = 0.013), with

adult females denning on steeper slopes than adult males (T_{62} = 2.97, P = 0.011). Den-

site slope of juveniles was similar to adult females ($T_{111} = 1.45$, $P = 0.319$) and adult

males ($T_{105} = 1.31$, $P = 0.391$) (Table 3.2).

Bears showed non-random selection for aspect ($X^2_8 = 15.96$, $P = 0.043$) with

adult females and juveniles using east and south-facing aspects and adult males using east

and west-facing aspects more than expected (Table 3.3). Both juvenile males and

juvenile females selected east and south-facing aspects. Dwarf shrub and sparse

vegetation were the two primary land covers of den sites for all gender/age classes.

However, percentage of dens in each land cover varied, with adult female dens relatively

equally distributed (45% dwarf shrub, 36% sparse vegetation), adult male dens primarily

in the dwarf shrub class (58% dwarf shrub, 17% sparse vegetation), and juvenile dens

primarily in the sparse vegetation land cover (55% sparse vegetation, 27% dwarf shrub)

(Table 3.3). Sparse vegetation was the most common land cover class for juvenile males

and juvenile females.

For maximum entropy modeling, I found no correlation between any variables for

adult female or juvenile den sites ($r \leq 0.70$). Elevation and land cover were correlated for

adult males ($r = 0.72$), thus, I did not run models containing elevation and land cover.

Best models for predicting den site use differed among adult females, adult males, and

juveniles (Table 3.4). Based on AUC values and classification efficiency, the global

model was most parsimonious for adult females (Fig. 3.1). This model was influenced

most by elevation (contribution = 79.3%), followed by slope (12.7%), land cover (5.6%),

and aspect (2.5%). Probability of den use increased with increasing elevation from 925

to 1,523 m, gradually decreased to 1,937 m, and declined sharply thereafter (Fig. 3.2).

Probability of den use also generally increased with increasing slope to 39°, declining

thereafter. Den use was associated with east or south-facing aspects, and dwarf shrub/sparse vegetation land covers.

I selected the model containing elevation for adult males. Probability of den use increased with increasing elevation from 300 to 1,334 m and declined for areas >1,334 m (Figs. 3.1, 3.3). I selected the model containing land cover (contribution = 90.6%) and elevation (9.4%) for juveniles (Figs. 3.1, 3.4). Probability of den use was greater in areas with sparse vegetation, closed low birch shrub, and dwarf shrub land covers. There was a comparatively wide range of elevations associated with juvenile den use, with probability of use increasing with increasing elevation from 300 to 1,500 m, followed by a gradual decline.

Table 3.2   Comparisons among grizzly bear den locations and habitat correlates for adult females ($n = 142$), adult males ($n = 36$), and juveniles ($n = 35$), Denali National Park and Preserve, Alaska, USA, 1990–1998.

Variable	Adult Female		Adult Male		Juvenile	
	$\bar{x}^a$	SE	$\bar{x}^a$	SE	$\bar{x}^a$	SE
Elevation (m)	1,412A	52	1,209B	76	1,329AB	66
Slope (°)	21.9A	1.1	15.6B	1.9	18.9AB	1.9

[a] Means not sharing a letter within rows differed significantly ($P < 0.10$).

Table 3.3   Number of grizzly bear den sites by aspect and covertype for adult females ($n = 142$), adult males ($n = 36$), and juveniles ($n = 35$), Denali National Park and Preserve, Alaska, USA, 1990–1998.

Variable	Class	Adult Female	Adult Male	Juvenile
Aspect	North	22	5	4
	East	43	15	10
	South	43	5	12
	West	34	11	7
	Flat	0	0	2
Covertype	Open woodland spruce	1	3	1
	Broadleaf/mixed forest	0	0	1
	Alder/willow shrub	4	1	0
	Closed low birch shrub	0	0	1
	Low shrub/birch/willow/sedge	6	4	2
	Dwarf shrub	64	21	9
	Sparse vegetation	51	6	18
	Snow/ice	16	1	3

Table 3.4   Candidate maximum entropy models for adult female, adult male, and juvenile grizzly bear dens, Denali National Park and Preserve, Alaska, USA, 1990–1998.

Age/Sex Class	Model[a]	AUC	SE	Z	P	Threshold	Class %
Adult Female	ESVA	0.926	0.002			19.900	83
	ESV	0.923	0.002	2.957	0.003	20.334	83
	EVA	0.920	0.002	5.624	<0.001	21.666	83
	ESA	0.919	0.002	2.673	0.008	21.118	83
	EV	0.916	0.002	9.373	<0.001	19.426	81
	SVA	0.910	0.002	11.153	<0.001	29.190	83
Adult Male	E	0.880	0.013			48.141	80
	EA	0.854	0.015	2.707	0.007	41.686	80
	ES	0.851	0.013	1.562	0.118	40.990	80
	ESA	0.840	0.014	4.050	<0.001	30.542	70
	SVA	0.838	0.022	1.841	0.066	30.647	80
	VA	0.831	0.027	1.849	0.065	33.814	80
Juvenile	EV	0.841	0.011			20.152	70
	SVA	0.824	0.012	1.893	0.058	18.824	80
	ESA	0.823	0.013	1.067	0.286	31.640	70
	EVA	0.823	0.013	1.071	0.284	19.478	80
	SV	0.823	0.015	1.963	0.049	18.778	70
	ESVA	0.819	0.012	3.088	0.002	14.922	70

[a] Model abbreviations: E = elevation, S = slope, V = land cover, A = aspect.
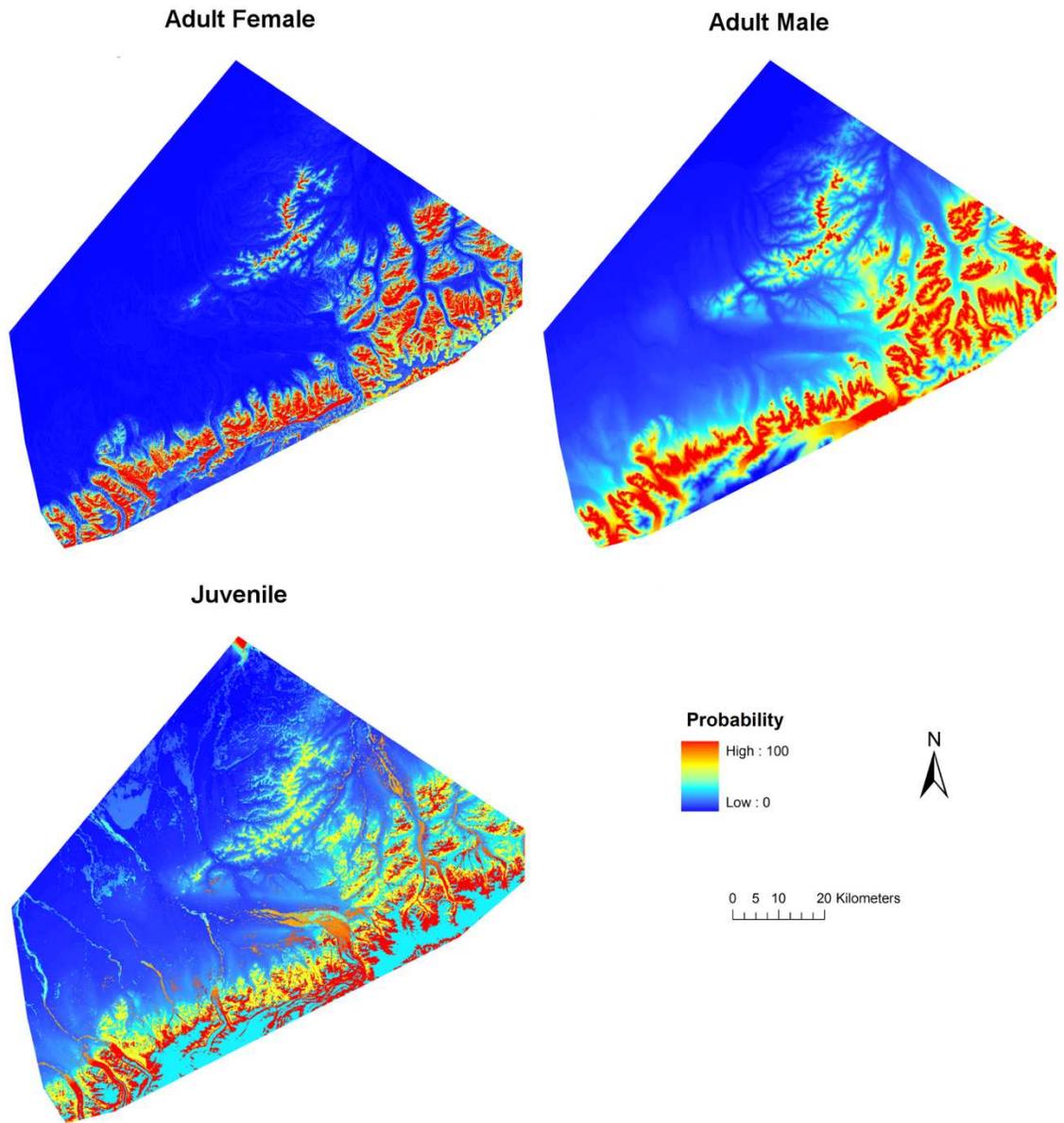
Figure 3.1   Probability of adult female, adult male, and juvenile grizzly bear denning
habitat, Denali National Park and Preserve, Alaska, USA, 1990–1998.
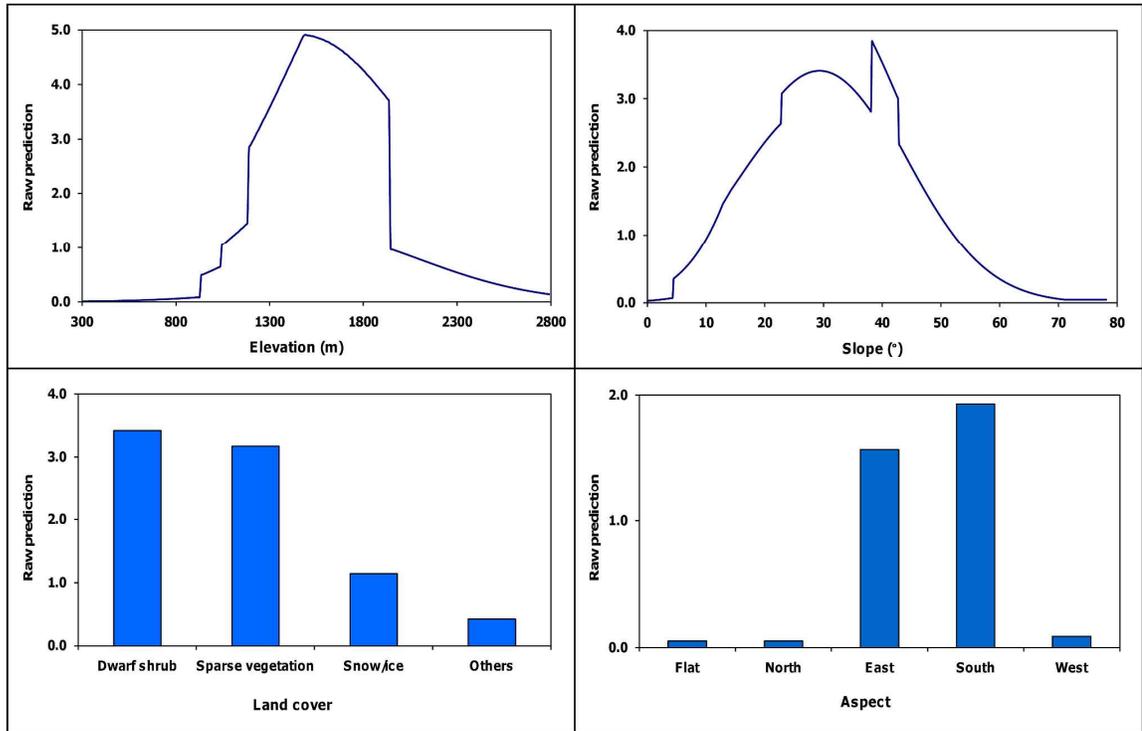
Figure 3.2   Relationships between the exponential contribution of slope, elevation, land cover, and aspect to the raw prediction score and the observed value for 142 adult female grizzly bear den sites, Denali National Park and Preserve, Alaska, USA, 1990–1998.

Figure 3.3   Relationship between the exponential contribution of elevation to the raw prediction score and the observed value for 36 adult male grizzly bear den sites, Denali National Park and Preserve, Alaska, USA, 1990–1998.

Figure 3.4   Relationships between the exponential contribution of land cover and elevation to the raw prediction score and the observed value for 35 juvenile grizzly bear den sites, Denali National Park and Preserve, Alaska, USA, 1990–1998.
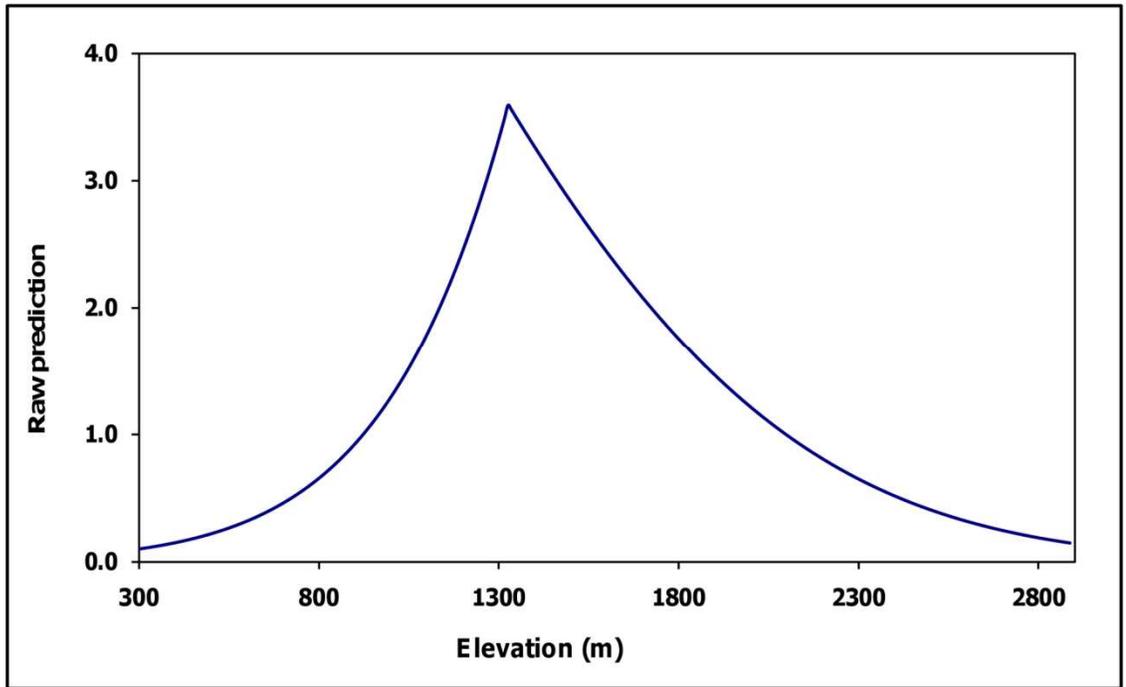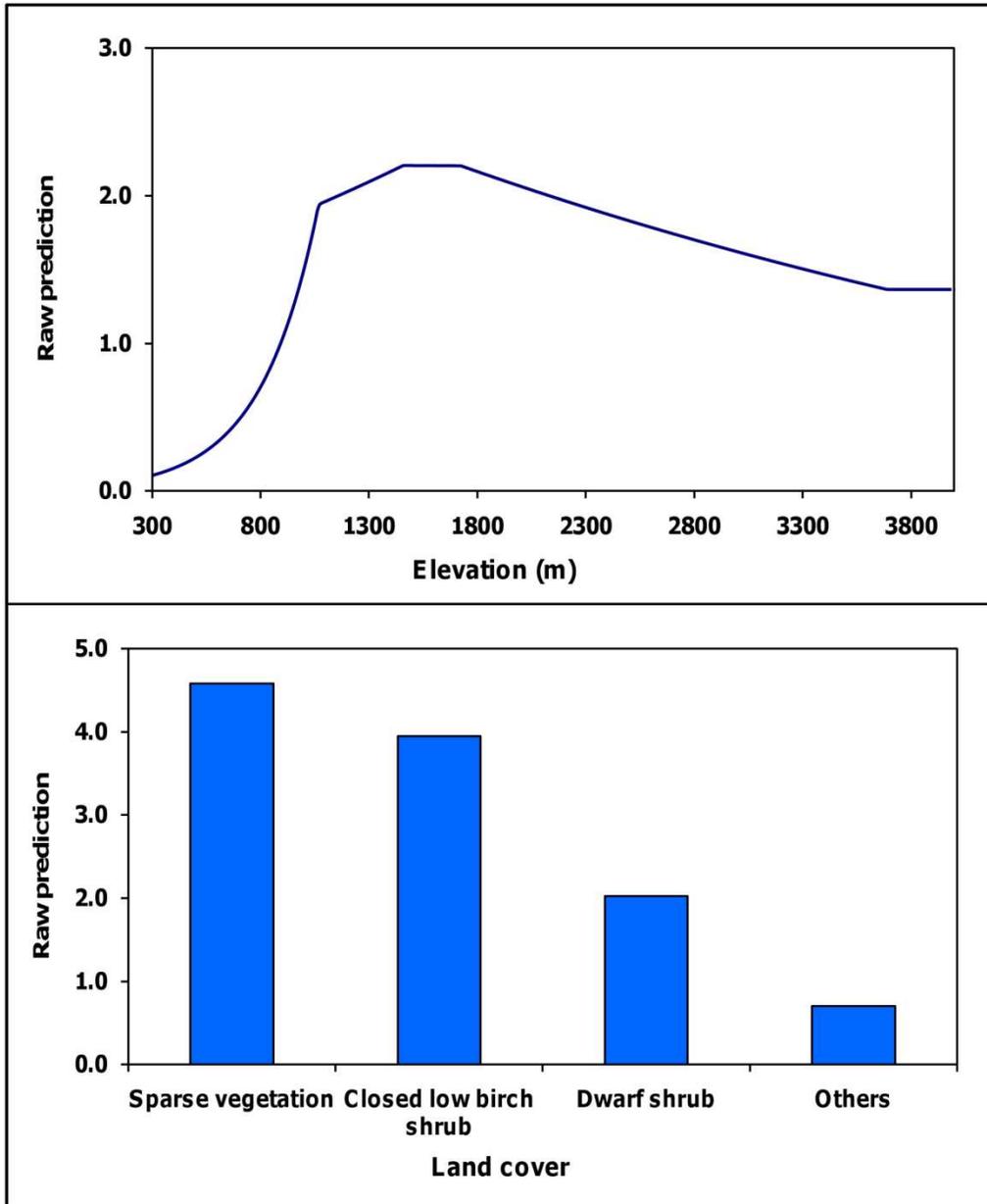
Discussion

Risk and den-site selection

Predation risk did not appear to influence juvenile den-site selection. Juveniles selected a wide range of elevations that did not differ from adult males. Thus, juvenile den-site selection did not appear to follow the ideal despotic distribution model. While it is possible that adult males selectively kill juvenile males to eliminate potential competitors and increase breeding opportunities, small sample size for juvenile den locations ($n = 35$, 20 male, 15 female) precluded rigorous testing between juvenile females and juvenile males. Thus, I was unable to test whether this potential source of predation risk affected juvenile male den location. However, my results supported the ideal despotic distribution model and the sex hypothesis of sexual segregation for adult females, in that den-site selection differed between adult females and adult males, with maximum probability of den use for adult females at higher elevations than for adult males. The sex hypothesis of sexual segregation, coupled with adult females denning for longer periods of time than adult males (Haroldson et al. 2002, McLoughlin et al. 2002b, Manchi and Swenson 2005), is the most likely explanation for observed adult female den use. As predation risk is similar for juveniles and adult females (the risk to the individual), I suggest that observed sexual segregation is a consequence of adult females avoiding adult males to reduce risk of infanticide (the added risk of losing their reproductive investment).

Although the mechanism for male den-site selection is unknown, I suggest the range of elevations selected by males was related to food availability at den emergence.

Grizzly bears in Denali National Park and Preserve emerge from dens around May (Mech et al. 1998), coinciding with caribou parturition on their calving ground in my study area (Adams et al. 1995). Den site elevation use of adult male grizzly bears overlapped extensively with the elevation range of the caribou calving ground, with greatest number of newborn calves generally occurring from 900 to 1,500 m (Adams et al. 1995). Mortality of caribou calves due to bear predation averaged 22% annually (Mech et al. 1998). I suggest this concentrated and available food source was exploited by adult male grizzly bears to increase lean body mass following den emergence (e.g., Belant et al. 2006), leading to improved condition. Improved body condition (e.g., larger size) provides males with greater breeding opportunities in many species (McCann 1981, Ruby 1984, Reid and Roitberg 1995, Bellemain et al. 2006a).

In addition to denning at higher elevations, adult females entering dens earlier and emerging later may also be in response to infanticide risk (Haroldson et al. 2002, McLoughlin et al. 2002b, Manchi and Swenson 2005). Adult females, particularly those with young, should delay denning to maximize foraging opportunities before winter as percentage body fat in fall influences proportion of lean body mass lost during hibernation, and therefore animal condition (Hilderbrand et al. 2000). However, I suggest that by moving to high elevation den locations early, adult females are further reducing the risk of infanticide, by moving through adult male denning areas before occupation by adult males. Likewise, it would be energetically advantageous for adult females to leave dens earlier to forage, because females with young lose more body mass than lone bears during hibernation (Hilderbrand et al. 2000). However, this would necessitate adult females moving through high concentrations of adult males in denning

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areas. Further, the most readily available food in the study area in early spring was caribou calves or carcasses of animals that died in winter. These concentrated food sources are likely to attract multiple bears, including adult males, similar to concentrations of salmon (Ben-David et al. 2004, Rode et al. 2006). These food resources are therefore risky for adult females with young (Luque and Stokes 1976, McLellan 1994, Chi 1999, Rode et al. 2006). Consequently, adult females may remain in high elevation dens to conserve energy, where longer snow cover increases thermal insulation and reduces energy loss, and wait for adult males to disperse from den areas and more dispersed food (e.g., herbaceous vegetation) to become available. I suggest that predation risk alone does not strongly influence den-site selection in grizzly bears. However, the added risk of infanticide appears to influence adult female den-site selection and contributes to spatial segregation between adult females and adult males.

Though not addressed in the original hypotheses, my results suggest adult females may further spatially segregate by occupying steeper slopes than adult males (Schoen et al. 1987). This difference, however, may also be an artifact of the observed elevation gradient among gender/age classes as higher elevations often exhibit steeper slopes. Though elevation and slope differed between adult females and adult males, it is important to note there was considerable overlap. I suggest that while adult females attempted to sexually segregate, they were constrained by topographic (i.e., elevation) and structural (e.g., slope) features. These requirements likely limited how high and steep adult females could den, as very steep slopes are structurally unstable and the highest elevations in the study area have permafrost or little topsoil conducive to den excavation. Adult females in this study exhibited greatest selection for a narrow band of

habitat near ridges (Fig. 3.5). Consequently, although segregation of adult females from adult males was observed, segregation may have been constrained by landscape features.

Den-site characteristics

      Elevation was an important indicator of den sites for adult females and adult males, with high probability of use associated with mid-elevation portions of the study area. These elevations likely provided good insulative snow cover while remaining free of permafrost (Pearson 1975). Although elevation was a predictor in the juvenile model, it only contributed 9.4% to model fit. The difference in contribution of elevation between juveniles and adult bears may be a consequence of inexperience. Resource use of juveniles often differs from adults and has been attributed to naïveté (Sjöberg and Ball 2000, Krebs et al. 2004), which may in part explain high observed variability in juvenile den elevation, resulting in low explanatory power.

      Slope was moderately important for predicting adult female denning habitat, contributing 12.7% to model fit. Strongest selection was for slopes between 22–39°. These values are within the range reported in other studies, and likely were selected in part for structural stability and drainage properties (Pearson 1975, Reynolds et al. 1976, Vroom et al. 1980, Servheen and Klaver 1983).

      Land cover was the best predictor of juvenile denning habitat (contribution = 90.6%). Sparse vegetation and closed low birch shrub were the most probable cover
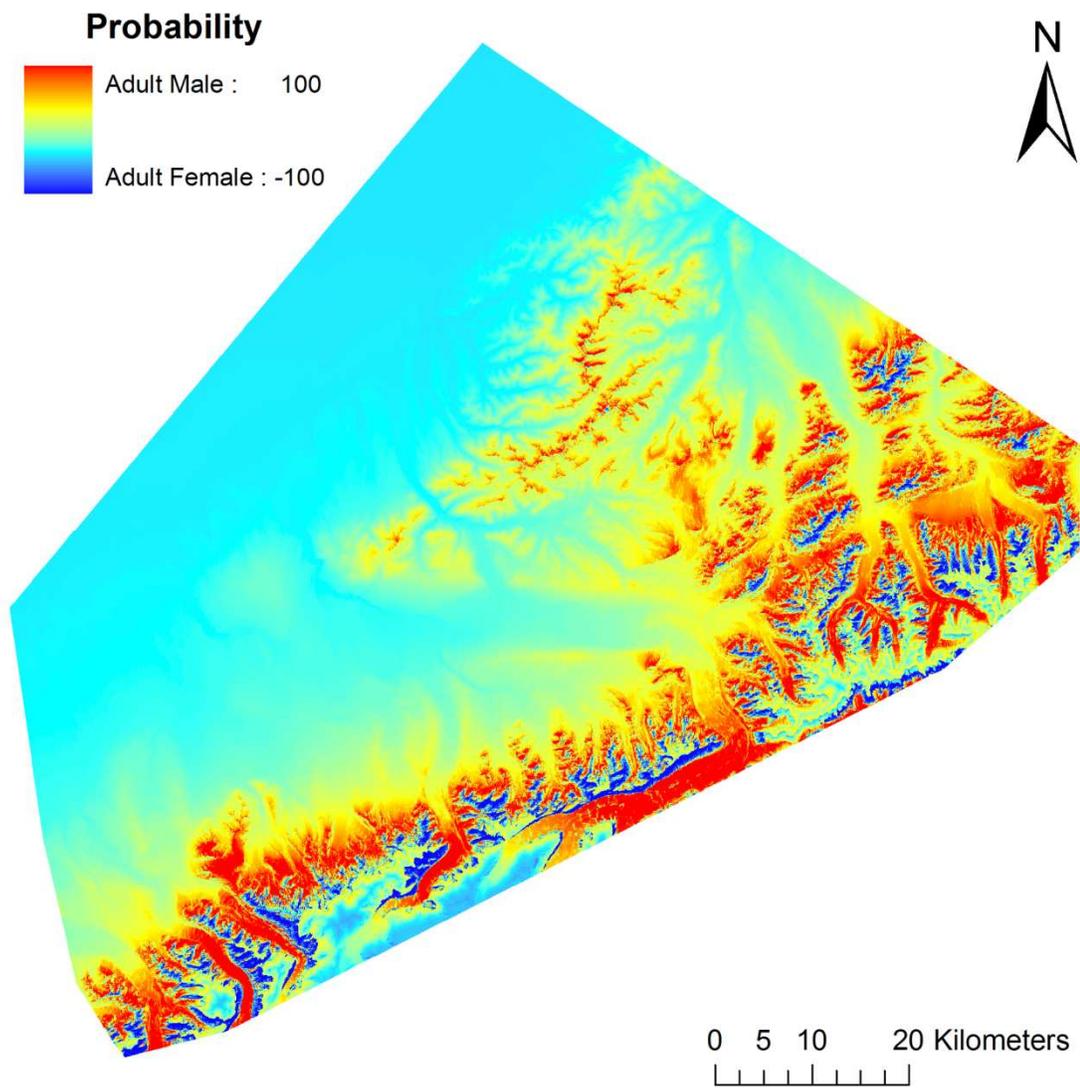
Figure 3.5   Shift in probability of suitable den locations between adult female and
adult male grizzly bears, Denali National Park and Preserve, Alaska, USA,
1990–1998.

types, followed by dwarf shrub. These covertypes are indicative of higher elevation sites generally chosen for den sites. Land cover was also present in my adult female model but only contributed 5.6% to model fit. Sparse vegetation, dwarf shrub, and snow cover types were probable denning habitat. These covertypes are consistent with den elevations, and I believe were an artifact of selection for elevation.

CHAPTER IV

CONCLUSIONS

Hierarchical habitat selection has been observed across a broad range of taxa (Bergin 1992, Rettie and Messier 2000, McLoughlin et al. 2004, Hwang et al. 2007, Squires et al. 2008, Baxter and Hauer 2011). I suggest that grizzly bears also exhibit hierarchical den-site selection. At the largest spatial extents bears appeared to select for thermal cover, suggesting thermal regulation was the most important limiting factor I evaluated for denning grizzly bears, as denning is primarily a mechanism for energy conservation (Nelson 1973, Harding 1976). Security and stability influenced selection at meso- and microscales; which of these latter factors is most limiting may depend on individual circumstances (e.g., bear age or gender, local environmental conditions).

Risk from conspecifics also influences resource selection in many species (Myllymäki 1977, Hrdy 1979, Packer and Pusey 1983, Colley et al. 1989, Gotceitas and Brown 1993, Beier 1995, Coulon et al. 1995, Van Schaik and Kappeler 1997, Ebensperger 1998, Pierce et al. 2000, Dahle and Swenson 2003a, Ferreras et al. 2004, Rode et al. 2006, Keehner 2009). With respect to grizzly bears, risk from conspecifics may contribute to spatial segregation during the denning season. This form of risk appeared to operate at a spatial scale intermediate to thermal cover and den stability. Adult male grizzly bears in Denali National Park and Preserve selected den sites in areas

with abundant, high quality food available at den emergence (i.e., caribou calves; Adams et al. 1995). I suggest adult males selected these areas to improve individual fitness and increase breeding opportunities (Hilderbrand et al. 1999, Bellemain et al. 2006a). That adult male and juvenile den-site selection was similar suggests predation risk was not a strong indicator of den-site selection by juveniles. However, risk of infanticide appeared to influence adult female den-site selection, with adult females selecting higher elevations and steeper slopes than adult males. I suggest sexual segregation is an important component of grizzly bear denning ecology, providing a mechanism by which adult females avoid infanticidal males. As adult male grizzly bears are the dominant gender/age group and adult female denning behavior appears suboptimal from an energetic perspective, observed sexual segregation supports the ideal despotic distribution model. While empirical evidence supporting sexual segregation to reduce infanticide is limited (Coulon et al. 1995, Ebensperger 1998), a growing body of literature suggests it occurs frequently across numerous taxa (Packer and Pusey 1983, Derocher and Stirling 1990, Coulon et al. 1995, Wielgus and Bunnell 1995, Pierce et al. 2000, Keehner 2009).

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