THE SPATIAL ECOLOGY AND MATING SYSTEM OF

BLACK BEARS (*Ursus americanus*) IN NEW MEXICO

by

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APPROVAL

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This dissertation has been read by each member of the dissertation committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the Division of Graduate Education.

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STATEMENT OF PERMISSION TO USE

DEDICATION

To three wonderful men with whom I have spent some of my most memorable days afield,

Mark, Don, and Dick

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GENERAL INTRODUCTION AND METHODS

Introduction

Although black bears (*Ursus americanus*) have been studied extensively throughout

North America, much concerning the social ecology and mating system of this species

remains unknown. Most studies have focused on population and spatial dynamics important

for management of this game species, and the field study which formed the basis of the

analyses in this dissertation was no exception. It was designed primarily to "study the

ecology and population dynamics of black bears for developing methods and analytical tools

to help estimate and predict trends in population size and structure in New Mexico, as

influenced by human-caused mortality and environmental variation." However, the capture

and monitoring of hundreds of bears within two distinct study areas, and subsequent analysis

of microsatellite DNA from these same bears, provided me with a variety of data with which

to investigate questions related to their social ecology and mating system.

Chapters 2 and 3 explore the spatial organization of black bear populations, and

provide necessary background for the analyses in Chapters 4 and 5. In Chapter 2, I describe

the movements and spatial interactions of resident black bears (i.e., those utilizing an

established home range) and investigate the influence of food and social factors on the

movements and interactions of males and females. In Chapter 3, I assess patterns of natal

dispersal and home range fidelity, based on radio-telemetry.   In Chapter 4, I utilize

microsatellite DNA to determine paternity of offspring and assess the influence of various

individual and population characteristics on male reproductive success. This analysis relies

heavily on a set of criteria developed from the findings in Chapters 2 and 3. Finally, in
Chapter 5, I investigate the effect of male-biased dispersal (as observed in Chapter 3) on the
spatial genetic structure of the populations to determine the potential for inbreeding.

<center>Methods</center>

The following are methods common to all or most chapters. Additional field and
analytical methods specific to the subject matter are presented within each subsequent
chapter.

Study Areas

I studied bears in two populations separated by ~475 km and tracts of unsuitable
habitat (Figure 1.1). The 310 km^2 Northern Study Area (NSA) was located in the Sangre de
Cristo Mountains of northern New Mexico. The 420 km^2 Southern Study Area (SSA) was
located in the Mogollon Mountains of west-central New Mexico.

Land use differed between the study areas. The NSA encompassed mostly private
and state lands, where recreation and cattle ranching were the primary land uses. The area
included part of Philmont Scout Ranch, a recreational high-adventure camp operated by the
Boy Scouts of America, which hosted up to 20,000 scouts each summer. It was immediately
adjacent to the towns of Eagle Nest and Ute Park, and was about 6 km from Cimarron. It
was bordered by a 2-lane highway, which received fairly high use year-round, and enclosed
numerous gravel roads, dirt roads, and trails. Access to private lands was limited and
vehicular access to the CNWA was restricted to the highway. The more remote SSA was
entirely within Gila National Forest, but included some private parcels. It was located about

3–12 km away from the closest towns of Mogollon, Alma, Glenwood, and Reserve. Livestock grazing and timber harvest were primary land uses, with some recreational use occurring during the summer and fall months. A 2-lane, partially paved loop road provided the main access into the study area. Numerous gravel roads, dirt roads, and trails were found on the study area, and access was usually unrestricted.

With the cooperation of private landowners, the entire NSA was closed to bear hunting so population dynamics could be studied in the absence of hunting. This closure was
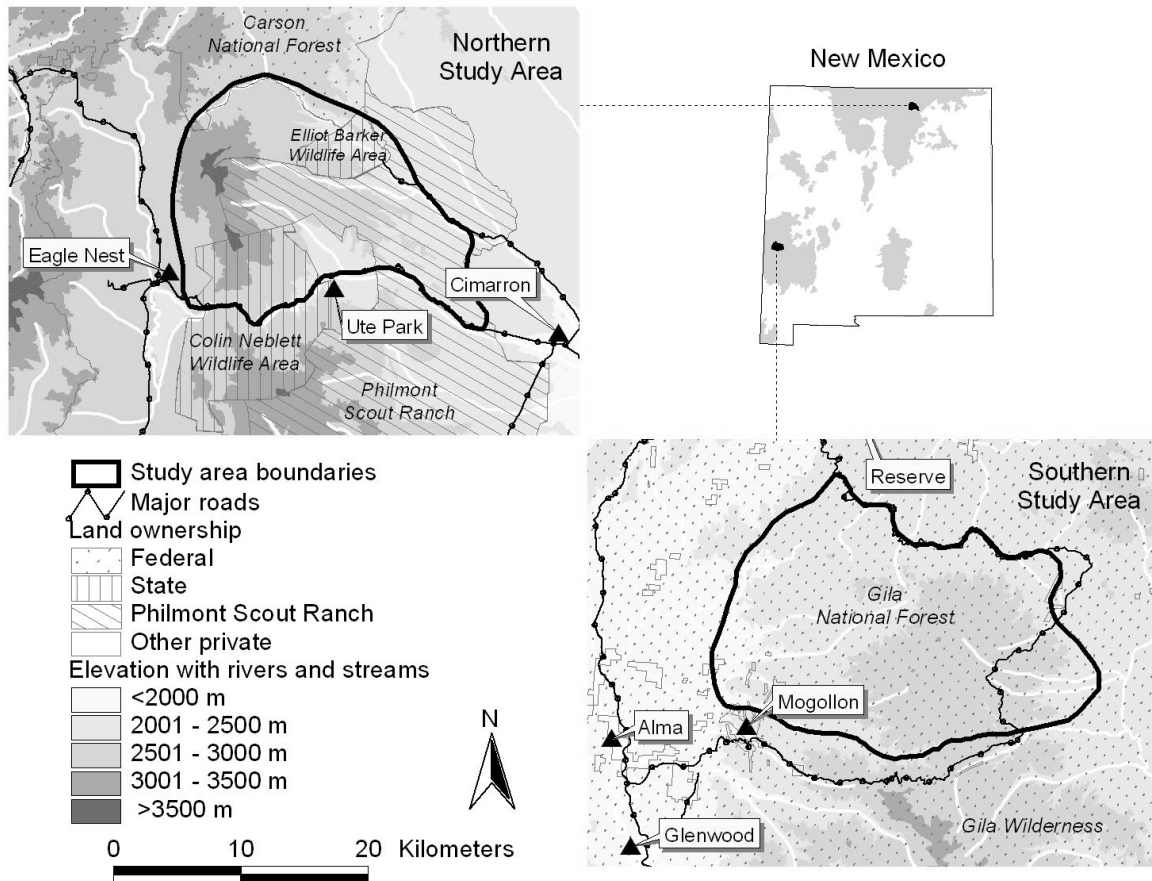
Figure 1.1. Location of the Northern and Southern Study Areas in New Mexico, showing their land ownership, terrain, and proximity to major roads and towns.

in effect from 1992 until 1998 when hunting was reestablished on some private lands. Prior to the study, state lands had been closed to bear hunting since the 1960s and the intensity of bear hunting on private land probably varied from moderate to high. The SSA was open to bear hunting throughout the study period. Historically, hunting intensity in the region was probably moderate to high. Using population reconstruction, estimated mean density of bears ≥1 year old was 17.0 bears/100 km^2 in the NSA and 9.4 bears/100 km^2 in the SSA (Costello et al. 2001).

Dominant habitat types in both areas included pinyon–juniper (*Pinus edulis–Juniperus* spp.) woodlands; oak–mountain mahogany (*Quercus* spp.–*Cercocarpus* spp.) scrub; ponderosa pine (*P. ponderosa*), mixed conifer (*Pseudotsuga menziesii–Abies concolor*), aspen (*Populus tremuloides*) and spruce–fir (*Picea engelmannii–Abies lasiocarpa*) forests; and meadows of mixed grasses (*Festuca* spp., *Muhlenbergia montana*, *Bouteloua* spp., and *Poa* spp.). Elevations ranged from 2,070 m to 3,793 m in the NSA and 1,750 m to 3,035 m in the SSA. Both areas included numerous permanent streams. In the SSA, some smaller streams were ephemeral, drying out annually or in drought years. Numerous constructed dirt tanks were found within the both areas, providing permanent or seasonal water for cattle and wildlife.

Climate varied with elevation, with slightly warmer and drier condition in the SSA (Table 1.1). Mean January temperatures were at or below freezing and snowfall was high in the upper elevations, especially in the NSA. July temperatures were generally mild with most rainfall occurring during July–August (Western Regional Climate Center [WRCC] 2001).

Table 1.1. Climate variables recorded at weather stations closest to the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico, 1939–2000.

Parameter	NSA		SSA	
	Eagle Nest (2506 m[a])	Cimarron (1939 m)	Beaverhead (2023 m)	Glenwood (1432 m)
Mean Jan temperature (^{0}C)	-7	0	-1	5
Mean Jul temperature(^{0}C)	16	21	19	24
Frost-free season (days)	70–120	145–190	110–155	180–230
Annual precipitation (cm)	37.8	41.4	37.6	40.4
Monthly snowfall Dec–Mar (cm)	25.4	15.0	10.5	4.0
Monthly rainfall Jul–Aug (cm)	6.9	7.0	6.6	6.8

[a] Elevation of weather station

Capture and Radio-telemetry

Between September 1992 and June 2000, 516 individual bears (198 F, 290 M, 28 unknown) were marked or uniquely identified, by means of trapping and den investigations, detailed in Costello et al. (2001), Costello et al. (2003), and Inman et al. (2007). The field team and I captured 300 individuals 517 times during active season trapping. Nearly all captured adult ($\geq$5 years) and subadult (2 – 4 years) females were radio-marked with collars or ear-tag transmitters ($n = 99$), but adult males were radio-marked as needed to maintain a sample of about 10 individuals each year ($n = 53$). Initially, captured subadult males were also radio-marked ($n = 29$), but only during 1992–1994. Using telemetry to locate dens, we handled or observed 342 bears in dens 683 times to document reproduction and fit or refit collars. Yearling females ($n = 28$) and males ($n = 30$) were radio-marked in the den when accessible. We chemically immobilized adult, subadult, and yearling bears, but handled 6- to 8-week-old cubs in the den without immobilization.

During trapping and den work, bears were sexed, measured, and marked with eartags and lip tattoos. We estimated age (based on body size and tooth eruption, wear, and coloration) and extracted a vestigial premolar tooth from most bears ($n = 292$) for age determination using cementum annuli counts (Willey 1974). We noted signs of estrus, lactation, or presence of offspring for female bears. We noted presence of wounds (lacerations and punctures) apparently inflicted during fights with other bears.

Radio-marked bears were located from fixed-wing aircraft on a 14-day schedule during the active season (i.e., outside of hibernation). We recorded locations using Universal Transverse Mercator (UTM) grid coordinates to the nearest 0.1 km, on U. S. Geological Survey 7.5-minute maps. We obtained 5,723 radio-telemetry locations for 239 bears (127 females, 112 males).

Microsatellite DNA Analysis

We collected samples from 430 bears (83% of individuals) to obtain microsatellite genotypes. During all years, we collected tissue samples obtained from punching holes in ears for ear-tagging ($n = 377$). Samples collected before 1998 were frozen, those collected after 1998 were stored in lysis buffer (Longmire et al. 1997). In addition, we froze whole blood obtained from bears captured during 1992-1996 ($n = 50$). Beginning in 1997, hairs with fresh follicles were pulled and stored in envelopes with silica dessicant beads ($n = 320$).

I extracted DNA from 1–4 samples for 422 individuals, with a preference for blood or tissue when available (samples were misplaced for eight individuals). I extracted DNA using DNEasy blood and tissue kits (Quiagen, Valencia, California, USA). I numbered DNA extractions separately from bear identification numbers, therefore the process of genotyping

repeated samples from the same bear was blind. The laboratory team and I amplified 11

microsatellite loci previously shown to have useful heterozygosity in bear populations:

CXX20 (Ostrander et al. 1993), G1D, G10L, G10P (Paetkau et al. 1995), G10J, G10O

(Paetkau et al. 1998), UarMu05, UarMu10, UarMu15, UarMu23, and UarMu59 (Taberlet et

al. 1997). Each polymerase chain reaction (PCR) contained ~50 to 150 ng of extracted DNA.

All 11 loci PCRs, with 5' end fluorescently-labeled forward primer, were performed using

the DNA Engine DYAD thermal cycler (Bio-Rad Laboratories) and visualized with the

3100-Avant Genetic Analyzer (Applied Biosystems). All PCRs contained 1X Gold Buffer,

locus-specific $MgCl2$ concentration (1.5–2.5 mM), 200 ng/μL bovine albumin serum (BSA),

1.0 mM dNTPs, 2.0 μM each of forward-labeled and reverse primers, 1.0 Unit AmpliTaq

Gold DNA Polymerase (Applied Biosystems), and deionized water for a constant reaction

volume of 15 μL. Following optimization, the thermal profile consisted of one cycle at 95°C

for 10 min, followed by 45 cycles at 95°C for 30 s, a locus-specific annealing temperature

(48–57°C) for 30 s, 72°C for 45 s, and a final extension at 72°C for 30 min. We combined

four loci into two PCR duplexes (Cxx20 with G10O and UarMU05 with UarMU23). PCR

products were combined, on the basis of size and fluorescent labeling, into three pools of 3–5

loci each for visualization, consisting of (1) G10L, G10P, G10H, and Mu59; (2) Cxx20,

G10O, G10J, UarMU05, and UarMU23, and (3) G1D, UarMU10, and UarMU15. All allelic

calls (i.e., determinations of the presence and size of an allele) were made using GeneMapper

3.7 (Applied Biosystems) with automatic allelic call setup. In addition to automatic allelic

calls, all allelic calls were manually checked for accuracy. We discarded entire multi-locus

genotypes when <8 of 11 loci amplified successfully for a particular sample ($n = 30$ or 6% of

476 total samples). Among the remaining samples, we calculated a genotyping error rate of

0.01 errors per allele by comparing genotypes of 41 pairs of samples taken from the same

individual. This error rate does not include the potential for alleles to match despite both

being incorrect. If errors are independent, this would occur in only one of 10,000

comparisons.

A COMPARISON OF THE MOVEMENT PATTERNS OF MALE AND FEMALE BLACK BEARS: ARE THEY GOVERNED BY FOOD OR SOCIAL FACTORS?

Abstract

I analyzed movements and dynamic interactions of 60 female and 17 male black bears, to test the hypothesis that space use by male black bears is driven by social factors during the mating season (den emergence–20 Jul) and food during fall hyperphagia (21 Jul–den entry), while that of female bears is driven by food throughout the year. As predicted, males moved slightly larger distances and exhibited higher attraction toward other males when estrous females were more limited during the mating season. Also as predicted, males moved 10–26% farther and exhibited lower attraction to other bears when oak production failed during the mast season. Contrary to my prediction, the presence of cubs was an equal if not greater influence than food on the movements and interactions of females. Despite having greater metabolic needs, females with cubs moved significantly smaller distances than other females and exhibited avoidance or reduced attraction to males during both seasons. Low food indices were associated with only slight increases in female movement parameters and interactions during the mating season, but a 25% increase in the median distance from home range center during the mast season. Evidence suggests both sexes utilize areas larger than necessary for fulfilling immediate metabolic needs. I suggest both sexes benefit from knowing and utilizing a large home range by the ability to efficiently exploit its resources using scramble competition. As a consequence, within-sex spacing patterns are similar for males and females, despite the different strategies employed for increasing their fitness.

Introduction

In selecting and utilizing a home range, an animal must take into account the needs of food, cover, and mates (Burt 1943). In polygynous mammals, where females assume the sole burden of raising offspring, food is most often assumed to be the primary factor determining movements and home range size of the females. In contrast, because males are capable of increasing their fitness through multiple mating, their movements and home range size are presumed to be governed by the distribution of both mates and food (Ostfeld 1985, 1986, Ims 1987, Wauters and Dhont 1992).

In black bears, and other bear species that hibernate, the central role of food may be intensified, due to the fact that bears must fulfill their annual energetic needs in the months that they are active. Throughout the hibernating period, usually lasting from 4–6 months, bears live entirely off stored body fat, and parturient females assume the added burden of lactation for approximately 3–4 months (Hellgren 1998). Strong correlative evidence of a negative impact of food shortage on cub production (Rogers 1976, Eiler et al. 1989, Elowe and Dodge 1989, McLaughlin et al. 1994, Costello et al. 2003) also supports the general assumption that use of space by black bears is largely tied to food, at least for females (Jonkel and Cowan 1971, Amstrup and Beecham 1976, Lindzey and Meslow 1977, Garshelis and Pelton 1981). Still, the large size of male home ranges, typically larger than expected based on the energetic demands of their body size relative to that of females (Sandell 1989, Powell et al. 1997, Koehler and Pierce 2003), suggests the distribution of potential mates may also be important in determining their movements (Rogers 1987a, Powell et al. 1997). Emphasizing this contrast between the sexes, Amstrup and Beecham (1976) claimed "it is

advantageous for male bears to be mobile and occupy large areas that overlap the ranges of many female bears…female bears should be less mobile than males and should occupy areas no larger than necessary to assure adequate nutrition for self-maintenance and development of young."

In a study of brown bears (*Ursus arctos*), Dahle and Swenson (2003) refuted the notion that female home range size was explained solely by metabolic needs, on the basis that home ranges of females with cubs-of-the-year were smaller than those of lone females and home ranges of females with yearlings did not differ from those of lone females. Although data is limited, studies of black bears have also generally documented smaller movements or home range size for females with cubs compared to other females, especially during the spring (Piekielek and Burton 1975, Lindzey and Meslow 1977, Hellgren and Vaughan 1990, Smith and Pelton 1990, Hirsch et al. 1999). However, exceptions to this pattern have been reported. Garshelis and Pelton (1981) detected no difference in home range size relative to offspring, and Alt et al. (1980) found that home range size was larger for individual females during periods when they were accompanied by offspring (either cubs or yearlings) compared to periods when they were not, but acknowledged a brief period of limited movements when cubs were very small. Limited mobility of young cubs is the standard explanation for the smaller movements of family groups, however it might also be explained by avoidance of other bears. Thus, it may be prudent to further investigate the determinants of female movements.

Seasonal shifts in movements or home range have been widely reported (Lindzey and Meslow 1977, Garhelis and Pelton 1981, Hellgren and Vaughan 1990, Smith and Pelton

1990, Samson and Huot 1998). But, with a few exceptions, some of the earliest radio-telemetry studies (often plagued by small numbers of bears monitored for short periods) still stand as the only published work to describe movement rates (Amstrup and Beecham 1976, Alt et al. 1980, Young and Ruff 1982, Garshelis et al. 1983, Warburton and Powell 1985, Rogers 1987a, Hirsch et al. 1999) or spatial interactions (Lindzey and Meslow 1977, Garshelis and Pelton 1981, Horner and Powell 1990, Samson and Huot 2001). In addition, many recent studies have focused predominantly or exclusively on females, but a comparison of the sexes can be a powerful tool to identify the factors most strongly controlling movements and space use.

My first goal is to utilize radio-telemetry data obtained during 1992–2000 within two regions of New Mexico to provide a comprehensive description of the movements and spatial interactions of black bears in arid New Mexico. My second goal is to compare the relative importance of food and social factors in determining the seasonal movements and spatial interactions of male and female bears. I hypothesize that space use by male bears is driven by social factors during the mating season and food during fall hyperphagia, while that of female bears is driven by food throughout the year.

Methods

Home Range Analysis

I compiled the following locations for each bear: active season telemetry fixes, capture and recapture sites, den locations, and mortality sites. Recapture locations were excluded if the bear was captured more than once at the same trap site during the same

trapping period. I restricted home range and movement analyses to those individuals with

$\geq$30 total locations and whose site fidelity indicated they were resident bears (see Chapter 2;

$n = 60$ females, $n = 17$ males). Preliminary analysis indicated that estimates of home range

size asymptoted around thirty fixes, so inclusion of bears with fewer than thirty fixes would

underestimate the true extent of their typical movements.   Among these bears, the

monitoring period averaged 4.4 years (range 1.9–7.3) and the number of locations averaged

53.4 (range 30–100).

It was obvious from field experience and a superficial examination of the spatial data

that resident bears in New Mexico, like bears elsewhere, usually concentrated their activity

within a relatively small area of multi-annual use during the spring and summer, but often

traveled widely during fall hyperphagia (Lindzey and Meslow 1977, Garhelis and Pelton

1981, Hellgren and Vaughan 1990, Smith and Pelton 1990, Samson and Huot 1998). For

home range analysis, my primary interest was defining this core area of multi-annual use, as

well as estimating a home range center. I used the kernel method (Silverman 1986) to

delineate 50% core home ranges (CHR) and 95% total home ranges (THR), using the Animal

Movements 2.0 extension (Hooge and Eichenlaub 2000) developed for use with ArcView 3.3

software (Environmental Systems Research Institute, Redlands, California). Initially, I

estimated the smoothing parameter using the reference smoothing parameter (h_{ref}) or least

squares cross validation (LSCV; Silverman 1986). However, I found the CHR was under-

smoothed for individuals that made few fall excursions and over-smoothed for individuals

that made frequent fall excursions. Although I understood the extent of long-range fall

movements should influence my estimate of THR, I did not believe these movements should unduly influence CHR. Therefore, I fit kernel ranges with a common smoothing parameter (see Breed et al. 2006 and Forester et al. 2006 for other examples) for each sex representing the rounded mean value of h_{ref} (3800 m for males and 1800 m for females) and found that this method provided me with the most realistic and consistent representation of the CHR (see Figure 2.1 for examples). I summarized home range size by sex, and compared overlap of CHR for pairs of neighboring individuals (i.e., overlap ≥ 0.01) occupying their range at the same time.
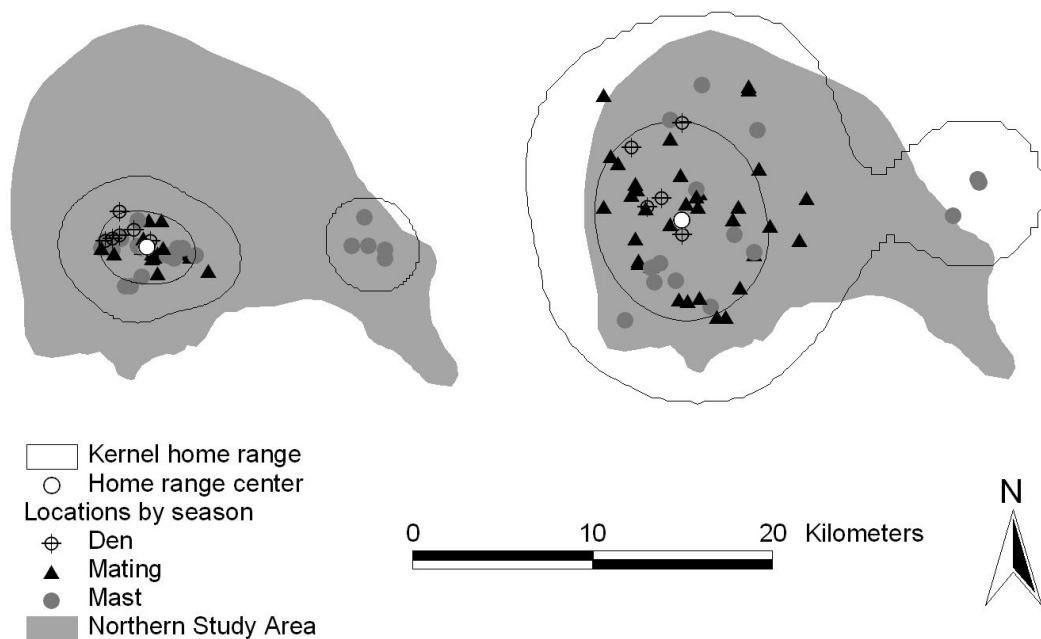
Figure 2.1. Examples of average-sized, multi-year kernel home ranges for female (left) and male (right) black bears in New Mexico. Bears were typically located within the core area during the mating season (den emergence–20 Jul), but often traveled widely during the mast season (21 Jul–den entry).

Movement Analysis

I described the annual movement patterns based on monthly periods, but undertook more detailed analysis based on season (mating or mast). The mating (i.e., pre-mast) season (den emergence–20 Jul) spanned the period of observed mating activity (which probably peaked in June) and was characterized by low availability of fruits and nuts. The mast season (21 Jul–den entry) began with the first ripening of summer fruits and continued throughout the fall, when mast from oak, juniper, and pinyon became available.

Movement analysis involved two parameters. The first parameter was the distance between each location and the home range center (i.e., activity radius, $n = 4013$; Dice and Clark 1953). I estimated the home range center as the center coordinates of the 50% kernel contour using a function of the Animal Movements extension that attributes polygon shapefiles with their center coordinates. When ranges were represented by two contours, the home range center was identified as the center of the contour that contained predominantly mating season locations.

The second parameter was distance between successive locations. We typically monitored bears every two weeks, so I restricted these analyses to observations when days between successive locations ranged from 7–21 days ($n = 2861$). Mean days between locations was 13.3 for this sample. The midpoint between successive locations was used to assign season for each observation. I used a natural log transformation to obtain normal distributions for distance from center and successive distance, thus analyses were based on the median.

Dynamic Interactions Analysis

I used the dynamic interactions routine in Ranges 6 (Kenward et al 1993) to obtain an estimate of the tendency for pairs of individuals to be close together at the same time within seasons. Using the Jacobs index (Jacobs 1974), this routine compares the mean distance between observed "same time" locations for a pair of individuals to the mean distance between all pairs of locations for these same individuals. Jacobs index values range from -1 to 1. Values closer to -1 indicate avoidance (i.e., observed mean distance was greater than expected), while values closer to 1 indicate attraction (i.e., observed mean distance was less than expected). I defined same time locations as those that were obtained on the same day (usually during the same telemetry flight of 2–4 hours) and used the index based on the geometric mean (Walls and Kenward 2001). I restricted this analysis to pairs of bears that had a reasonable chance of interacting, which I defined as CHR overlap of ≥0.20. I excluded pairs of bears with <5 locations obtained at the same time, thus number of same time locations per season, ranged from 5–36, with a mean of 13.6.

Analysis of Food Versus Social Factors

I assigned a variety of annual and individual explanatory variables (Table 2.1), pertaining to food or social factors, to the location data (see below). My movement response variables (median distance from center and median successive distance) were based on multiple observations for each individual that varied over time for the explanatory variables. In contrast, my dynamic interaction response variable was a single index for each pair of individuals calculated separately for each explanatory variable. Due to this difference in the nature of the data, I used two different approaches to determine which explanatory variables

Table 2.1 Explanatory variables (and their signs) predicted to influence movements and dynamic interactions of black bears, during the mating season (den emergence–20 Jul) and mast season (21 Jul–den entry), based on whether food or social interactions were more important.

Sex	Season	Food	Social factors
Male	Mating	AGE (+), PRECIP (-)	AGE (+), ESTRUS (-)
	Mast	AGE (+), OAK (-)	
Female	Mating	AGE (+), OFFSPRING (+), PRECIP (-)	OFFSPRING (-)
	Mast	AGE (+), OFFSPRING (+), OAK (-)	OFFSPRING (-)

were most important in determining space use and interactions. I used model selection (Burnham and Anderson 2002) to analyze the effects of explanatory variables on the size of movements, but used traditional hypothesis testing to determine whether or not each covariate affected the Jacobs index of dynamic interactions. For model selection, I formulated a set of candidate mixed-effects models (with bear as a random factor) for each response (Table 2.2) and used Akaike information criteria (AIC) to compare models. Because some explanatory variables were sex-specific, I ran male and female models separately. For dynamic interactions, I divided the data into two groups relative to each explanatory variable and ran the routine separately. Restricting analysis to pairs of bears observed in both groups, I then used paired-t tests to determine if there was a difference in the Jacobs index relative to the explanatory variable. This analysis was run separately for male-male, female-female, and male-female pairs.

The first explanatory variable was AGE. I obtained cementum annuli age estimates ($n = 76$) or field-based age estimates ($n = 1$) for all bears in the analyses. Age ranged from 0–27 years for females and 3–23 years for males. My estimates of age were generally

Table 2.2. Set of candidate model for predicting movements of male ad female black bears during the mating season (den emergence–20 Jul) and mast season (21 Jul–den entry).

Model	Male		Female	
	Mating	Mast	Mating	Mast
AGE	X	X	X	X
PRECIP	X		X	
PRECIP + AGE	X		X	
ESTRUS	X			
ESTRUS + AGE	X			
ESTRUS + AGE + PRECIP	X			
ESTRUS + PRECIP	X			
OFFSPRING			X	X
OFFSPRING + AGE			X	X
OFFSPRING + AGE + PRECIP			X	
OFFSPRING + PRECIP			X	
OAK		X		X
OAK + AGE		X		X
OAK + OFFSPRING				X
OAK + AGE + OFFSPRING				X

reliable (Costello et al. 2004) and available for each bear during each year. In contrast, we obtained only periodic measures of weight or chest girth. As age and body size were correlated (see Chapter 4), I resolved to use age, but not body size as a covariate. In the mixed models predicting movements, I entered AGE as a continuous variable with a quadratic function, allowing for an asymptote or decline associated with physical senescence. I did not examine dynamic interactions relative to age. I presumed if food was a determinant

of space use, movements would be positively associated with age as larger bears would require larger areas to fulfill their nutritional requirements. If social factors determined space use, mating season movements of males might be positively associated with age, as older, larger males might be successful in mating with more females over a larger area (Table 2.1).

Presence of offspring (OFFSPRING) was assigned as follows: no offspring, cubs, yearlings, or unknown. We documented the reproductive status of nearly all females during visits to winter dens (except if dens were not found or were inaccessible), but the status of newly captured bears (i.e., those not previously observed in the den) was only known if offspring were observed at the capture site. For females known to have cubs in the den, I used different criteria for assigning reproductive status during the two seasons to account for cub mortality. Cub survival averaged only 55%, however I was unable to establish when cubs were lost by individual females. As many females that lost entire litters were known to have bred again, I made the assumption that most cub mortality occurred during the mating season. For females with cubs during the observation year and yearlings during the following year, OFFSPRING was assigned as cubs for both seasons of the observation year. For females with cubs during the observation year, but no yearlings during the following year, OFFSPRING was assigned as cubs during the mating season and no offspring during the mast season. Yearlings become independent of their mother during the pre-mast season, therefore OFFSPRING was assigned as yearlings only for the pre-mast season. OFFSPRING assignments among the female observations were 41% no offspring, 36% cubs, 21% yearlings, and 2% unknown during the pre-mast season, and 68% no offspring, 23% cubs, and 9% unknown during the mast season. I entered OFFSPRING as a indicator variable in

the mixed models. For analysis of dynamic interactions, I ran the data separately for pairs when no cubs were present and for pairs when cubs were present with one or both females. If food was the determinant of space use, the energetic needs of females with offspring would necessitate use of larger areas than those of lone females, thus movements and interactions would be positively associated with OFFSPRING. If social factors determined space use, females with cubs would reduce movements to avoid encounters with other bears, thus movements and interactions would be negatively associated with OFFSPRING (Table 2.1).

I assigned an estimate of the annual proportion of females in estrus (ESTRUS) to each male observation during the mating season. I calculated ESTRUS using reproductive data obtained during den visits during the following winter and expressed it as $1-P_Y$, where P_y = the proportion of adult females with yearlings (I presumed any mature female that did not have cubs throughout the observation year was available for breeding). I obtained estimates ranging from 0.60–1.00 with a mean of 0.78. The estimates fell into two distinct groups, those below the average (actually ≤0.73) and those above the average (actually ≥0.84), so I entered this as a categorical variable for low or high proportion of females in estrus. Low and high proportion accounted for 59% and 41% of the sample. I presumed males would be compelled to range over larger areas to locate potential mates when a lower proportion of females were in estrus, thus movements would be negatively associated with ESTRUS. In addition, more males would be attracted to the same females during years when a lower proportion of females were in estrus, therefore male-male interactions would also be higher during those years (Table 2.1).

During spring and summer in New Mexico, the bear diet is dominated by grasses and forbs (Costello et al. 2001). We did not conduct any surveys to quantify the annual abundance of these foods, but I supposed the biomass of plant foods would be determined by moisture. Thus, I used precipitation (PRECIP) as an index of food abundance and determined whether precipitation was above or below long-term averages (dating back to 1939 or earlier). I obtained monthly total precipitation records for two weather stations near each of my study areas (Eagle Nest and Cimarron 4 SW for the NSA, Beaverhead R S and Glenwood for the SSA; WRCC 2001). I used data for Jan–Jul (of the observation year) and Oct–Dec (of the previous year) for the years 1993–1999. Summing precipitation across these months would account for winter snow and spring and early summer rainfall. Months with >5 days of missing data were omitted from long-term averages (WRCC 2001), so I used the same rule for my analysis. I substituted the long-term average for the observed value for those months with >5 days of missing data (18 of 280 [6%]), unless the average was less than the observed value. Summing the 10 months of precipitation, I classified each year as above or below the average, and by the number of substituted months. The two weather stations near each study area were in agreement (as to above or below average) for 12 of 14 (86%) pairs of observations. For years when observations were not in agreement, I used the data from the station with fewer months with missing data or the station at higher elevation (where more bears resided). Observations were equally divided between above and below average precipitation. If food was a determinant of space use, I predicted below-average precipitation would result in lower plant biomass and promote use of larger areas by bears in

search of food. Thus movements and interactions would be negatively associated with PRECIP (Table 2.1).

During the mast season, bears foraged on various mast-producing plants, of which oaks were most important for determining body condition, natality, and recruitment (Costello et al. 2001, Costello et al. 2003). Specifically, failure of acorn crops resulted in 60–70% reductions in reproductive rates compared to other years. We conducted annual surveys of mast production in each area (see Costello et al. 2003). For the present analyses, I assigned each mast season location as to whether or not it occurred during a year of oak failure (OAK). Observations consisted of 26% oak failure and 74% non-failure. Again, if food was a determinant of space use, I presumed oak failure would promote use of larger areas by bears in search of food. Thus, movements and interactions would be negatively associated with OAK (Table 2.1).

Overall, I predicted that the best models would include different explanatory variables depending on whether food or social factors influenced space use, as outlined in Table 2.1. As food was hypothesized to be the driving factor for females throughout the year, I predicted the best models would include AGE, PRECIP, OAK, and OFFSPRING. Again, as the energetic needs of females with offspring would necessitate use of larger areas than those of lone females, I hypothesized the coefficient for OFFSPRING would have a positive sign. Based on my hypothesis that space use by male bears would be driven by social factors during the mating season and food during fall hyperphagia, I predicted best models would include AGE and ESTRUS during the mating season and AGE and OAK during the fall.

Results

Estimated size of the CHR varied from 65.5–118.2 km^2 for males and 13.4–42.2 km^2 for females. Median CHR size was 87.1 km^2 for males and no difference was detected between study areas ($F_{1,15} = 0.413$, $P = 0.53$). Median CHR size of females was smaller in the NSA (16.6 km^2) than in the SSA (18.7 km^2; $F_{1,58} = 5.19$, $P = 0.03$). For neighboring bears, within-sex overlap of the CHR was comparable between males and females (Figures 2.2 and 2.3). Median overlap of a female by a neighboring female was 0.16 (range 0.01–0.97) and overlap of a male by another male was 0.25 (range 0.01–0.78). Median overlap of females by males was 0.59 (range 0.04–1.0), but median overlap of males by females was only 0.10 (range 0.01–0.51).
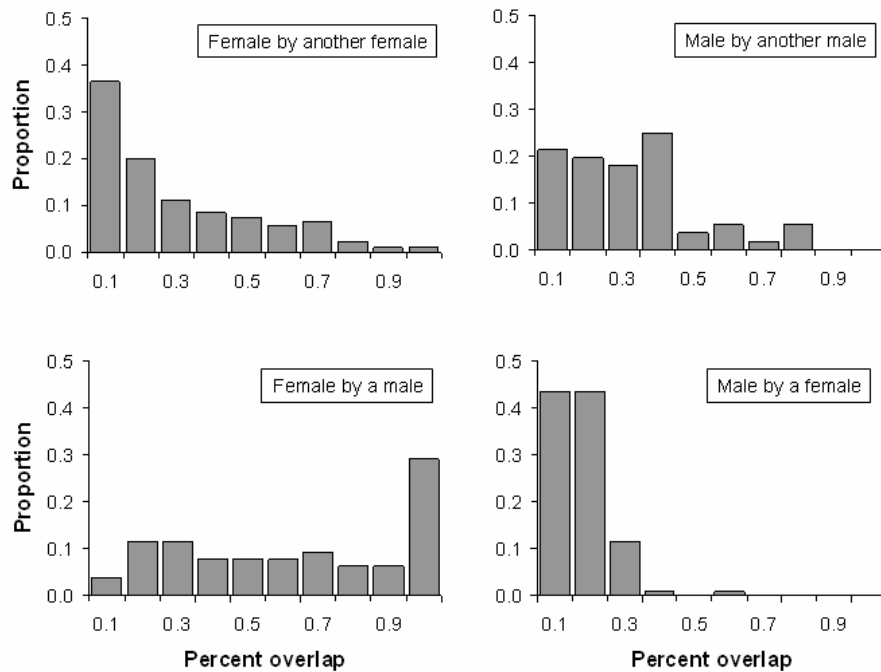
Figure 2.2. Histograms of percent overlap of core home ranges by neighboring male and female black bears.

Estimated size of the THR varied from 291.0–843.9 km^2 for males and 47.7–238.7 km^2 for females. Like CHR, THR differed between study areas for females ($F_{1,58}$ = 15.3, P = 0.001), but no difference was detected for males ($F_{1,15}$ = 0.37, P = 0.56). Median THR size was 99.7 km^2 for SSA females and 73.3 km^2 for NSA females. Median THR for all males was 462.7 km^2.
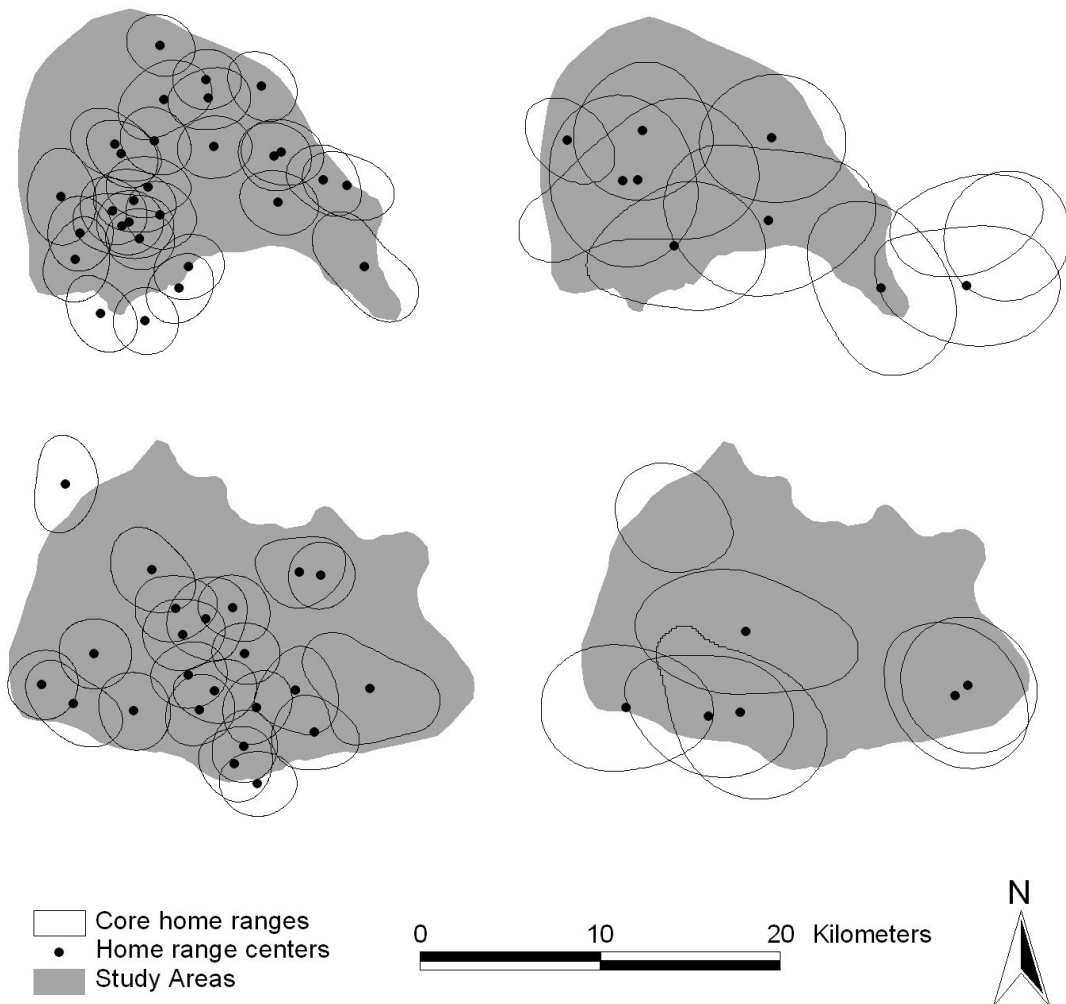
Figure 2.3. Overlap of multi-year core home ranges and proximity of home range centers for black bears: (top) Northern Study Area females (left) and males (right); (bottom) Southern Study Area females (left) and males (right). Maps depict the maximum number of ranges that were occupied simultaneously and overlapped the study areas.

Distance from home range center ranged from 0.3 km to 55.4 km, with an extreme outlier of 134.9 km. Median radius was larger for males than for females throughout the year (Figure 2.4). Median radius increased during fall months for both sexes, as bears entered hyperphagia. Proportion of locations representing excursions (movements outside of CHR contours) was similar between sexes, except during June and July, when males left their CHR more often than females (Figure 2.4). Proportion of locations outside of the CHR was consistent throughout Jun–Oct for males, however median distance from home range center was significantly higher during the mast season. Among females, proportion of excursions and mean distance from home range center increased during fall months.

Distance between successive locations ranged from 0.10 to 55.4 km, with an extreme outlier of 129.66. Median distance between locations was larger for males than for females throughout the year (Figure 2.4). However, median distance was generally highest during the mating season for males, while it was highest during the mast season for females.

Among pairs of bears with CHR overlap of ≥0.20, overall Jacob index values ranged from -0.29 to 0.92 during mating season and from -0.22 to 0.76 during the mast season. Mean index values were positive for all sex categories, however the CI for male-female pairs overlapped zero during the mating season (Figure 2.5). Index values were lowest for male-female pairs ($F_{2, 344} = 11.5$, $P < 0.001$) and higher during the mast season than the mating season ($F_{1, 344} = 26.2$, $P < 0.001$).

Factors Affecting Movements

Using model selection on the basis of AIC scores, intercept-only models were among the best models for predicting movements of males during the mating season (Table 2.3),
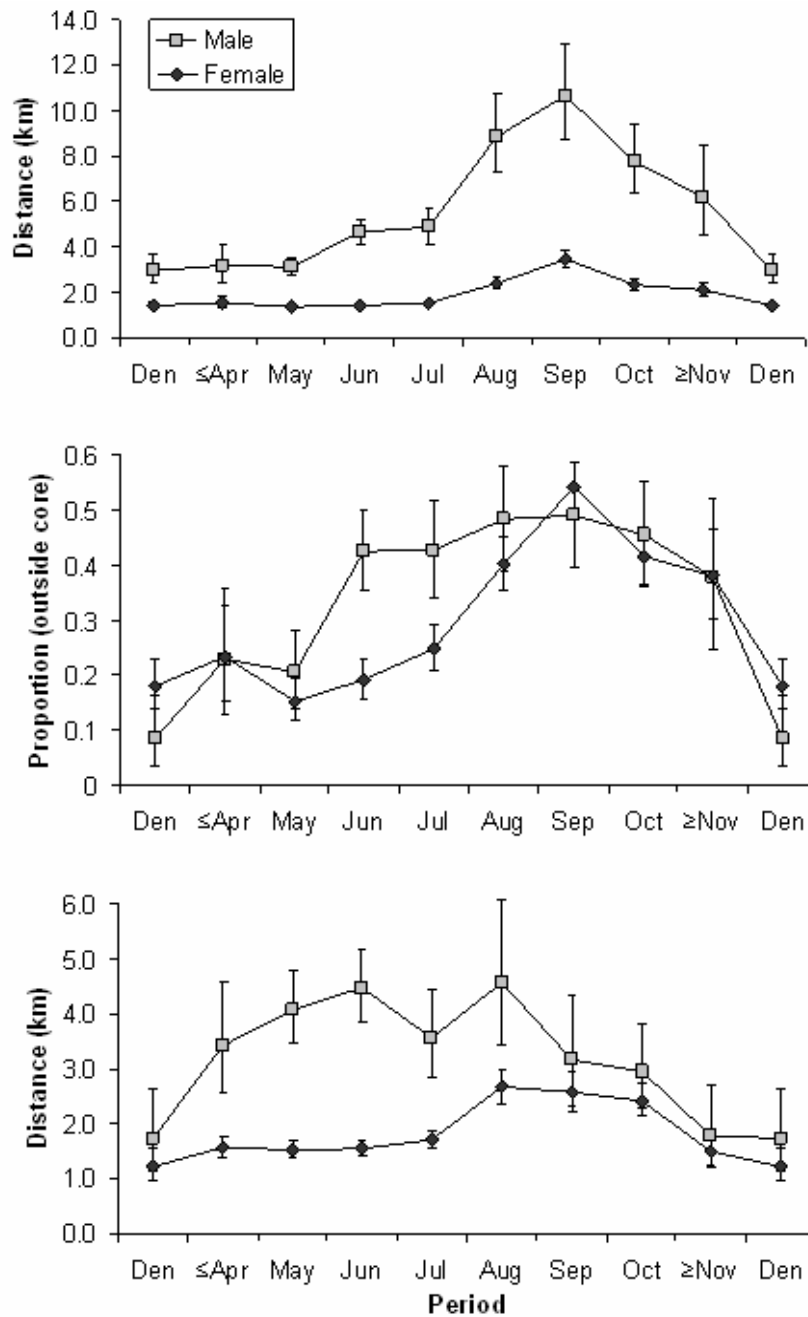
Figure 2.4. Seasonal movement patterns of black bears, by sex and month: (top) median distance (±95% CI) between each location and the home range center ($n = 4013$); (center) proportion of locations (±95% CI) occurring outside of core home range contours ($n = 4013$); and (bottom) median distance (±95% CI) between successive locations obtained 7–21 days apart ($n = 2861$). Distance between successive locations for the den period pertains to individuals that moved from one den to another.
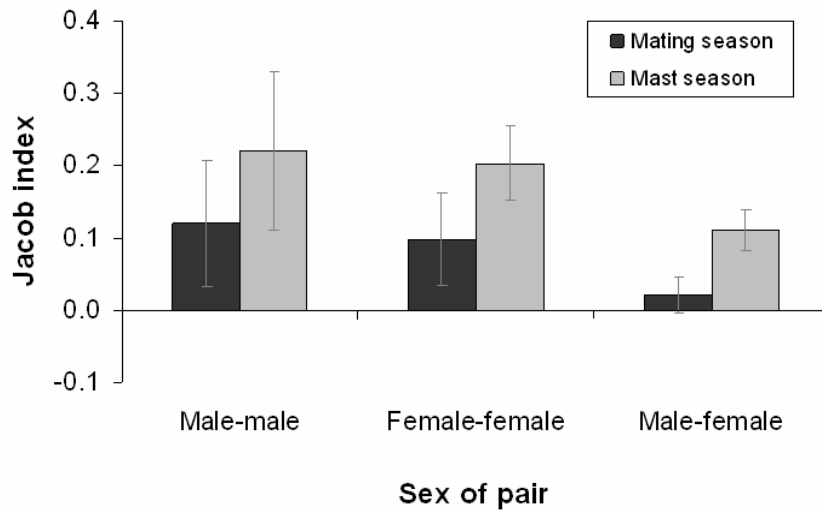
Figure 2.5. Mean (95% CI) Jacobs index of dynamic interactions, by sex, between pairs of black bears with core home range overlap of ≥0.20. Jacobs index values closer to -1 indicate avoidance, while those closer to 1 indicate attraction.

suggesting that daily movement patterns were not strongly affected by any of the independent variables. Based in these models, median distance from center was 3.9 km (CI: 3.3–4.5 km) and median distance between successive locations was 4.0 km (CI: 3.7–4.5 km). The explanatory variables found among the best models were ESTRUS and PRECIP. As predicted, estimates of the coefficients for ESTRUS were negative (suggesting males moved farther when estrous females were less available), however the CIs for the coefficients overlapped zero. Based on the ESTRUS models, median distance from center was 13% higher and successive distance (Figure 2.6) was 5% higher during years when a lower proportion of females were in estrus compared to years when a higher proportion of females were in estrus. Contrary to my prediction, the PRECIP model indicated successive distance was 16% higher during years of high precipitation compared to years of low precipitation, however the CI for the coefficient overlapped zero. During the mating season, 67% of male

Table 2.3. Best AIC-ranked models for predicting movements of male and female black bears during the mating season (den emergence–20 Jul) and mast season (21 Jul–den entry). Models reported had a ΔAIC of ≤2.00 or a model weight of ≥0.10.

Sex	Season	Response	n	Model	k	AIC	ΔAIC	Model weight
Male	Mating	Distance from center	463	ESTRUS	2	1128.57	0.00	0.43
				Intercept	1	1128.75	0.18	0.39
		Successive distance	352	Intercept	1	949.11	0.00	0.45
				ESTRUS	2	949.76	0.65	0.33
				PRECIP	2	951.57	2.46	0.13
	Mast	Distance from center	434	OAK	2	1214.28	0.00	0.94
		Successive distance	321	Intercept	1	1099.85	0.00	0.70
				OAK	2	1101.57	1.72	0.29
Female	Mating	Distance from center	1233	OFFSPRING	4	2669.11	0.00	0.85
				OFFSPRING + PRECIP	5	2672.62	3.51	0.15
		Successive distance	1046	OFFSPRING	4	2573.66	0.00	0.88
				OFFSPRING + PRECIP	5	2577.71	4.05	0.12
	Mast	Distance from center	1500	OAK + OFFSPRING	4	4341.63	0.00	0.58
				OAK	2	4342.47	0.84	0.38
		Successive distance	1097	OFFSPRING	1	3309.72	0.00	0.42
				Intercept	3	3309.85	0.14	0.39
				OAK	2	3312.56	2.85	0.10

locations were found within the CHR and this proportion did not differ relative to ESTRUS

($\chi^2_1 = 0.73$, $P = 0.39$) or PRECIP ($\chi^2_1 = 2.1$, $P = 0.15$).

OAK was the only covariate among the best models for predicting movements of males during the mast season (Table 2.3). As predicted, oak production had a negative association with the distance males moved from their home range center during the mast
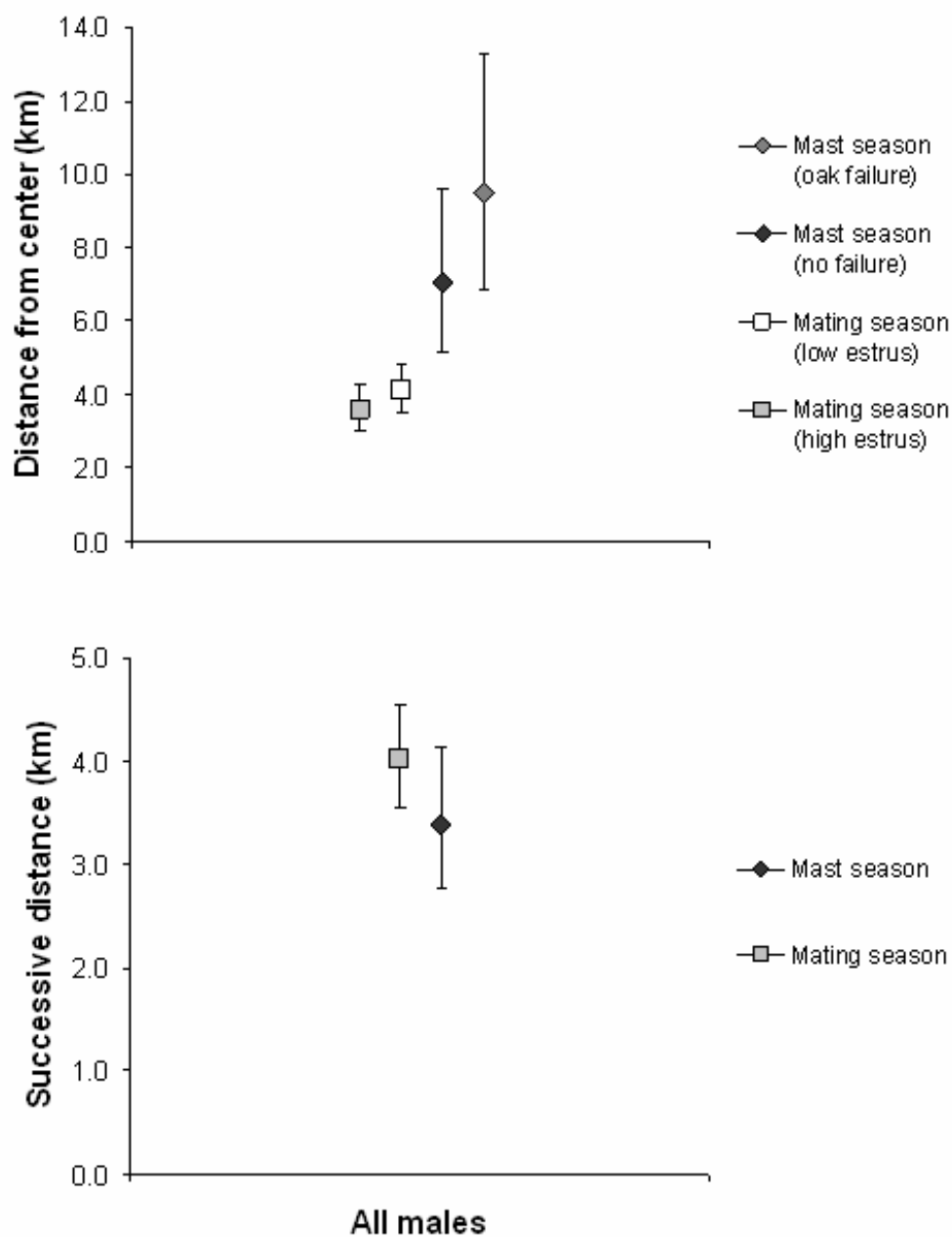
Figure 2.6. Median (95% CI) movement distances of male black bears during the mating season (den emergence–20 Jul) and mast season (21 Jul–den entry) based on the best AIC-ranked models for each season: (top) median distance from home range center was influenced by ESTRUS during the mating season and OAK during the mast season; (bottom) median distance between successive locations was not influenced by any explanatory variable during either season.

season. Based on the oak model, median distance from center was 8.2 km (CI: 6.0–11.2)

overall and it was about 26% larger during years of oak failure than during other years

(Figure 2.6). The intercept model was the best model for predicting successive distance. The

OAK model was second best and the coefficient for OAK was also negative in this model,

however the CI overlapped zero. Based on this model, median successive distance was 3.4

km (CI: 2.7–4.1) overall, and it was 10% larger during years of oak failure. Males were

found within their CHR 40% of the time during years of oak failure, but 60% of the time

during other years ($\chi^2_1 = 14.5$, $P < 0.001$).

The best models for predicting movements of females during the mating season

included the explanatory variables OFFSPRING and PRECIP (Table 2.3). Top models

indicated the median distance from the home range center was 1.5 km (CI: 1.3–1.6) and

median distance between successive locations was 1.7 km (CI: 1.5–1.8 km). Movement

estimates were lower for females with cubs than for lone females or females with yearlings,

supporting the hypothesis that social factors governed movements, rather than food

resources. Based on the top models, median distance from center for females with cubs were

26% smaller compared to females with yearlings, 23% smaller compared to females with no

offspring, and 23% smaller compared to females of unknown reproductive status (Figure

2.7). Median successive distance for females with cubs was 25% smaller compared to

females with yearlings, 17% smaller compared to females with no offspring, and 33%

smaller compared to females of unknown reproductive status. The second-best models also

included PRECIP. As predicted, the sign of the coefficients were negative (indicating bears

moved farther when food was more limited), however the CIs overlapped zero. Estimates
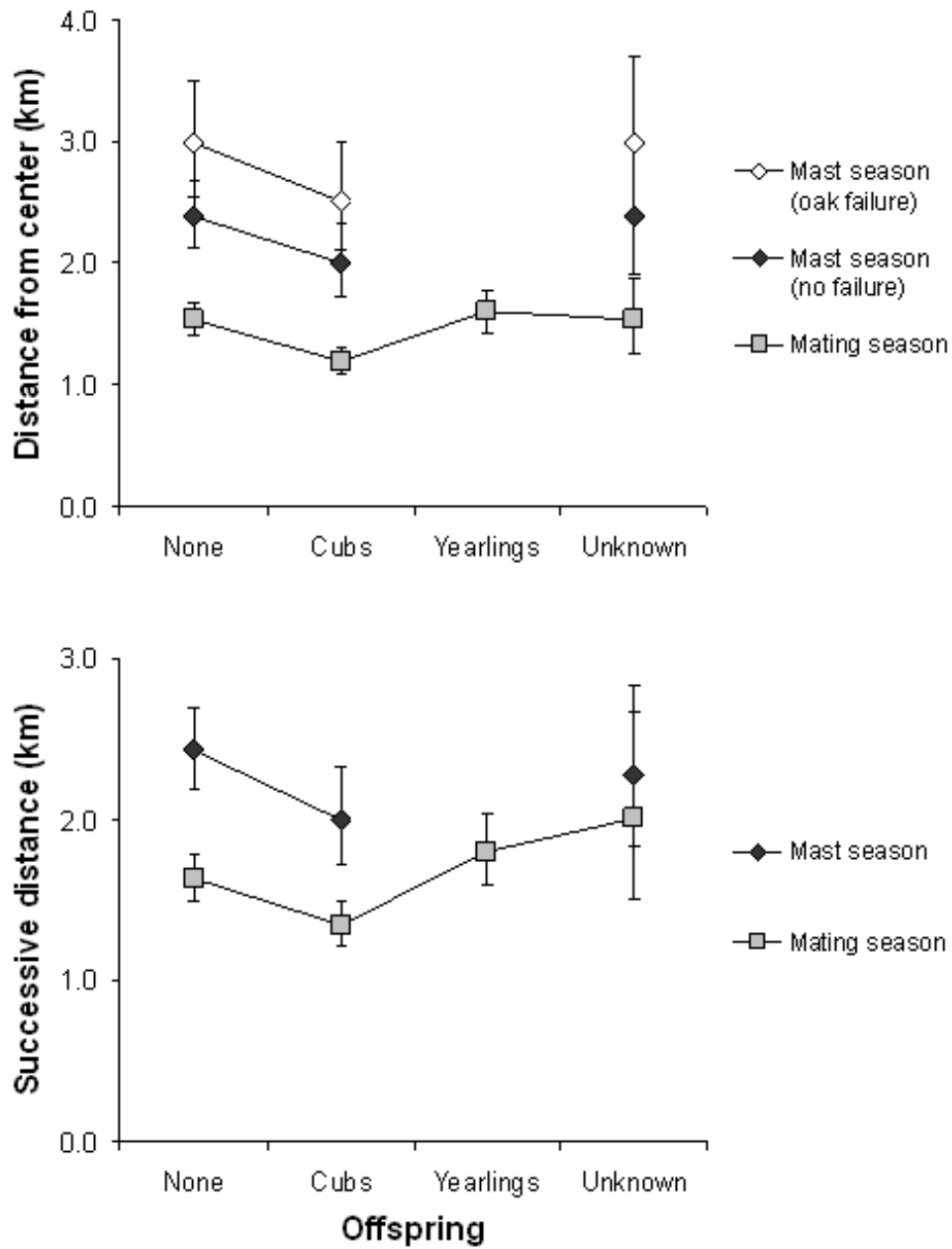
Figure 2.7. Median (95% CI) movement distances of female black bears during the mating season (den emergence–20 Jul) and mast season (21 Jul–den entry) based on the best AIC-ranked models for each season: (top) median distance from home range center was influenced by OFFSPRING during the mating season and OFFSPRING and OAK during the mast season; (bottom) median distance between successive locations was influenced by OFFSPRING during both season.

from these models indicated distance from center was 4% higher and successive distance was <1% higher during years of below-average precipitation compared to years of above-average precipitation. Comparing proportion of locations within the CHR, no difference was found relative to PRECIP ($\chi^2_1 = 0.7$, $P = 0.41$), but females with cubs were located within their CHR 88% of the time, while other categories of females were located in their CHR 75–77% percent of the time ($\chi^2_3 = 27.4$, $P < 0.001$).

For females during the mast season, the top model for predicting distance from center included both OAK and OFFSPRING (Table 2.3). Based on this model, median distance from center was 2.5 (CI: 2.2–2.8) km overall, and it was 25% larger during years of oak failure than during other years. It was also 16% smaller for females with cubs compared to females with no offspring or females of unknown reproductive status (Figure 2.7). Offspring was the only covariate in the best model for predicting successive distance. Based on this model, median successive distance was 2.2 (CI: 2.0–2.5) km overall, and it was 18% smaller for females with cubs compared to females with no offspring and 12% smaller compared to females of unknown reproductive status (Figure 2.7). Females were found within their CHR 50% of the time during years of oak failure, but 60% of the time during other years ($\chi^2_1 = 14.5$, $P < 0.001$). Proportion of locations within the CHR did not differ relative to OFFSPRING ($\chi^2_2 = 0.08$, $P = 0.96$).

Factors Affecting Dynamic Interactions

During the mating season, mean Jacobs index for male-female pairs was slightly positive when females did not have cubs, but slightly negative when females had cubs (paired $t_{34} = -1.8$, $P = 0.08$; Figure 2.8). Mean values were positive for both circumstances
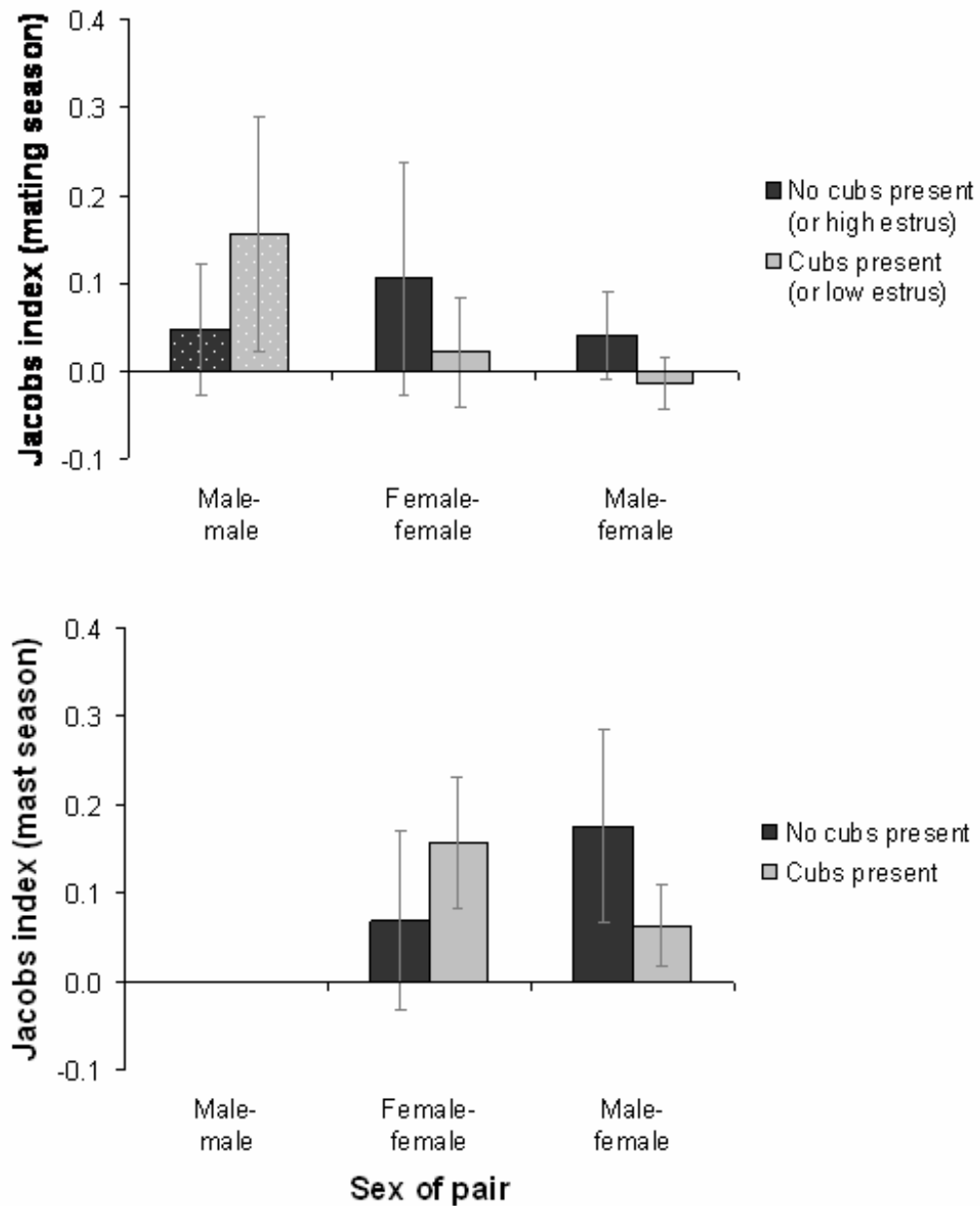
Figure 2.8. Influence of social factors on mean (±95% CI) Jacobs index of dynamic interactions for pairs of black bears during the mating season (top) and mast season (bottom). The presence of cubs was associated with lower interactions of male-female pairs during both seasons ($P \leq 0.08$), but no significant difference was detected for female-female pairs ($P \geq 0.20$). The proportion of females in estrus was negatively associated with interactions of male-male pairs during the mating season (top, shaded with dots), however the difference was not significant ($P = 0.17$).

during the mast season, but the mean was lower when females had cubs (t_{16} = -2.0, P = 0.07).

Among female-female pairs, no difference in mean index was detected between years when

one or both females had cubs versus years when neither female had cubs, during the mating

season (t_{18} = 1.2, P = 0.23) or the mast season (paired t_{18} = -1.3, P = 0.20). Among male-

male pairs, I detected no difference in the mean index during the mating season comparing

years when a high percentage of females were in estrus to years when a lower percentage of

females were in estrus (t_{15} = -1.4, P = 0.17).

A pattern of greater attraction between bears during years of below average

precipitation (i.e., lower food production) compared to years of above average precipitation

(i.e., higher food production) was observed for all sexes (Figure 2.9), however the difference

was more significant for male-male pairs (t_9 = 1.8, P = 0.09) and male-female pairs (t_{50} = 1.7,

P = 0.09) than for female-female pairs (t_{23} = 0.9, P = 0.36). The opposite pattern was

observed for oak production, where mean indices were lower or equal during years of failed

oak production compared to other years (Figure 2.9). The difference was significant for

male-male pairs (t_7 = -2.3, P = 0.05), but was not significant for female-female pairs (t_7 = 0.1,

P = 0.90) or male-female pairs (t_{15} = 1.0, P = 0.34).

Discussion

The movements of black bears in New Mexico varied according to the seasonal needs

of mating, hyperphagia, and hibernation. The annual pattern began with most bears denning

close to their home range center within their CHR. Post-denning movements were generally

small, but increased during the mating season, especially for males. During fall hyperphagia,
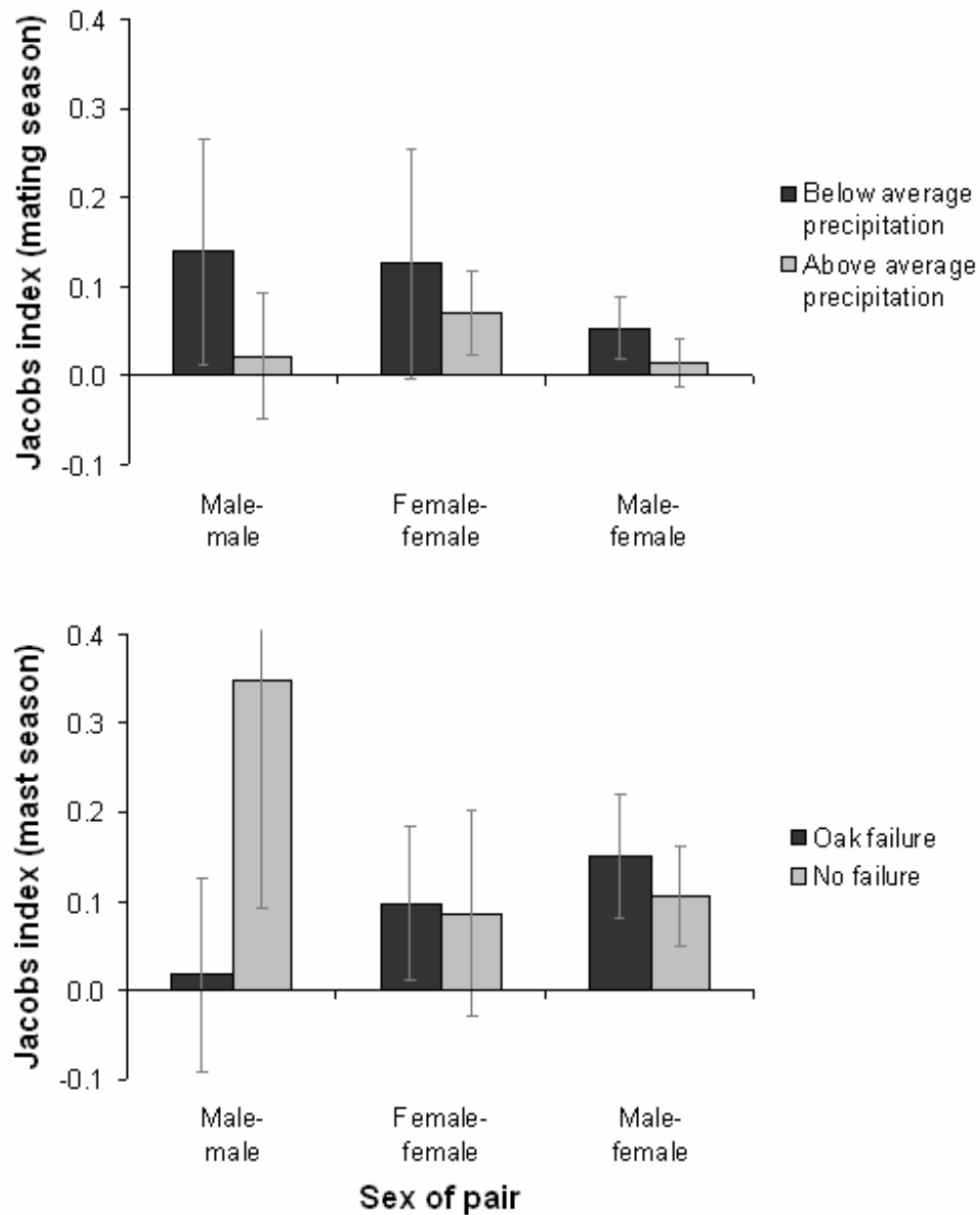
Figure 2.9. Influence of food on mean (95% CI) Jacobs index of dynamic interactions for pairs of black bears during the mating season (top) and mast season (bottom). Below average precipitation (i.e., lower food production) was associated with higher interactions of male-male and male-female pairs ($P = 0.09$), but no significant difference was detected for female-female pairs ($P = 0.36$). Failure of oak production was associated with lower interactions for male-male pairs ($P = 0.05$), but no significant differences were observed for female-female pairs ($P = 0.90$) or male-female pairs ($P = 0.34$).

when bears were building up fat stores for hibernation, bears often ranged far from their CHR. In the days prior to denning, bears typically returned to their CHR and reduced their movements.

Within seasons, I observed interesting variation in the movements of male and female black bears, which reflect differences in the way the sexes increase their fitness. My hypothesis regarding the role of food and social factors in determining space use of male and female bears was only partially supported. As predicted, movements and interactions of males, who rely on scramble competition for reproductive success, were influenced predominantly by social factors during the mating season, and by food resources during the mast season. But, contrary to my prediction, social factors were an equal if not greater influence than food on the movements and interactions of females, during both seasons.

My analyses revealed that the mating season strategy of males was to exhibit high mobility, but concentrate their movements within or near their CHR. Two thirds of mating season locations were found within the CHR. Although males spent significantly more time outside of their CHR during June and July compared to females, the mean distance from home range center was significantly less than that observed during the mast season. But, the distance between successive locations was higher during the mating season than during the mast season, indicating males were repeatedly traversing their CHR. Mean movement rates of males, measured in 1- to 2-day increments, were also highest during the breeding season in Pennsylvania (Alt et al. 1980), Alberta (Young and Ruff 1982), and Michigan (Hirsch et al. 1999). Within a mating season that spans more than three months, and one in which females may come into estrus at any time, this canvassing behavior probably maximizes a

male's chances of encountering familiar females at the time that they come into estrus. Consistent with this canvassing strategy, my analysis also hinted that males may travel greater distances and show greater attraction to one another during years when fewer females are in estrus, however overlapping margins of error left some uncertainty about the validity of these patterns. I found no differences in the movements patterns relative to age (i.e., body size), suggesting all resident males use the same canvassing strategy regardless of age or size. Kovach and Powell (2003) also found that black bears of all size categories searched widely for receptive females during the mating season, and rejected the hypothesis that males used conditional mating tactics according to body size.

I found no evidence that food scarcity caused males to increase their movements during the mating season, which highlights the supremacy of breeding in determining the magnitude of mating season movements. This, and the lack of evidence that movements increased with body size, support previous suggestions that the mating season home range size is larger than that needed for metabolic requirements (Sandell 1989, Powell et al. 1997, Koehler and Pierce 2003). Powell et al. (1997) also found that spring and summer food availability, weight, and age were uncorrelated with seasonal or annual home range size of males. Nonetheless, I did detect an affect of food in the dynamic interactions of males, who showed greater attraction to other males during years of lower food availability. Thus, it appears the magnitude of male movements during the mating season is not determined by food availability, even when food is scarce. But, while exploiting foods present within the areas they canvas for estrous females, perhaps males are more apt to be attracted to the same patches of food when production is low.

This weak association with food during the mating season contrasted sharply with the mast season, when males were observed to spend 20% more time outside of their CHR, stray 26% farther from their home range center, and exhibit less attraction to one another during years of oak failure. This divergence in the role of food in determining movements and interactions suggests that males have the capacity to devote the bulk of their energy to mating during the mating season and feeding during the mast season. In other words, they may function as "capital breeders" (Stearns 1989, Jönsson 1997). I do not argue that males ignore food during the mating season. Our ability to capture males using baited traps shows their willingness to investigate food resources. However, with the capacity for weight gain and efficient use of fat stores displayed by bears (Hellgren 1998), it is likely most adult males are capable of withstanding a period of low food intake without reducing their survival. Noyce and Garshelis (1998) found that adult males tend to lose weight between winter and summer, and they cited several lines of evidence to support the notion that breeding males may curtail feeding, including reduced use of garbage dumps (Herrerro 1983, Rogers 1987a, Garshelis 1989), formation of a false annulus in tooth cementum indicating food stress (Coy and Garshelis 1992), and low serum urea levels indicating low ingestion rates. The period following the mating season is usually typified by the increasing availability of carbohydrate- and fat-rich foods (Eagle and Pelton 1983, Noyce et al. 1997, Inman and Pelton 2002). So, unlike many ungulate males, whose winter survival is decreased due to the reduced energy intake during the rut (Barboza et al. 2004, Forsythe et al. 2005), male bears are likely able to replenish, if not increase their fat stores immediately following breeding. The possible lack of food intake required for breeding success may be a factor promoting the large body size of

male bears (i.e., sexual dimorphism). Fasting endurance increases with body size, because larger mammals have a proportionately greater mass of body fat and proportionately lower energy demands (Lindstedt and Boyce 1985).

I hypothesized that food would play the central role in determining movements and interactions of females throughout the year. But, similar to the pattern of males, the importance of food was far more obvious during the mast season. I found strong evidence that females moved farther when food was scarce in the fall, but weaker evidence that the same was true during the spring. There was no evidence that movements increased with the increased metabolic needs of large body size (i.e., AGE) or the presence of offspring. This contradicts the hypothesis that females "should occupy areas no larger than necessary" (Amstrup and Beecham 1976) and suggests younger, smaller females and older females without offspring use areas larger than needed for fulfilling their immediate energetic requirements. What might account for this behavior? Certainly, it is possible that estrous females canvass in a manner akin to males, to advertise their receptivity and attract males of the highest quality. However, this behavior does little to explain the movements of reproductively immature females, whose movements were not found to be smaller than older females. Nor does it explain the smaller movements of females with cubs during the mast season, when mating behavior is absent. It is more likely females move throughout an area larger than their present needs require in order to familiarize themselves with the resources available within their vicinity. Many of the foods bears consume, especially mast species, are unpredictable in time and space (Eagle and Pelton 1983, Inman and Pelton 2002). Thus, females benefit from utilizing a large home range by the ability to efficiently exploit its

resources, especially food. Females are highly philopatric, and most often establish a home range overlapping that of their mother (Rogers 1987ab, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Beck 1991). It is also possible females establish a home range large enough to accommodate these future female offspring.

During both seasons, females with cubs were observed to reduce their movements, despite having higher energetic demands than lone females. This was probably made possible due to their efficiency in exploiting food resources gained from previous exploration. The reduction in movements might be simply explained by the lower mobility of small cubs, coupled with the need to take part in the stationary behavior of sucking. However, like Dahle and Swenson (2003), I would argue that these limitations should be minimal by the fall months, when cubs are 8–11 months old. Therefore, the more restricted movements of females with cubs, which we observed to be similarly reduced during both the mating and mast seasons, may be because mothers concentrate their activity toward the center (and most familiar) part of their home range to avoid threatening encounters with other bears, especially males. This idea is supported by the analysis of dynamic interactions, which indicated attraction of male-female pairs was reduced when females were accompanied by cubs. In fact, the only avoidance we observed (i.e., mean Jacobs index <1) was between males and those females accompanied by cubs. Intraspecific predation of cubs has been observed in black bears (LeCount 1987, Garrison et al. 2007) and brown bears (Troyer and Hensel 1962, Mattson et al. 1992, Olsen 1993, Swenson et al. 2001), and some argue that infanticide is primarily perpetrated by males in an effort to increase their reproductive success by mating with the mother of the cubs (Bellemain et al. 2006a). If

females are indeed limiting their movements to protect their cubs from infanticidal bears, the persistence of this behavior beyond the mating season would suggest predation on cubs is not entirely motivated by sexual selection.

For both sexes, it appears the most likely function of the CHR is to provide an efficient means to exploit local resources, be they estrous females or foods, rather than a means to ensure exclusive use of those resources. The canvassing movements I observed among males, coupled with known marking behavior among bears (Burst and Pelton 1983), might suggest territorial behavior. However, there is no evidence to suggest that males defend their home range, even during the mating season. Overlap of multi-annual CHRs was as high as 78% between males. This was observed despite radio-telemetry monitoring of just a fraction of males. In an analysis of male reproductive success (Chapter 4), the average female was overlapped by different 14.7 males, including both resident adults and transient subadults. Evidence indicated that males were unable to ensure dominate mating with the females residing closest to them, much less all of the females within their sizable home range.

Like males, females displayed high levels of home range overlap with one another (as much as 100%), indicating a lack of territorial behavior. In the past, some authors have argued that females are more territorial than males, but share space with relatives (Jonkel and Cowan 1971, Young and Ruff 1982, Rogers 1987a). We observed high overlap by females, even when DNA evidence suggested they were unrelated. In fact, 50% of females that overlapped another female by ≥ 0.50 ($n = 32$) were likely unrelated to that neighbor (i.e., the r coefficients for the pair was 0; see Chapter 5). This proportion of unrelated neighbors did

not differ from that of all females that overlapped by even a small amount ($n = 196$; 58.7%

unrelated; $\chi^2_1 = 1.0$, $P = 0.31$). Thus, it would appear that females are equally likely to

tolerate a non-relative as a relative within their home range.   Schenk et al. (1998) also found

low relatedness among females with overlapping home ranges in Ontario. Much of the

debate on whether or not female bears are territorial has focused on the observed overlap of

their ranges. Few, if any, have considered the issue from a cost-benefit viewpoint. I would

argue the fitness benefits of defending a territory to ensure exclusive access to spring foods,

which are largely ubiquitous and of comparatively low quality in New Mexico, would be

quite small compared to the potential fitness costs of defense.   Instead, it appears females

simply use scramble competition to obtain their necessary food intake, similar to the way

males compete for mates. As a consequence, the intra-sexual spacing patterns are similar for

males and females, despite the different strategies employed for increasing their fitness.

TELEMETRY-BASED ESTIMATES OF DISPERSAL, HOME RANGE ESTABLISHMENT, AND FIDELITY IN BLACK BEARS

Abstract

I examined patterns of dispersal, home range establishment, and home range fidelity in black bears using radio-telemetry data for individuals whose natal range was known ($n = 43$), individuals whose natal range was identified using microsatellite DNA ($n = 13$), and individuals whose natal range was unknown ($n = 86$). Like previous studies, I found that natal dispersal was highly male-biased. Males emigrated between the ages of 1 and 3 years and were observed to move 6.6–61.2 km from their natal range. Young males also displayed low year-to-year fidelity to a home range. Dispersing males moved their range 15.1–67.7 km between successive years. This floating period lasted from a few months to several years, but most males settled into a permanent home range by 4 years, and all males settled by age 7 years. Females were more philopatric and settled 0.3–7.3 km from their natal range. Only one female moved her range >20 km at the age of 5 years. The adaptive significance of male-biased natal dispersal is discussed.

Introduction

Patterns of dispersal affect the dynamics and spatial genetic structure of populations. Despite its importance, dispersal is among the most difficult aspects of animal movement to document. The difficulty and expense of tracking dispersing animals has limited the amount of data on this behavior in large carnivores, where its documentation requires long-term monitoring, the ability to repeatedly identify individuals, and usually, use of radio-telemetry.

Radio-telemetry is the only reliable means of documenting dispersal movements in black bears, due to their secretive nature and low sightability. However, many researchers have been reluctant to radio-collar juvenile bears, particularly males, due to the risk of collar injuries resulting from rapid growth during a time when long-range movements may hinder maintenance of telemetry contact. Thus, few studies have measured rates or correlates of dispersal in black bears.

Dispersal is often treated as a single event, but it can be considered a process composed of three stages: emigration, movement, and immigration (Bowler and Benton 2005). In the case of natal dispersal in black bears, these stages include movements away from the mother's home range, a period of roaming (often called 'floating'), and finally settlement in an adult mating range. Various field studies of black bear movement have documented parts of this sequence, but none have provided a detailed picture of the entire process.

Most studies of black bear dispersal have focused primarily on the emigration phase. By revealing high levels of emigration by young males but little emigration by females, these studies have shown that rates of dispersal in black bears are male-biased. In data from Minnesota, Massachusetts, Alaska, and Colorado, only 6% of 79 juvenile females emigrated from their natal range, while 100% of 62 juvenile males emigrated from their natal range (Rogers 1987b, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Beck 1991). Of 54 cases where age was reported, 11% of males emigrated as yearlings, 67% as 2-year-olds, 19% as 3-year-olds, and 2% as 4-year-olds (Rogers 1987b, Schwartz and Franzmann 1992,

Beck 1991). Ages of female emigrants were not systematically reported, but at least one

emigrated by age 2 years (Elowe and Dodge 1989), and three others emigrated at 3–4 years

(Rogers 1987b). Reported straight-line dispersal distances ranged from 3–15 km for

dispersing females and 13–219 for dispersing males (Rogers 1987b, Elowe and Dodge 1989,

Beck 1991). Other studies have found that radio-collared juvenile males (whose natal ranges

were unknown) often roam widely, and this roaming is probably associated with natal

dispersal (Garshelis and Pelton 1981, Pacas and Paquet 1994, Wertz et al. 2001).

Dispersal often carries a mortality cost (Waser et al 1994), and in the studies

summarized above, most dispersing males died, shed their transmitters, or were lost from

telemetry contact before settlement could be documented. Thus, the period of floating and

dispersal distance could be determined for only a small fraction of dispersing bears.

Information about the timing of home range establishment and long-term fidelity to home

ranges is lacking. Rogers (1987b) reported that age of home range establishment ranged

from 2–7, with most males settling by age 4. However, his methodology for obtaining this

estimate was unclear and it appeared to be based primarily on capture-recapture data.

Several studies have reported that home ranges were stable for adult bears, but most were

based on only 1–2 years of monitoring (Amstrup and Beecham 1976, Alt et al. 1980, Wertz

et al. 2001), so their analytical power was low.

The goal of this paper is to provide a more comprehensive picture of the entire

process of dispersal, based on a study of two black bear populations in New Mexico. Like

previous studies, I will determine the timing and distance of emigration based on movements

from natal ranges. But I will also estimate the period of floating and the timing of home

range establishment based on fidelity of individuals to their home ranges over time.

Although this study was plagued by many of the same constraints as previous research, I

believe this novel approach will provide better insight into black bear dispersal patterns.

These analyses were particularly critical for establishing baseline data for other work,

including analyses of paternity and male reproductive success (Chapter 4) and analyses of

spatial genetic structure and inbreeding avoidance (Chapter 5).

Methods

I compiled telemetry, capture, recapture, den, and mortality locations for all radio-

marked bears and classified them by season (see Chapter 2): den, pre-mast or mating (den

emergence to 20 July), and mast (21 July to den entry). Recapture locations were excluded

when bears were captured more than once at the same trap site during the same trapping

period. I restricted analyses of dispersal and home range fidelity to 187 bears (105 F, 82 M)

with ≥ 3 locations obtained within the pre-mast season of ≥ 1 year. Although this number of

locations was low, it was equally low for most bears. Mean number of pre-mast locations

among this sample was 6.1 (SE = 2.1) and mean number of total locations used for annual

ranges was 10.9 (SE = 4.0). For each bear-year (n = 477), I calculated an annual 50% kernel

home range (Silverman 1986), using the Animal Movements extension (Hooge and

Eichenlaub 2000) developed for use with ArcView software (Environmental Systems

Research Institute, Redlands, California). I calculated h_{ref} for each individual, and used the

rounded mean value for all males (3800 m) and all females (1800 m) as the smoothing

parameter (Chapter 2). Use of a common smoothing parameter, rather than the least squares cross validation, minimized the effect of sample size on home range size. Eighty-five percent of annual ranges were represented by a single contour (one contiguous area). When ranges were represented by 2, or more rarely 3, contours, one contour typically contained predominantly pre-mast season locations, while the other(s) typically contained mast season locations. I estimated the home range center as the center coordinates of the 50% kernel contour containing the pre-mast season locations using the Animal Movements extension.

I analyzed dispersal using two samples. The "known" sample (n = 73 bear-years) included annual ranges of 43 bears first handled as cubs in the den. These bears were monitored from age 1 year with radio-telemetry and their natal range was known from monitoring their mother. Adding to this known sample, the "expanded" sample (n = 95 bear-years) included annual ranges of another 13 bears (22 bear–years) whose mothers were identified unambiguously by analysis of microsatellite DNA (Chapter 4). For bears with mothers identified using DNA, I assumed their natal range was the same as their mother's established range. For both samples, I determined whether annual home ranges overlapped the natal ranges and the mean distance between centers of the annual range and the natal range.

Finally, I analyzed home range fidelity for 135 bears (49 bears from the previous samples, plus 86 other bears) with annual home ranges obtained for ≥2 successive years (n = 316 bear-years). For these, I determined whether successive annual ranges overlapped and the mean distance between successive home range centers.

Results

Among the known sample, sample size decreased with age, as expected due to mortalities and transmitter failures (Figure 3.1). Natal dispersal was male-biased. All yearling males resided within their natal range for most of the year, but 20% of 2-year-old males ($n = 10$), and 100% of 3-year-old males ($n = 3$) moved sufficiently far that their annual range (defined by a 50% kernel) did not overlap their natal range. Male dispersal distances ranged from 22.4–61.2 km, with a mean of 40.4 km ($n = 5$). Males began dispersal movements during fall as yearlings ($n = 2$), during fall as 2-year-old ($n = 1$), or during spring as 3-year-olds ($n = 2$). In contrast, all females overlapped or remained very near their natal range for as long as they were monitored. The single female yearling (from the SSA) whose annual range did not overlap her natal range moved only 5.2 km. All females monitored until age 3 years maintained overlap with their natal range; distance from natal to annual range centers ranged from 0.3–5.0 km, with a mean of 2.1 km ($n = 7$).

Among the expanded sample, natal dispersal was similarly male-biased (Figure 3.2). This analysis indicated 25% of 2-year-olds ($n = 12$), 75% of 3-year-olds ($n = 4$), and 100% of ≥4-year-old males ($n = 2$) dispersed from their natal range. However, mean dispersal distance decreased to 34.0 km ($n = 8$) with the addition of these bears, primarily because an 8-year-old male from the SSA (whose mother was identified using DNA) resided only 6.6 km from his suspected natal range. As in the known sample, most females remained within or near their natal range. One 8-year-old female from the NSA dispersed 7.3 km, so that her annual range did not overlap her suspected natal range.
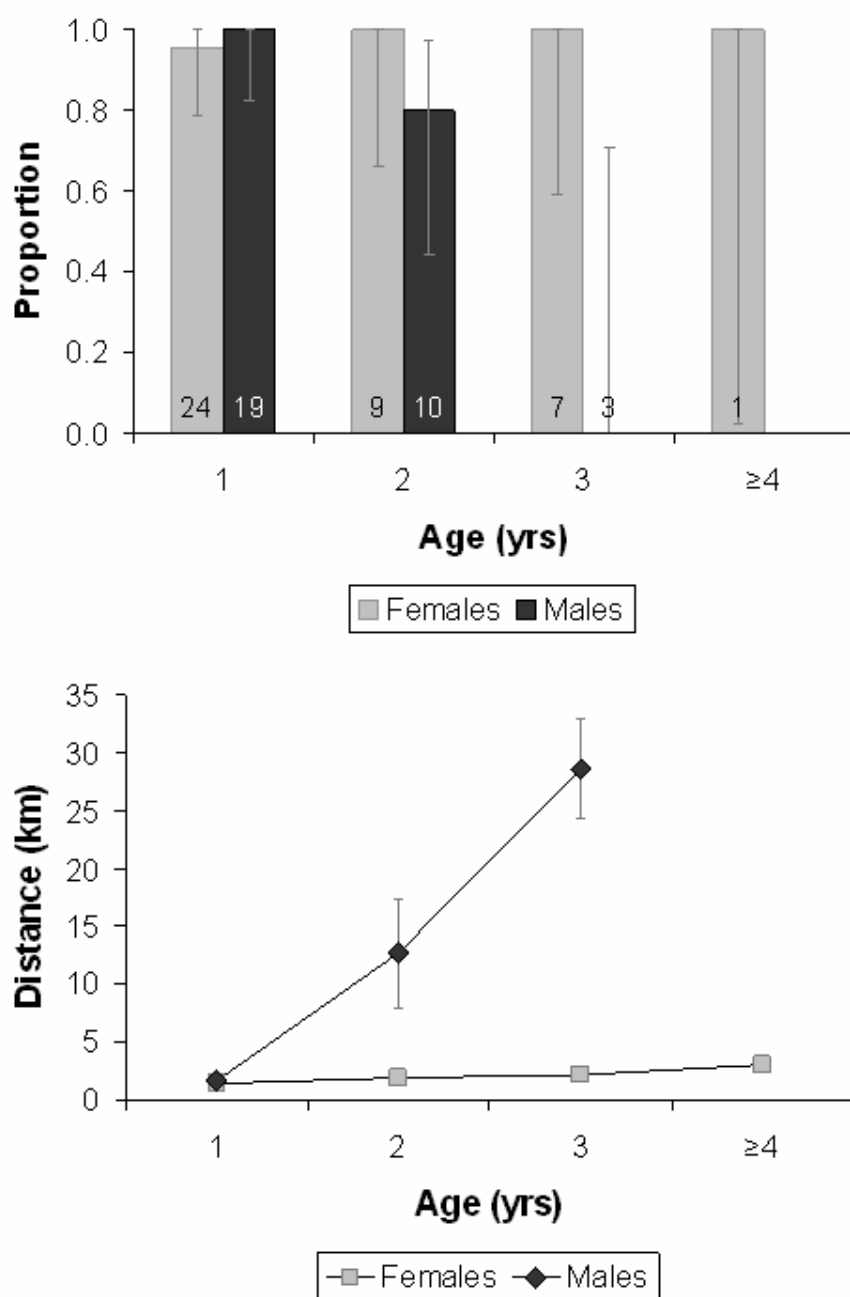
Figure 3.1. Black bear emigration from the natal home range (known sample): (top) proportion (±95% CI) of individuals occupying an annual home range that overlapped the natal range; and (bottom) mean (±95% CI) distance between center of the natal range and the annual range.
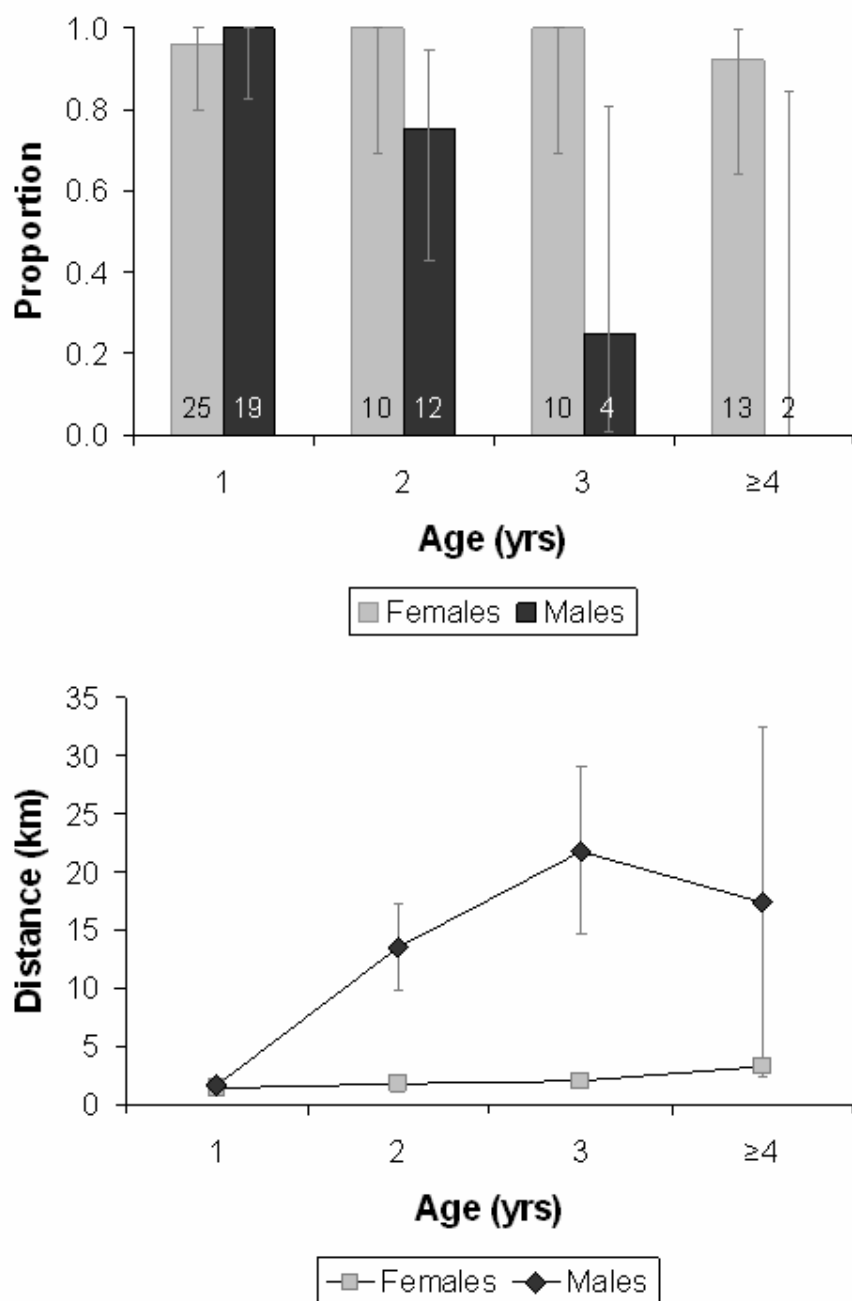
Figure 3.2. Black bear emigration from the known or suspected natal home range (expanded sample): (top) proportion (±95% CI) of individuals occupying an annual home range that overlapped the natal range; and (bottom) mean (±95% CI) distance between center of the natal range and the annual range.

Among all bears monitored in ≥2 successive years, young males displayed low year-to-year fidelity to a home range (Figure 3.3). From age 2–6 years, 17–67% of males were observed to use ranges that did not overlap that of the previous year. Movements were most common among 3- and 4-year-olds. Dispersing bears moved from 15.1–67.7 km between years, with a mean of 46.1 ($n = 8$). Long-distance inter-annual dispersal was rare among females. A NSA female dispersed 20.1 km from her previous range at age 5. She remained in this new range for at least two years. By age 7, no bears of either sex were observed to permanently disperse from their previous year's home range, although two bears made unusual movements. A 19-year-old male moved about 20.1 km from his previous range during the entire mating season of 1996, but returned to his established home range later that year and continued to use it throughout the next three years. A female on the SSA displayed an unusual multi-annual home range that included two contours separated by 32.7 km. One contour was found within the SSA boundary, but the other was found within a wilderness area to the south. Locations from all seasons and all years were found within each contour, indicating the split home range did not simply represent seasonal movements. Although she used both regions throughout all years that she was monitored, her annual range contours were typically located within only one region or the other. Thus, her annual range center was located within the study area during both 1994 and 1999, but was located within the wilderness area during 1995 and 1998. Interestingly, the yearling range of her female offspring born during 1994 was found within the SSA, but the yearling range of her female offspring born during 1998 was found within the wilderness.
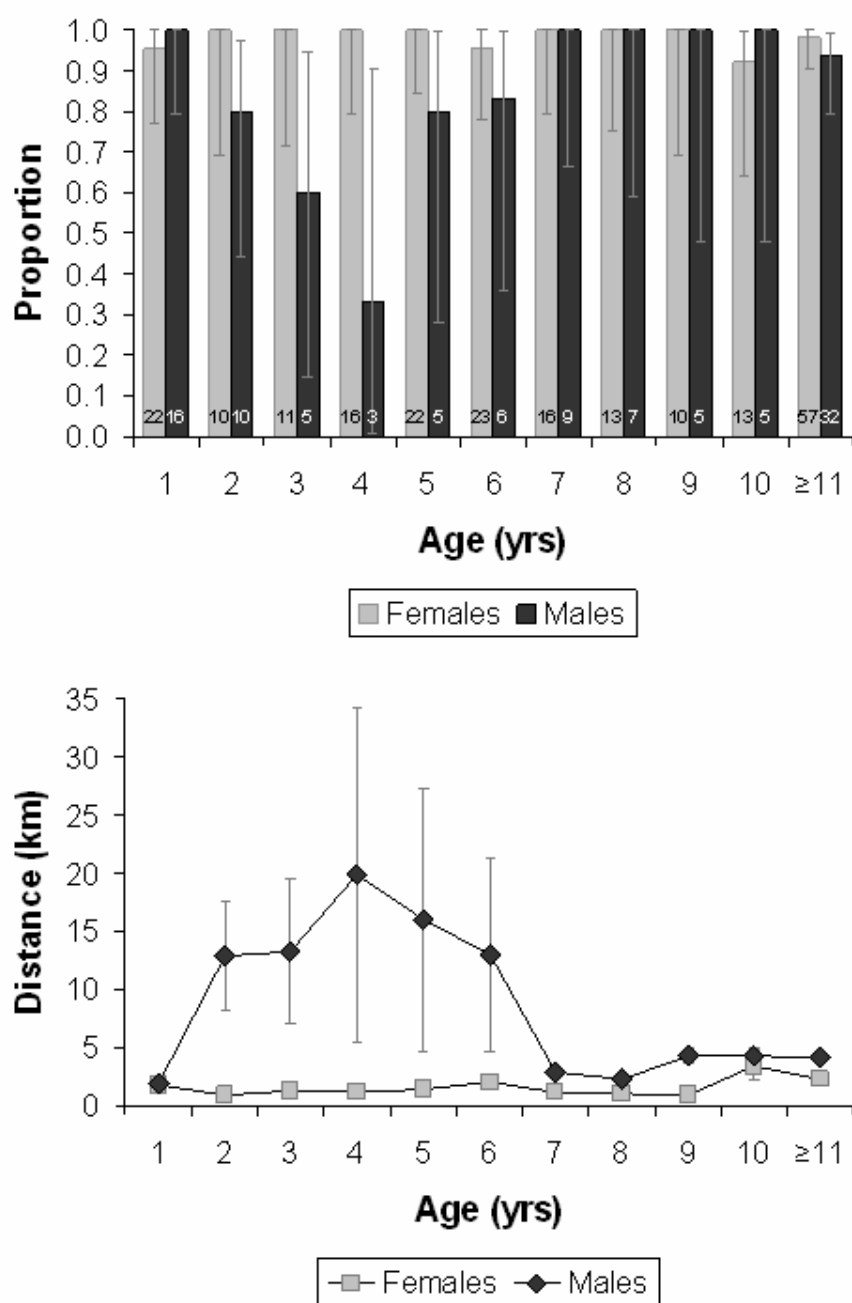
Figure 3.3. Patterns of home range fidelity for radio-marked black bears: (top) proportion (±95% CI) of individuals that occupied an annual range that overlapped the previous year's annual range; and (bottom) mean (±95% CI) distance between the center of the annual home range and that of the previous year.

Discussion

The movements patterns I observed corroborated previous studies of black bear dispersal patterns, which have demonstrated nearly universal dispersal among males and a high degree of philopatry among females (Rogers 1987b, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Beck 1991). Male biased dispersal is common among mammals in general, and among other carnivores (Waser and Jones 1983). Most male bears emigrated distances equal to about 2–6 home range diameters (see Chapter 2) from their natal range. Emigration distances of up to about five mating range diameters were also found in Minnesota (Rogers 1987b). Although long-distance emigration appeared to be the norm, evidence indicated one of eight males (an individual whose natal range was estimated using DNA) dispersed only 6.6 km, less than a single adult home range diameter. Relatively short dispersal distances were also documented for a few individuals in other studies (11–13 km; Rogers 1987b, Beck 1991). Similar to other studies, female dispersal was rare, and permanent movement in excess of 10 km was observed for only one female.

Like previous studies, I had difficulty determining the floating period for dispersing male bears, because I was unable to monitor individuals into adulthood (due to collar loss and the end of the study). But several lines of evidence indicated the floating period varied from a few months to a few years. Among the five males monitored since birth, three settled in a new home range (possibly the permanent range) within the year of emigration, while the other two remained transient during the emigration year and into the next. The combined patterns of emigration and fidelity indicated all males emigrated by the age of 4 years, but some males did not settle until the age of 6 years. This suggested at least some males floated

for two or more years. I documented one male (whose natal range was unknown) that was transient for three years between the ages of 3 and 6 years. Despite traveling a roundabout path with movements summing to >400 km, the endpoints for this bear were only 2.7 km from one another. This illustrates that dispersal distances determined solely from an initial movements away from a natal area might be misleading. Roundabout movements, such as these, may account for some of the shorter dispersal distances observed among males. This also suggests that dispersing bears probably sample a larger set of potential ranges, mates and environmental conditions than would be inferred from patterns of settlement alone.

I observed settlement of most bears by age the age of 4 years and by all bears by the age of 7 years. Home range establishment is important for reproduction, and may be a prerequisite for reproduction in both sexes. Clearly all philopatric females were present within their permanent home range prior to their first breeding, but even the single female that evidently dispersed as a 5-year-old first bred as a 6-year-old after establishing her new home range. Among males, evaluation of first breeding relative to home range establishment is far more problematic, but synchrony in observed timing suggests males also established home ranges prior to or coincident with first breeding. Age of first breeding in males ranged from 3–9 years, with an unbiased mean estimate (Garshelis et al. 1998) of 6.5 years (based on a sample of males whose reproductive history could be estimated starting at age 3 years; Chapter 4). Underscoring this, I observed no floating after first breeding, but I was aware of several young males that showed fidelity to a home range in the absence of any documented reproduction. Once a home range was established, I found no evidence that bears of either sex undertook secondary, or post-reproductive dispersal.

The adaptive significance of male-biased natal dispersal in bears is unknown, but possible explanations include inbreeding avoidance and mate competition (Rogers 1987b). Given that an extreme sex bias has been repeatedly observed under a variety of habitat and population conditions, inbreeding avoidance (Greenwood 1980, Dobson and Jones 1985, Pusey 1987) might be considered the simplest explanation for male-biased dispersal in black bears. The typical male dispersal distances observed among the various studies (i.e., >20 km) would serve to minimize the encounter rate between males and their philopatric, close female kin. Within our study populations in New Mexico, the mean distance between home range centers of mating pairs ranged from 0.6–17.8 km, with a mean of 5.9 km (Chapter 4). An analysis of the spatial genetic structure of our study populations revealed that dispersal patterns produced a low potential for close inbreeding, despite additional evidence of some short-distance dispersal among males (Chapter 5). That is, there was little evidence that mechanisms additional to dispersal, such as kin recognition by phenotypic matching, would be needed to avoid close inbreeding.

Other findings point to mate competition (Greenwood 1980, Dobson and Jones 1985, Dobson 1982) as a possible driving force for dispersal in black bears. Males engage in scramble competition for mates (Kovach and Powell 2003, Chapter 4), thus they might disperse in hopes of finding a range with adequate food and mates, but few competing males (Rogers 1987a). Our paternity analysis indicated young males (<7 years old) were more likely to father offspring when density of older, larger males (≥7 years old) was lower (Chapter 4). Increased immigration by juvenile males into areas where adult male density was low has been observed (Kemp 1976, Young and Ruff 1982, Rogers 1987a), and our

analysis of spatial genetic structure suggested short-distance dispersal by males was more common in the lower-density SSA than the higher-density NSA. This suggests young males may choose to stay close to their natal range, if chances for immediate breeding are available.

It is most likely male-biased black bear dispersal has multiple causes (Dobson and Jones 1985), including inbreeding avoidance and mate competition. I suspect the selection pressures of both of these factors have produced a fixed tendency for transiency in young males. This behavior may provide individual fitness benefits by allowing a male to select the mating range that will maximize his breeding potential and avoid inbreeding with close kin, but it also may provide inclusive fitness benefits by reducing the likelihood of inbreeding among his female kin. Repeated observations that at least some males disperse only short distances from their natal range might be explained by the relative costs of inbreeding and mate competition. Male reproductive success is highly variable and determined, in part, by the number of other males competing for breeding opportunities (Chapter 4). In polygynous species with no paternal care, inbreeding is less costly to males than to females (Waser et al 1986). In a qualitative sense, the costs of mate competition can be measured in the number of offspring, while the cost of inbreeding can be measured by the quality of offspring. Therefore, dispersing males might maximize their fitness by establishing a home range where mate competition is low, even if close female relatives are present.

DETERMINANTS OF MALE REPRODUCTIVE SUCCESS IN BLACK BEARS

Abstract

The promiscuous mating system, sexual size dimorphism, and male-biased operation sex ratio of black bears are consistent with intense sexual selection. Using DNA microsatellite analyses and field data, we examined annual male reproductive success in this solitary carnivore, and investigated individual and population characteristics that affected reproductive skew. We identified the likely father for 78 of 120 genotyped cubs born within two populations in New Mexico during 1994–2000. We calculated reproductive success for 106 males known or presumed present within designated mating regions during those years. Evidence indicated male-male competition was intense. Age was a strong determinant of reproductive success and intermediate-aged bears appeared to have a considerable reproductive advantage. Peaks in reproduction, mean weight, and frequency of bear-inflicted wounds occurred at about the same age (10–12 years), suggesting body size and fighting were important for obtaining mating access. Proximity of a male's home range center to that of an estrous female was also a significant factor determining reproductive success. Success of young males (<7 years old) was negatively associated with mature male (≥7 years old) density, and increasing density shifted the peak reproductive age higher. The dispersed distribution of females likely limited the capacity of large males to dominate reproduction. As a consequence, reproductive success was determined by a complex set of variables, including individual attributes (i.e., age, body size, and fighting ability), proximity to estrous females, and the number of other males competing for breeding opportunities.

Introduction

In polygynous species, reproductive success is expected to vary more among males than females (Clutton-Brock 1988). Particular physical or behavioral traits of males may confer an advantage in obtaining or defending mates, or signal genetic quality to females leading to sexual selection for those traits (Darwin 1871, Fisher 1915, Fisher 1930). Notable among these traits is body size (Andersson 1994). Sexual size dimorphism in many species is attributed to sexual selection for large body size in males. Higher reproductive success by large males has been observed in numerous species, from fruitflies (*Drosophila melanogaster*; Partridge et al. 1986) to gray seals (*Halichoerus grypus*; Anderson and Fedak 1985). Alternative mating strategies have evolved to enhance the reproductive success of smaller males. For example, younger, subordinate bighorn rams (*Ovis canadensis*) often use tactics less dependent on body or weapon size to achieve mating opportunities, such as coursing (i.e., sneaking) and blocking (i.e., sequestering females until they are receptive; Coltman et al. 2001).

The relative advantage of large body size, and the expression of alternative mating tactics, is dependent on the operational sex ratio (OSR; ratio of fertilizable females to sexually active males) and the spatial and temporal distribution of mates (Emlen and Oring 1977, Isvarin 2005). Emlen and Oring (1977) proposed that "the capacity for males to monopolize mates would be lower when females are uniformly distributed in space, than when they are clumped in distribution". These factors have been shown to mediate reproductive skew associated with body size, age, or dominance. For example, reproductive success of younger, subordinate male reindeer (*Rangifer tarandus*) increased when male-

female ratio became more even (Røed et al. 2002). Similarly, a pronounced skew in mating success was observed at high male density in European sousliks (*Spermophillus citellus*), but a normal distribution of mating was observed at low density (Millesi et al. 2004). Counter to these studies, changes in density or OSR may have the opposite effect, depending on the mating tactics employed by smaller, subordinate males. In European bitterlings (*Rhodeus sericeus*), sneaked fertilizations increased with male density, because the presence of many rival fish caused territorial males to draw away from courting and spawning to engage in aggression against rivals (Reichard et al. 2004). This pattern would appear more likely in species that congregate for breeding, than for species where receptive females are spatially and temporally dispersed.

Using DNA microsatellite analyses and various field data, we examined the individual and population characteristics that affected annual male reproductive success in a solitary carnivore, the black bear. The promiscuous mating system of black bears includes aspects that are consistent with intense sexual selection, including considerable sexual size dimorphism (with males weighing 1.2–2.2 times more than females; Alt 1980, Noyce and Garshelis 1998) and a male-biased OSR (created by multi-year birth intervals and asynchronous estrus). The dispersed distribution of female bears likely limits the ability of any male to monopolize breeding, because males would have to alternate between searching and guarding behaviors to maximize fitness. One strategy for monopolizing spatially-dispersed females is territoriality (Emlen and Oring 1977), but the considerable home range overlap that typically exists between neighboring males suggests bears do not employ this strategy (Lindzey and Meslow 1977, Garshelis and Pelton 1981, Chapter 2). Nonetheless, it

is possible males exhibit a degree of space-related dominance and attempt to restrict males from mating with females residing near the center of their home range. Alternatively, males may simply roam widely in search of females and rely on scramble competition for success (Schwagmeyer and Wootner 1986).

In black and brown bears, it has long been presumed that older, larger male bears are more successful in reproduction. Hornocker (1962) provided the first detailed record of brown bear breeding behavior. This established the promiscuous nature of their mating system; indicated larger, dominant bears had greater access to females; but also showed that smaller subordinate males obtained breeding opportunities (also see Craighead et al. 1995a). Later observations proved similar for black bears (Barber and Lindzey 1983, Rogers 1987a). Higher success of large males has recently been substantiated with DNA evidence in a short-term study of black bears in North Carolina (Kovach and Powell 2003), a short-term study of brown bears in Alaska (Craighead et al. 1995b), and a long-term study of brown bears in Scandinavia (Zedrosser et al 2007). Although each of these papers discussed factors that may affect the skew in age-related or size-related reproductive success, ours is the first paper designed to test possible effects.

The aim of this chapter was to test the following predictions. First, we hypothesized male reproductive success would be positively associated with age and body size (with a potential decline due to senescence). Second, we hypothesized that males would exhibit space-related dominance and restrict other males from mating with females residing near the center of their home range. Thus, we predicted that the male whose home range center is closest to a given female would be most likely to father her offspring. Third, due to the

dispersed distribution of females, we hypothesized the capacity of older, larger males to dominate reproduction would be affected by the spatial or temporal variation in the number of older, large males and the OSR. We predicted that dispersing or newly resident males would rarely father offspring, but would be more likely to father offspring when (1) many females are in estrus at the same time (i.e. the OSR becomes more even), (2) density of older, larger males is low, and (3) when a resident male dies leaving a potential home range vacancy.

Methods

Paternity Analysis

Using multi-locus genotypes, we analyzed paternity (and maternity, when necessary) using CERVUS 3.0 software (Marshall et al. 1998, Kalinowski et al. 2007). This program uses allele frequencies to calculate a likelihood of determination score (LOD) for each candidate parent. It uses simulation to derive criteria for parentage assignment, based on the difference between the highest and second highest LOD scores (ΔLOD). For our analyses, potential parents were those bears ≥2 years old (not known to be dead) during the mating season when the offspring was conceived (the year prior to the birth of the individual). For simulations, we set the strict confidence level to 0.95 and the relaxed confidence level to 0.85; the proportion of candidates sampled to 0.80; the number of candidate parents to 49 for fathers and 33 for mothers (i.e., the maximum number of candidates present within trapping areas assuming 80% of bears were sampled); the number of cycles to 10,000; the error rate to 0.01; the loci typed to 0.99; and the proportion of candidate parents related to the mother (by

0.25) as 0.05 for males and 0.10 for females (reflecting female-biased philopatry). We ran

alternate simulations with lower estimates for the proportion of candidates sampled (0.50,

0.15), for use with individuals whose birthplace was unknown or whose birth year was before

1994, however results did not differ. We accepted any parent assigned with strict

confidence, as well as fathers assigned by relaxed confidence that were common to

littermates.

Reproductive Success

To quantify reproductive success, and the factors related to it, it was critical to

correctly identify the set of males that could have fathered offspring (i.e. the denominator), as

well as those that did father offspring (i.e. the numerator). We also had to spatially and

temporally limit our analyses to those offspring for whom this set of males could be reliably

estimated. Because we radio-marked only a fraction of the bears, and could not verify the

location of each individual during each year, we used information from the analysis of space

use and dispersal to develop criteria for our sample.

The dispersal analysis indicated no females dispersed from natal areas; 1- to 3-year-

old males were actively dispersing from natal areas; most males settled within a home range

by age 4; and all males settled within a home range by age 7 years (Chapter 3). The space

use analysis indicated bears typically remained within or near their core home range during

the mating season, but traveled more widely in search of mast, such as acorns, during fall

hyperphagia (Chapter 2). The significance of these findings is that we could presume most

adult bears captured during the mating season were local residents, but we could not make

this same presumption for bears captured during the mast season or for subadult male bears

captured during any season. Finally, in our areas hunting and depredation mortality was
well-documented (i.e., known) and mortality from other sources was rare (≤0.06/year;
Costello et al. 2001). Our criteria for defining the set of males present and offspring
produced required several steps:

(1) We restricted our analyses to those years when we were actively trapping,
investigating dens, and monitoring bears with radio-telemetry. We estimated male presence
during 1993–1999, corresponding to birth years 1994–2000.

(2) For each population, we defined a sampling region by buffering pre-mast season
trap-sites by 4.0 km, which was the median distance between each location and the home
range center for radio-marked males (i.e., activity radius; Chapter 2).

(3) We compiled records of males documented as present, from trapping or radio-
telemetry, within the sampling regions during the mating season of each year. This yielded a
sample of 130 males present during 255 bear-years.

(4) We then developed age-specific criteria (Table 4.1) to infer probability of
presence (P_p) of these individuals during other years based on our knowledge of bear
movements and survival. Examples are shown in Figure 4.1. Males known present when ≥5
years old were presumed present in prior years back to age 4 years (see M168). Males
known present when ≥4 years old were presumed present in subsequent years until the end of
the sampling period (see M113) or until they were known to have died (see M145). Males
known present only as 2- or 3-year-olds were not presumed present during other years (see
M329). Males captured only during the mast season were not presumed present during the
mating season of any year. Males recaptured during the mast season were counted as present

Table 4.1. Age-specific criteria for inferring mating season presence of male black bears in years prior and subsequent to years of known presence. Products of specific probabilities were used to estimate the overall probability of presence for each male for each year.

	Prior year		Subsequent year		
Age (yrs)	Presumed present	Probability[1] (presence)	Presumed present	Probability (presence)	Probability[2] (survival)
2–3	No		No		
4	No		Yes	0.86	0.94
5	Yes	0.86	Yes	0.88	0.94
6	Yes	0.88	Yes	0.91	0.94
7	Yes	0.91	Yes	1.00	0.94
≥8	Yes	1.00	Yes	1.00	0.94

[1] Probabilities are the proportion of radio-marked black bears that used the same home range from that of the previous year (Chapter 2).
[2] Probability is estimated survival rate of male bears, excluding mortality from hunting or depredation ($n = 104$ bear-years; Costello et al. 2001).

during that year if they had previously been captured during the mating season of another year ($n = 10$ individuals). For estimating P_p, consider the following example. M331 was captured as a 6-year-old during the mating season of 1995 (corresponding to birth year 1996). We back-dated to age 5 years in birth year 1995 ($P_p = 0.88$) and to age 4 years in 1994 ($P_p = 0.88 * 0.86 = 0.76$). We forward-dated to age 7 years in 1997 ($P_p = 0.91 * 0.94 = 0.86$), 8 years in 1998 ($P_p = 0.91 * (0.94)^2 = 0.80$), 9 years in 1999 ($P_p = 0.91 * (0.94)^3 = 0.76$), and 10 years in 2000 ($P_p = 0.91 * (0.94)^4 = 0.71$). If bears were captured during multiple non-successive years, between-year P_p was set at 1.00 (see M115). Adding years of presumed presence increased the sample to 486 bear-years for the same 130 males. This sample, which included bears for which we did not obtain a genotype, was used for density estimation (see below). Our genotyped sample was 121 bears in 478 bear-years.
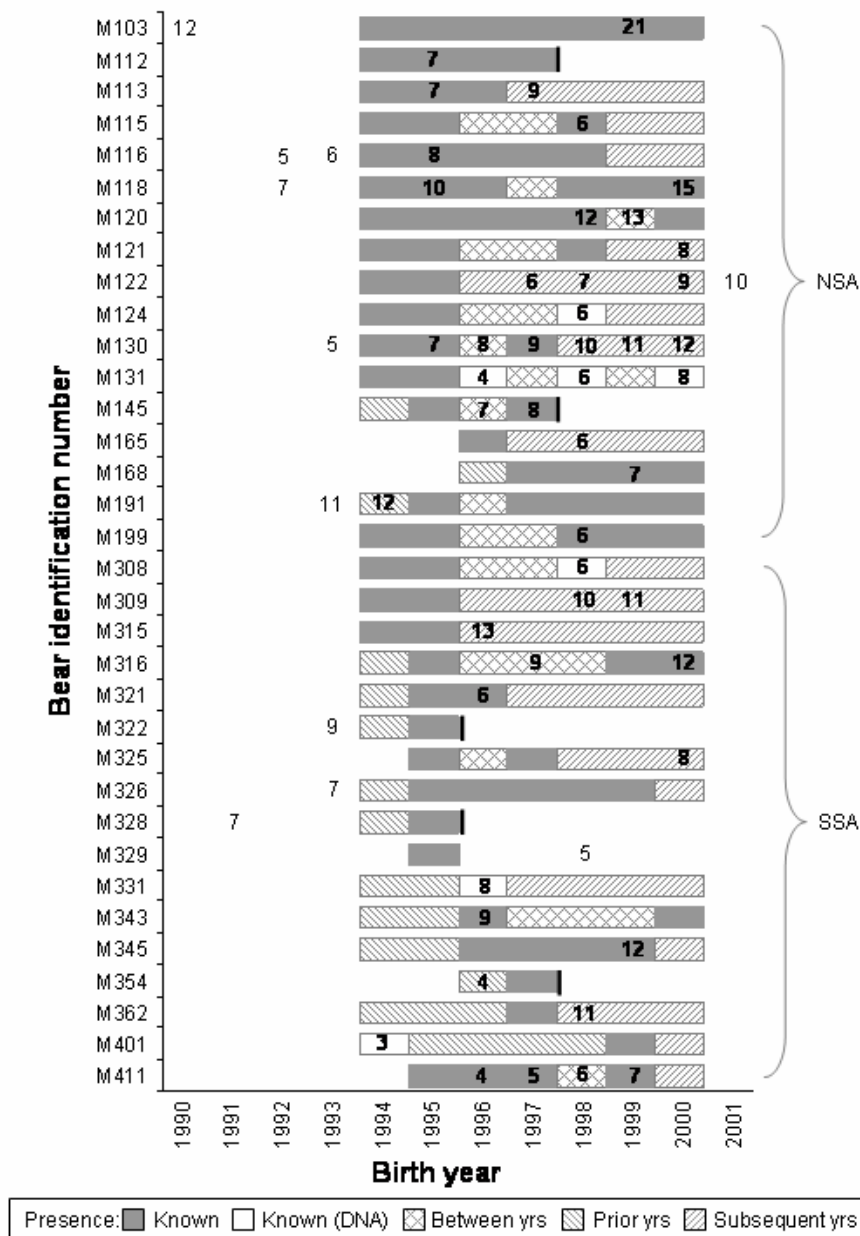
Figure 4.1. Mating season presence and reproduction, by birth-year, for 34 black bears identified as fathers. Bars represent presence of males during the sampling period. Males known present during a given year were presumed present during prior years, subsequent years, and years between using age-specific criteria. Numbers signify the age of males at the time of successful breeding, with bold numbers representing reproduction that occurred within our sampling region during the sampling period. A dark line at the right margin of a bar denotes a known mortality. Patterns of presence displayed for these successful males were representative of 87 other males who did not sire any genotyped offspring.

(5) For these males, we used capture, den, and telemetry location data to define an annual or multi-year core home range. We did the same for mothers of genotyped cubs born during 1994–2000. Using the Animal Movements extension (Hooge and Eichenlaub 2000) developed for ArcView software (Environmental Systems Research Institute, Redlands, California), we calculated the center of a 50% fixed kernel utilizing a common smoothing parameter for each sex (see Chapter 2) for most bears ($n = 75$ males, $n = 54$ females). For the remaining bears, we had limited location data, either because they were not radio-marked or they shed their radio-transmitter prematurely. For these bears, we estimated the home range center as the arithmetic mean of their x and y coordinates ($n = 55$ males). For individuals with ≥ 30 locations, the outer boundary of this kernel was used as the estimate of core home range ($n = 17$ males, $n = 43$ females). For individuals with <30 locations, we defined the core home range as a circle around the home range center, with an area equal to the mean kernel home range size for each sex (Chapter 2).

(6) We restricted our analyses to genotyped offspring of females whose home range center was within 2.4 km of our sampling region ($n = 120$ cubs in 76 litters). This distance was the median mating season activity radius of females (Chapter 2).

(7) We defined a mating region for each year by combining the estimated core home ranges of those mothers identified above.

(8) We then restricted the set of males present to those whose estimated home range overlapped the annual mating region, or those located within the region during the mating season of that year. This reduced the sample to 104 individuals known or presumed present during 336 bear-years.

(9) We merged paternity data with male presence data and recorded zeros for all males that were present, but did not sire genotyped offspring. At this point, we found that some of the identified fathers were not presumed present within mating regions. These included one male whose home range did not overlap the mating region; one male captured only during the mast season (Figure 4.1, see M331); three males captured as 2- or 3-year-olds and not forward-dated to their eventual age of reproduction (see M124, M131, and M308); and one male captured as an 8-year-old and not back-dated to age 3 years when he reproduced (see M401). Because the DNA analysis confirmed their presence during years when we were unaware of it, we revised their presence for other years using the same criteria explained above. This added 23 bear-years to the sample. The final sample included 106 males presumed present during 359 bear-years.

Effects of Covariates

Using our restricted data set, we aspired to relate male reproductive success to several covariates. We used mixed-effects logistic regression models (with bear as a random factor) to predict the probability that a male would father offspring (R version 2.4.1; lmer function; Venables et al. 2006). We used logistic regression models to the probability that an offspring was fathered by a young male (SPSS version 11.5.0 (Chicago, Illinois, USA). We used Akaike Information Critera (AIC) to compare models (Burnham and Anderson 2002).

Covariates included individual characteristics and population characteristics common to all individuals within a year. We used observed values for individual characteristics, but rounded values for population characteristics and pooled across years and study areas. This allowed us to reduce sampling error due to variation in offspring sample sizes by year. To

accommodate model comparison, we used data from birth years 1995–2000 only, because some covariates were unknown for birth year 1994.

First, we hypothesized male reproductive success would be positively associated with age and body size (with a potential decline due to senescence). Ideally, we wished to relate both age and body size to reproductive success. We obtained cementum annuli age estimates ($n = 100$) or field-based age estimates ($n = 6$) for all males in our restricted data set. As such, our estimates of age were generally reliable (Costello et al. 2004) and available for each male during each year. In contrast, we obtained only periodic measures of weight or chest girth. As age and body size were correlated, we resolved to use age, but not body size as a covariate. However, to help make inferences about the role of body size in determining reproductive success, we used linear regression to examine the relationship between age and mating season weight. For this model, as well as models for reproductive success, we entered age as a quadratic function, allowing for an asymptote and possible decline associated with senescence. The age model served as the basis for subsequent models predicting the probability of male reproduction.

Second, we hypothesized that males would exhibit space-related dominance and restrict other males from mating with females residing near the center of their home range. Thus, we predicted that the male whose home range center is closest to a given female would be most likely to father her offspring. To test this prediction, we measured the distance between the home range center of each male present within the mating region and each female with sampled cubs. By necessity, this sample required an observation for each male-female pair, therefore $n = 1572$. We ranked the each male according to distance to each

female with a maximum value of 11 (i.e. bears ranked 11–38 were pooled into one group), and we used this ranked distance to predict the probability that a male would sire offspring by year. We excluded males with distances greater than the maximum distance of successful fathers.

Third, we hypothesized that the advantage of large body size would vary with the OSR and the number and distribution of competing males. We predicted that dispersing or newly resident males would rarely father offspring, but would be more likely to father offspring when (1) many females are in estrus at the same time (i.e. the OSR becomes more even), (2) density of older, larger males is low, and (3) when a resident male dies leaving a potential home range vacancy. To test these predictions, we ran a set of competing models, built upon the age model, to predict the probability that a male would sire offspring ($n = 337$ bear-years). For each breeding season, we calculated proportion of females in estrus using reproductive data obtained during den visits the following year (Costello et al. 2003) as $1-P_Y$, where P_y = the proportion of adult females with yearlings. We rounded to the nearest 0.1 and obtained values ranging from 0.6–1.0. To obtain a density estimate, we compiled the records of mature males known or presumed present within sampling regions, then summed their values for P_p (probability of presence; see step 3 above). To ensure values were comparable between study areas, we divided the summed values of P_p by the area of the sampling regions. We then entered estimated density as values of 1–3 corresponding to low (<3.0 bears/100 km^2; actual values 2.6–2.7), moderate (3.0–3.9 bears/100 km^2; actual values 3.0–3.3), or high ($\geq$4 bears/100 km^2; actual values 4.0–4.5). As previously stated, deaths of bears from hunting and depredation were well-documented, and other deaths were relatively rare.

During 1993–1999, we documented deaths of 12 mature males residing within sampling regions. We entered this variable into models as a binomial.

Finally, using the data set with male-female pairs, we compared a set of models including age, ranked distance, and the population covariates to determine if male reproductive success was determined by a simple or more complex set of variables.

Results

Paternity Analysis

We obtained genotypes for 407 bears (79% of individuals uniquely identified during the study), with estimated or known birth years ranging from 1973–2001. Among this full data set, we identified a single likely father for 106 bears (26%; Table 4.2). We did not identify the father of any bear born prior to 1990. As expected, paternity assignment was substantially higher among the restricted data set (i.e., cubs born of known mothers within the sampling regions during 1994–2000), where we identified fathers for 78 of 120 genotyped bears (65%). This set represented 45% of offspring identified in the field within our sampling region during 1994–2000 ($n = 173$), corresponding to at least one cub from 55% of litters ($n = 101$). Accounting for the remainder of cubs, we failed to obtain a DNA sample or an acceptable genotype for 31% and failed to confidently identify a father for the other 23%.

We identified 17 fathers in the NSA and 19 fathers in SSA (Figure 4.1). These males fathered offspring with 1–8 different females ($\bar{x} = 1.9$) and produced a total of 1–16 cubs ($\bar{x} = 2.9$). By year, these males fathered cubs with 1–3 females ($\bar{x} = 1.2$) and sired 1–4 cubs

Table 4.2. Outcome of microsatellite paternity analysis of black bears sampled on the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico.

Data set	Category	NSA		SSA		Total	
		n	Father identified	n	Father identified	n	Father identified
Full[1]		212	31%	195	21%	407	26%
	Mother known	88	59%	56	50%	144	56%
	Mother identified	16	69%	9	67%	25	68%
	Mother unknown	108	2%	130	5%	238	4%
Restricted[2]		78	64%	42	67%	120	65%
	Mother known	75	65%	40	65%	115	65%
	Mother identified	3	33%	2	100%	5	60%

[1] Included all genotyped bears (birth years ranging from 1973–2001)
[2] Included offspring of mothers residing within sampling regions and born during 1994–2000.

($\bar{x} = 1.6$). Age of fathers at the time of breeding ranged from 3–21 years ($\bar{x} = 8.2$). Nineteen of 36 (53%) fathers bred more than once; the time between their first and last detected litter ranged from 0–9 years ($\bar{x} = 3.2$). Among fully-sampled, multi-cub litters with at least one father identified, multiple paternities were apparent in six of 22 (27%) NSA litters and three of 10 (30%) SSA litters.

Patterns in Body Size and Evidence of Fighting

We observed an asymptotic relationship between age and breeding season weight (Figure 4.2), with males reaching 95% of peak weight (113 kg) by 7 years of age. Predicted mean weight of 3-, 4-, 5-, and 6-year-old bears was 66%, 79%, 86%, and 92% of peak, respectively. Weight declined only slightly among bears ≥14 years old. Observations of
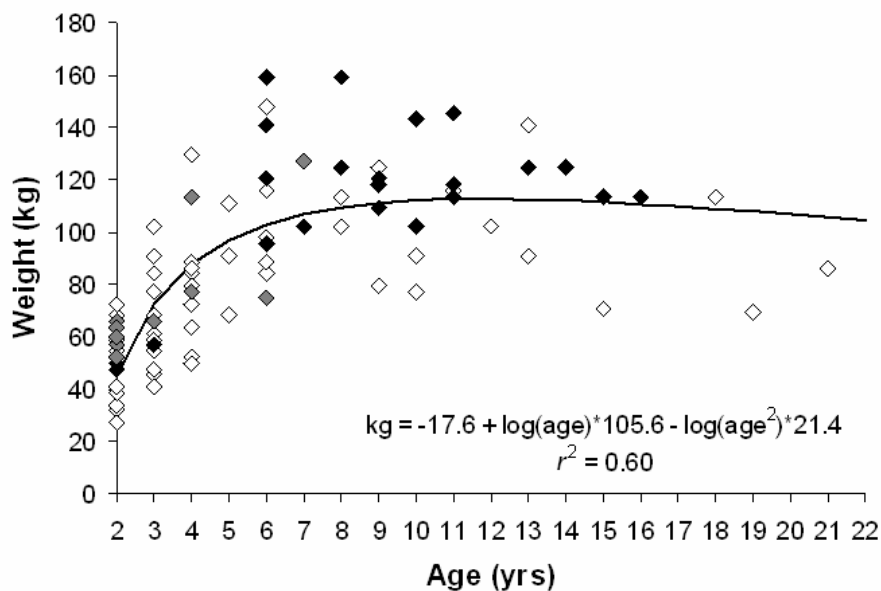
Figure 4.2. Relationship of mating season weight to age for male black bears: (gray) males that fathered cubs when young (<7 years old); (black) males that fathered cubs when mature (≥7 years old); and (white) males that did not father cubs or males for whom we did not have DNA samples. Weights were obtained only periodically, therefore weights displayed for successful males may have been obtained in years other than the one in which the male bred.

wounds (apparently inflicted from other bears) were more common during the mating season

and peaked at 11 years of age (Figure 4.3).

Patterns in Reproductive Success

Using our restricted data set, we documented reproduction by 13% of males known or

presumed present within mating regions each year and our estimate of reproductive success

was 0.22 offspring/male/year. Point estimates were slightly lower for the SSA, but

differences were not significant; 11% versus 16% for percent reproducing and 0.16 versus

0.27 offspring/male/year.
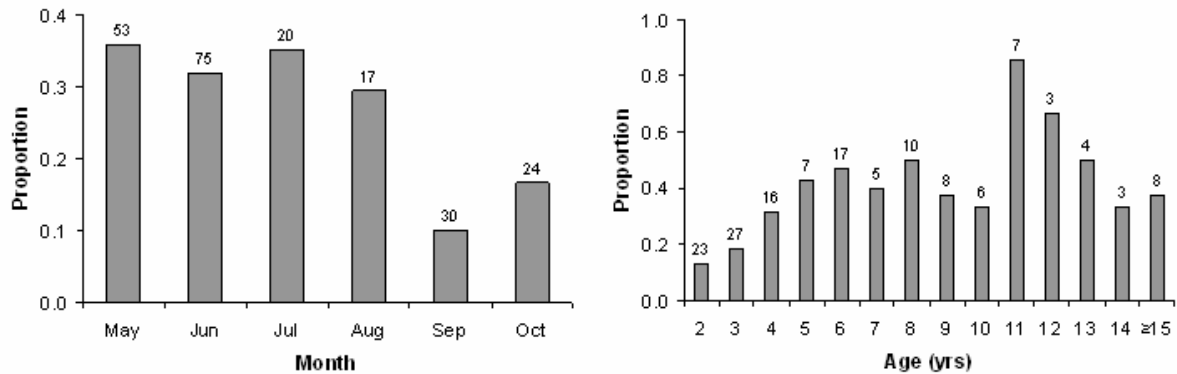
Figure 4.3. Proportion of male black bears (≥2 years old) observed with wounds apparently inflicted during fights with other bears: (left) by month; and (right) by age during the mating season only (den emergence to 20 Jul). Sample sizes are noted above bars.

Our age-specific criteria appeared to be a reasonable means of identifying males present within mating regions. Forty-two percent of males known to have fathered cubs were identified as present only by means of back-dating, forward-dating, or counting between known years. Comparing annual estimates of male versus female reproductive success, we found good correlation for annual percent of individuals reproducing ($r = 0.63$, $P = 0.02$) and number of offspring per individual ($r = 0.66$, $P = 0.02$). As reproductive success was known to vary with food availability, these correlations indicated our process for identifying males present for breeding did not create a detectable bias.

As expected, the quadratic age function was a significant predictor of the proportion of males fathering cubs during 1993–1999 (Table 4.3, Appendix A). The age model indicated reproductive success peaked at about 10 years of age (Figure 4.4).

Fifty-nine percent of cubs were fathered by males residing within one home range radius of the mother, but some successful males resided as many as two home range
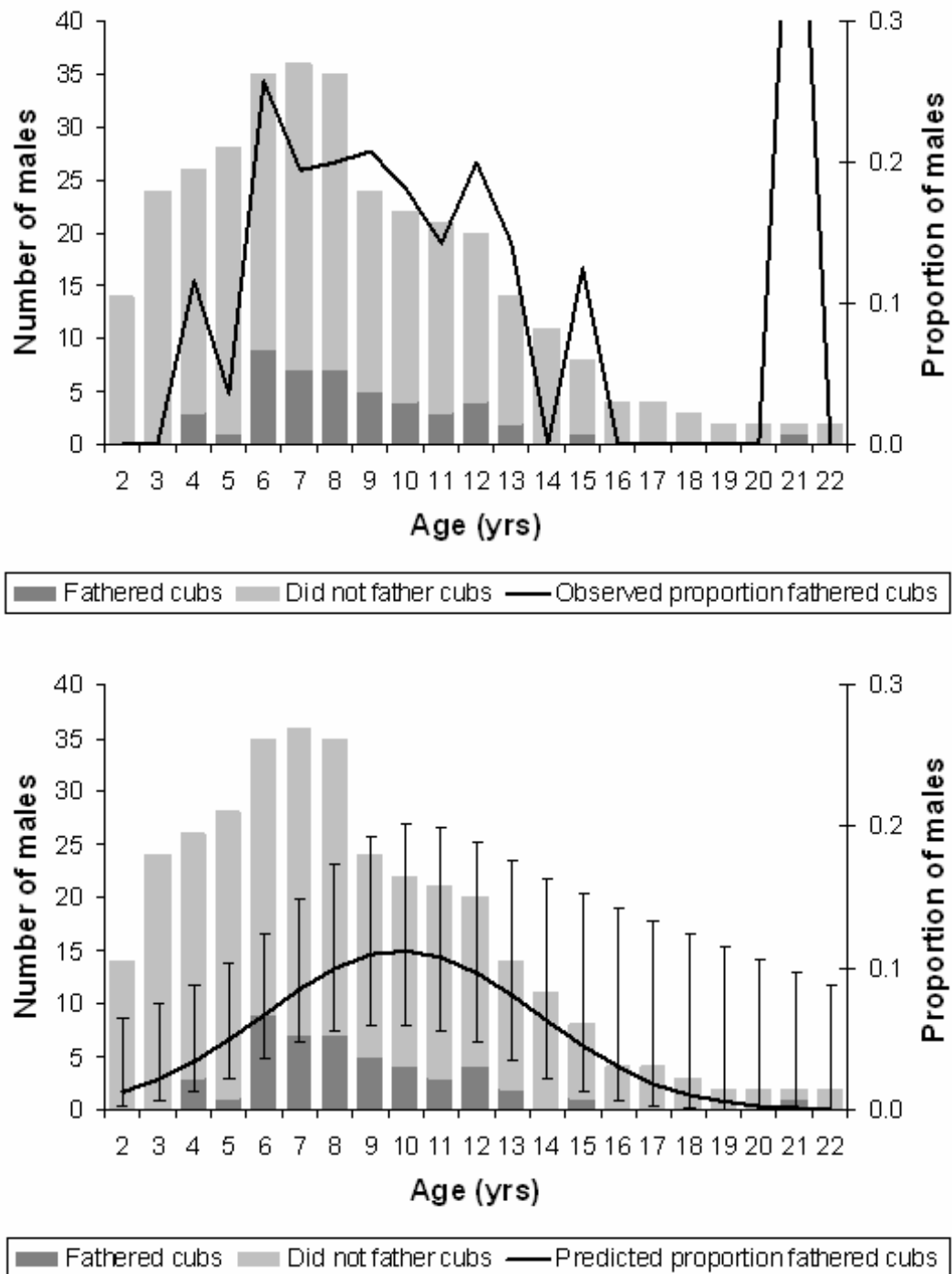
Figure 4.4. Number and proportion of males present that fathered genotyped cubs sampled within mating areas: (top) observed proportion and (bottom) model-predicted proportion (±95% CI) proportion as a quadratic function of age.

Table 4.3. Results of AIC model selection for logistic regression models predicting probability that a male fathered offspring. The top set of models included an observation for each male during each year. The bottom set of models included an observation for each male-female pair during each year.

Model	n	Groups	k	AIC	ΔAIC	Model weight
Age + age^2 + density + age*density	337	103	5	242.8	0	0.63
Age + age^2 + death + age*death	337	103	5	244.7	1.9	0.24
Age + age^2	337	103	3	246.9	4.1	0.08
Age + age^2 + estrus + estrus*density	337	103	5	248.5	5.7	0.04
Intercept only	337	103	1	251.9	9.1	0.01
Age + age^2 + distance^e + density + age*density	1572	103	6	427.4	0	0.56
Age + age^2 + distance + death + age*death	1572	103	6	429.3	1.9	0.22
Age + age^2 + distance	1572	103	4	429.5	2.1	0.20
Age + age^2 + distance + estrus + age*estrus	1572	103	6	433.3	5.9	0.03
Age + age^2	1572	103	3	456.1	28.7	0.00
Intercept only	1572	103	1	459.7	32.3	0.00

diameters away (Figure 4.5). Ranked distance for successful males ranged from 1–23 (Figure 4.5). Ranked distance was a significant factor determining reproductive success by age (Table 4.3, Appendix A). Males residing closer to the female had higher success, particularly the closest male who gained paternity in 10 of 56 cases (18%).

Two characteristics of male populations influenced the proportion of cubs sired by young males. A higher proportion of young males fathered offspring in years following the death of ≥1 mature male, and during years of lower mature male density (Figure 4.6). These trends were also apparent in analyses of reproductive success by age, where peaks in
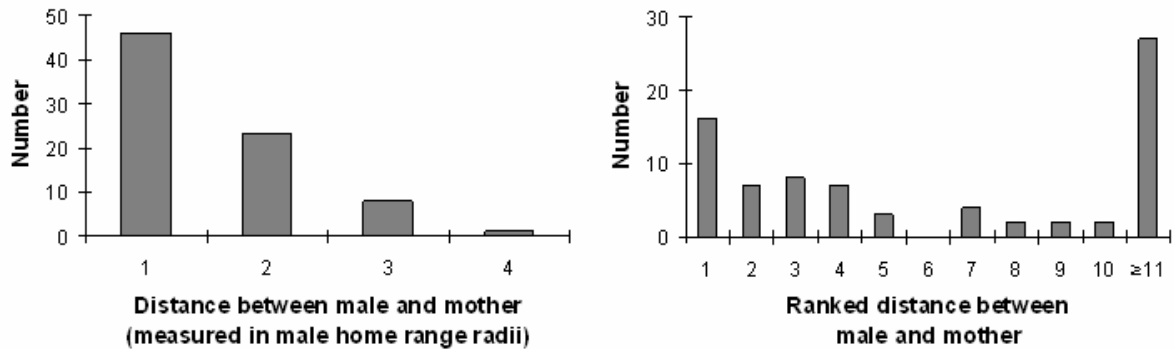
Figure 4.5. Number of cubs fathered by male black bears: (left) relative to distance of the male home range center to that of the mother (measured in home range radii); and (right) relative to distance ranked (from smallest to largest) among all males present.

reproduction shifted toward a younger age in apparent response to deaths or lower densities

of mature males (Table 4.3, Appendix A). Proportion of females in estrus did not influence

the proportion of cubs sired by young males (Figure 4.6), and it was not a significant

predictor of reproductive success by age (Table 4.3, Appendix A).
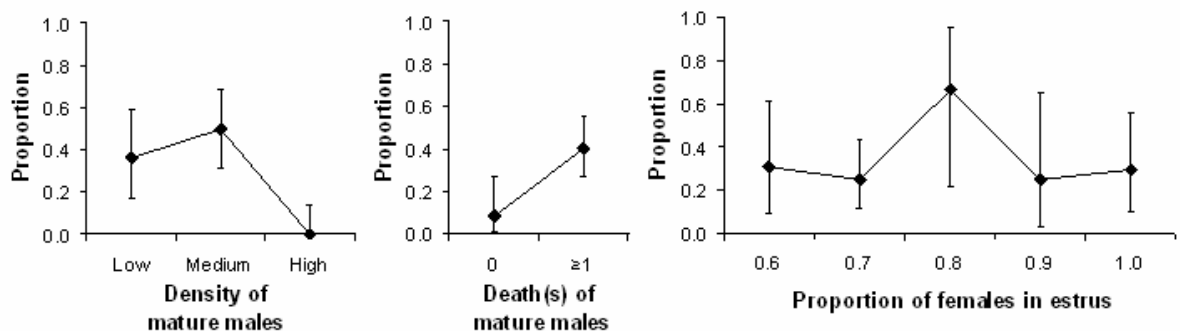
Figure 4.6. Observed proportion of cubs sired by young (<7 years old) male black bears: (left) relative to estimated density of mature ($\geq$7 years old) males during the breeding season; (center) relative to documented deaths of mature males during the previous year; and (right) relative to the proportion of females in estrus.

More complex models, which included age, either density or death of mature males, and ranked distance to the female were superior to simpler models according to AIC (Table 4.3). Based on the best model (age + age^2 + distance + density + age*density), the size advantage of intermediate-aged bears was most pronounced for those individuals residing closest to a female (Figure 4.7). Younger males had an advantage when mature male density was lower, even when they were not the closest male to a female.

Discussion

All lines of evidence indicated male-male competition was intense. On average, each estrous female had 14.7 different males overlapping her home range. As a consequence, most males apparently failed to reproduce on an annual basis. Even among the most successful age classes, fewer than 20% of bears were known to sire offspring each year. Our estimates of reproductive success were unquestionably biased low, because we did not obtain genotypes for all cubs born within sampling regions, much less within home ranges of all males bears present within the regions. However, we did obtain genotypes for over two thirds of cubs known born within study areas during 1994–2000, and this sample was likely unbiased relative to our covariates.

Reproductive success of males appeared to be determined by a complex set of variables, including individual attributes of males (i.e., age, body size, and probably fighting ability), their proximity to estrous females, and the number of other males competing for breeding opportunities. Although reproductive success was clearly enhanced for intermediate-aged bears (presumably at their physical prime), these individuals were by no
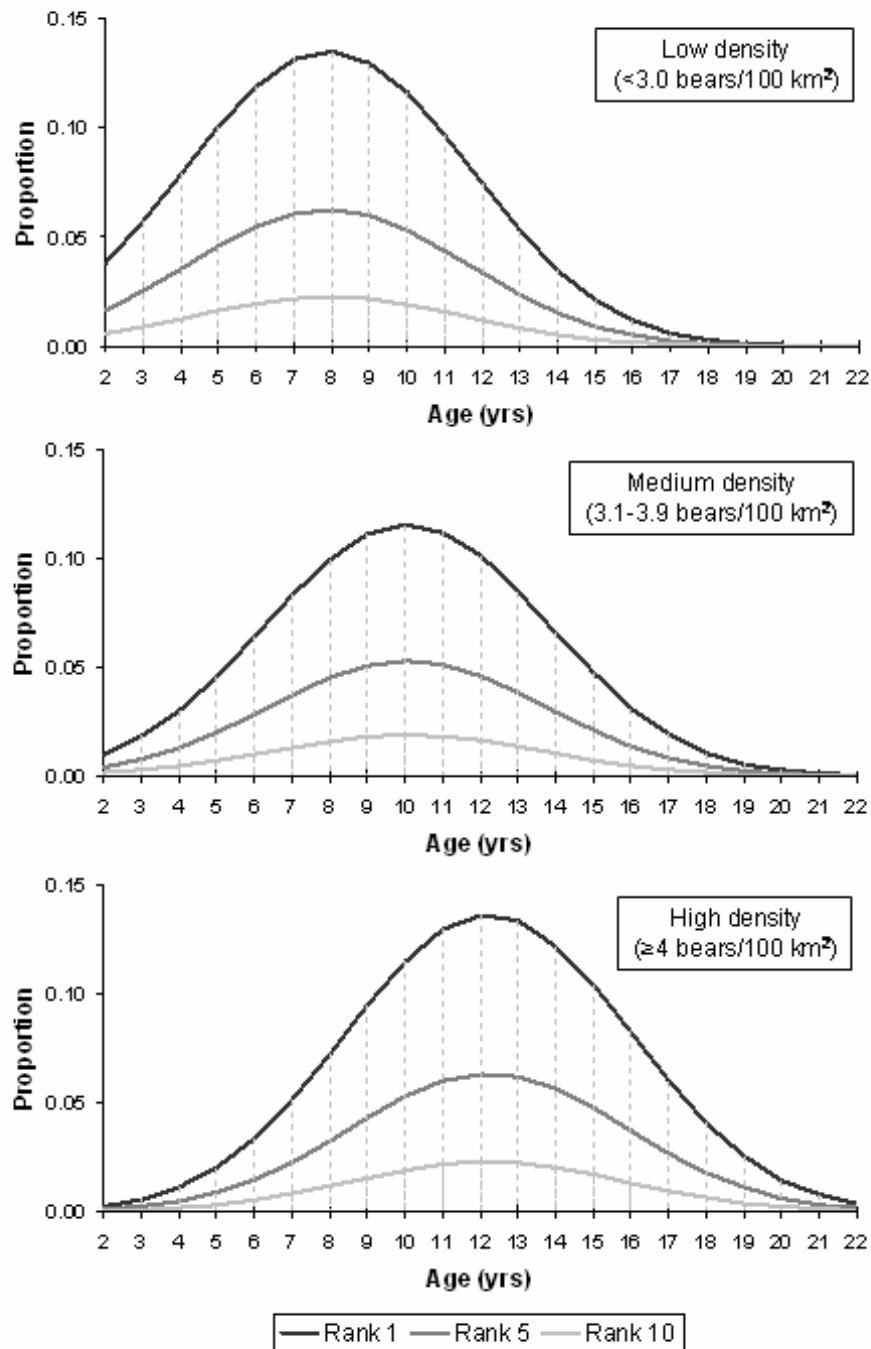
Figure 4.7. Model-predicted proportion of males black bear that fathered cubs, as a function of age, distance from the male home range center to that of the female ranked among all males present, and estimated density of mature (≥7 years old) males during the breeding season.

means guaranteed reproduction. Of 56 males present within mating regions between the ages of 8 and 13 years, only 33% were known to sire offspring. Similarly, males residing closest to an estrous female appeared to have an advantage, but were successful in only a minority of cases. Only 21% of 78 cubs were sired by the closest male, 53% by one of the closest five males, and 65% by one of the closest 10 males. Over 40% of cubs were sired by males apparently roaming outside of their core home range.

Circumstances necessitate a substantial search effort for receptive females by males. The mating season is quite long, spanning 3–5 months, with a peak in late May–June. Individual females may come into estrus at any time during this period. Females are spatially dispersed during the mating season, unlike during fall when they may congregate in patches of high quality food. As a consequence of this unpredictability, it appears a strategy of staying home and guarding females within a home range is less effective than roaming. Unlike females who typically made few excursions outside of their core home range until the onset of the mast season, males in our study areas were located outside of their core home range about 40% of the time throughout June–October (Chapter 2). In addition, distance between successive locations was highest during the mating season, suggesting males were actively searching for mates, both inside and outside of their core home range. That males were more likely to mate with females close to them was probably explained by higher encounter rates with these females, rather than spatial dominance. It appears that encountering and courting a female before rivals arrive may be an important aspect of success. Half of the 10 closest-ranking males that were successful in siring offspring were young males. It does not appear that resident males have the capacity to exclude other males

from their home range or its resident females, as is observed in territorial solitary carnivores, such as cougars (Murphy 1998), or territorial social carnivores, such as dwarf mongooses (Keane et al. 1994). It also appears roaming strategies do not differ between young and mature bears, as distribution and mean values for ranked distance did not differ between successful males of the two groups. Kovach and Powell (2003) also found that black bears of all size categories searched widely for receptive females, but large males had significantly higher encounter rates with females during their receptive periods, indicating superior ability to locate estrous females and to repel other bears from her vicinity. Bellemain et al. (2006b) found proximity was a significant determinant of paternity of brown bears, but attributed it to mate choice by female brown bears as a counter-strategy to infanticide.

Although encountering a female first may provide an unencumbered opportunity for breeding, the appearance of rivals (particularly at high male densities) would necessitate direct competition between males, either to exclude rival males from mating or to garner female preference by displaying physical superiority. Previous studies have shown that bears use physical and vocal displays, as well as fighting to exert dominance over conspecifics (Hornocker 1962, Stonorov and Stokes 1972, Herrero 1983). We found that age was a strong determinant of reproductive success, and intermediate-aged bears appeared to have a substantial reproductive advantage. The observed peak in reproductive success occurred at about the same age as peaks in mean weight and proportion of bears wounded (10–12 years), suggesting body size and fighting were important for obtaining mating access. Mating season weights of successful males were largely distributed above the median (Figure 4.2).

Reproductive success among older bears appeared to decline more than expected if body size were the sole determining factor. We fully expected reproductive senescence among only the very oldest bears, because they showed signs of deteriorating health. Based on their large body and skull size, aggressiveness in traps, and presence of fighting wounds, we had assumed bears were in prime condition and most competitive at about 12–16 years. However, there was a relatively sharp decline in reproductive success of bears ≥14 years old. Perhaps this is explained by sperm competition, which is assumed to be an important determinant in reproductive success of male bears (Kovach and Powell 2003, Zedrosser et al. 2007). Or perhaps older males retained body size, but intermediate-aged bears won out owing to superior endurance and a willingness to engage in physical contests with any male. Darwin (1871) listed "courage and pugnacity" along with the many physical attributes developed through sexual selection. Garshelis and Hellgren (1994) observed a peak in blood testosterone concentration among 6- to 8-year-old male bears in Minnesota followed by a decline in 9- to 15-year-olds. As a primary function of testosterone is to facilitate aggression (Wingfield et al. 1990), this observation coupled with our evidence of maximum fighting among intermediate-aged bears, may suggest these bears had the highest reproductive success because of their fighting superiority.

Another possible explanation for the success of intermediate-aged males is that females showed a preference for intermediate-aged individuals, as has been observed in lekking sandflies (*Lutzomyia longipalpis*; Jones et al. 2000). Age-related sexual selection may function in two opposing directions. First, it has been suggested that females may prefer older males that have demonstrated genetic quality merely by surviving (Manning 1985,

Brooks and Kemp 2001, Proulx et al. 2002). An alternative hypothesis suggests females may prefer younger or intermediate-aged males, as older males may be compromised by lower fertility and an accumulation of mutations (Brooks and Kemp 2001). Beck and Powell (2000) found the strength of age-related selection would depend on age-specific survival rates, e.g., when adult survival was high and juvenile survival was low, female preference for older males was unlikely to evolve. Like other bear populations, we observed the lowest survival rates in juvenile bears; 0.55 for cubs (Costello et al. 2001) and 0.84 for yearlings (Costello et al. 2001). Most mortality among these age classes was from natural causes. In contrast, most mortality of adult bears was human-caused and the adult male survival rate, excluding human-caused mortality, was 0.94 (Costello et al. 2001). Therefore, longevity may not be a particularly strong signal for male quality in bear populations. To a female selecting a mate, the fact that a male has reached the age of sexual maturity may be demonstration enough of genetic quality.

As expected, we observed low reproductive success among younger, smaller males. The absence of reproduction by some young males was probably due to sexual immaturity. Age of sexual maturity, based on presence of fully formed spermatozoa, has been found to range from 2–3 years in a single study of black bears (Erickson et al. 1964) and 2–7 years in various studies of brown bears (Pearson 1975, White et al 1998, Tsubota and Kanagawa 1991). In a study of black bears in Michigan, evidence suggested black bears <60 kg were sexually immature (Erickson et al. 1964). Garshelis and Hellgren (1994) found lowest levels of blood testosterone in 1- to 2-year-old black bears, and low levels in 3-year-olds, as compared to bears considered adult (≥4 years old). Postponement of reproductive maturity

may be adaptive trait, as resources otherwise used for mating attempts can be used for body growth which will enhance future reproduction (Jarman 1983). The youngest age of male reproduction we observed was 3 years, the same as previously reported for *Ursus* (Kovach and Powell 2003, Zedrosser et al. 2007), indicating that some males reach reproductive maturity by this age.

There were interesting patterns in the reproductive success of these younger bears, associated with factors of male demography. Higher density of large, mature males appeared to impede reproduction by young males. We can only speculate about the means by which young males gained mating opportunities, however it is doubtful small males directly challenged older males as much as three times their size. Given the relatively high survival of adult males, it is unlikely a small male would risk injury or death for a current reproductive opportunity given the potential for later reproduction once he has attained large body size (Jarman 1983). However, weights of successful young males were distributed above the median estimate more often than not (Figure 4.2), suggesting the successful young males may have had a size advantage over other males in their cohort. We did observe fighting wounds on males as young as 2 years, possibly incurred in attempts to sneak mating. The relationship with density suggests success of young male is probably contingent on the spatially and temporally dispersed distribution of receptive females. At low densities, subordinate males may find unattended females more often than at high male densities and this may provide them with mating opportunities.

We found male reproductive success was correlated with female reproductive success, but were surprised to find it was not associated with proportion of females in

estrous. Neither did evidence support our hypothesis that young males would have higher reproductive opportunities in years when a higher proportion of females were in estrus. The apparent de-coupling of proportion of females in estrous and reproduction may be explained by the effect of food availability on reproductive output. In bears, timing of breeding and parturition are independent owing to delayed implantation (Wimsatt 1963). This process allows breeding to occur early in the active season when it would not interfere with the prolonged fall foraging necessary to build up fat stores for hibernation. Female black bears give birth in winter dens, and in addition to their own metabolic requirements must fulfill the energetic demands of gestation and lactation during the hibernating phase. Even after mating occurs, it is postulated that delayed implantation may also allow females, with fat stores insufficient for gestation and lactation, to forego reproduction by not implanting the blastocyst (Bunnell and Tait 1981). No hard evidence of this process had been found, however lack of litter production has been linked to poor nutritional status (Kolenosky 1990, Noyce and Garshelis 1994, Samson and Huot 1995). In our study areas, natality declined by about 60% following failures in acorn production (Costello et al. 2003). Male reproductive success was evidently constrained by this extrinsic factor of food availability. In all likelihood, males that successfully bred females in the spring and summer were, nonetheless, unsuccessful in producing cubs due to reduced parturition following acorn failures.

Adult male bears have often been given credit for regulating population density, primarily through killing or evicting younger males from their home ranges (Bunnell and Tait 1981). However, this premise has also received criticism, and Taylor (1994) argued strongly that evidence of density-dependence has not been adequately demonstrated in bears.

Indeed, little evidence exists for a pattern of spatial dominance among male bears. The sizeable home range overlap observed among males suggests they do not have exclusive use of food resources within their range and regularly tolerate the presence of other males (Lindzey and Meslow 1977, Garshelis and Pelton 1981). In our study, core home range overlap of neighboring males was as high as 78% (Chapter 2). Adding to this, results from this study indicate males are incapable of maintaining exclusive access to females within their range, even at its very core. Therefore, the premise that large, dominant males benefit by evicting younger males from their home range has little merit.

Instead, our results suggest an indirect, and less lethal, mechanism by which the presence of mature males might influence *local* population density and composition, contingent on immigration of dispersing males. This idea was also proposed by Rogers (1987a). Dispersal from natal areas is high for male bears, and dispersing males are known to travel large distances before settling in a more permanent home range (Chapter 3). Besides selecting for areas with adequate food and cover, young males also likely select for sites based on opportunities for reproduction. Our results indicated higher densities and lower turnover of mature males reduced the immediate chances of mating for young males, making areas with high male density less appealing than areas with low male density for establishment of a home range. Localized loss of mature males from hunting or other human-caused mortality may, therefore, encourage immigration of young males. In a species where alleviating conflict with humans is an important aspect of their conservation, this possibility has management implications. At the wildlife-human interface, presence of large numbers of young male bears is undesirable, because of their higher tendency to investigate

and exploit sources of anthropogenic foods (Rogers 1976). Among our study bears, 46% of 32 individuals known or suspected of nuisance activity were young males. Our results suggest management strategies aimed at maintaining populations dominated by mature bears in areas close to humans, while focusing hunting effort (particularly trophy hunting) in more remote areas may play a role in reducing bear-human conflict. Of course, this strategy would require concurrent efforts to reduce availability of anthropogenic foods to bears, so as to ensure mature bears were not removed as a result of nuisance behavior. Existence of mature bear populations may also serve to dampen the typical upsurge in nuisance behavior observed during periods of natural food shortage (Rogers 1976). Older and larger individuals, with more adequate fat reserves, may be more likely to endure these periods without resorting to anthropogenic foods.

SEX-BIASED NATAL DISPERSAL AND INBREEDING AVOIDANCE IN AMERICAN BLACK BEARS AS REVEALED BY SPATIAL GENETIC ANALYSES

Abstract

We tested the hypothesis that sex-biased natal dispersal reduces close inbreeding in American black bears, a solitary species that exhibits nearly complete male dispersal and female philopatry.   Using microsatellite DNA and spatial data from reproductively mature bears (≥4 years old) we examined the spatial genetic structure of two distinct populations in New Mexico from 1993–2000. As predicted, relatedness (r) and the frequency of close relationships (parent-offspring or full sibling) decreased with distance among female dyads, but little change was observed among male or opposite-sex dyads. Neighboring females were more closely related than neighboring males. The potential for inbreeding was low. Most opposite-sex pairs that lived sufficiently close to facilitate mating were unrelated and few were close relatives. We found no evidence that bears actively avoided inbreeding in their selection of mates from this nearby pool, as mean r and relationship frequencies did not differ between potential and actual mating pairs (determined by parentage analysis). These basic patterns were apparent in both study areas despite a nearly two-fold difference in density. However, the sex bias in dispersal was less pronounced in the lower-density area, based on proportions of bears with male and female relatives residing nearby. This result suggests that male bears may respond to reduced competition by decreasing their rate or distance of dispersal. Evidence supports the hypothesis that inbreeding avoidance is achieved by means of male-biased dispersal, but also indicates competition (for mates or resources) modifies dispersal patterns.

Introduction

Patterns in natal dispersal and philopatry affect the demography and genetic structure of populations, as well as the evolution of social behavior (Waser and Jones 1983). In many species, one sex is typically philopatric, while the other is prone to dispersal. Male-biased dispersal and female-biased philopatry are common characteristics of mammals, while the opposite is typical of birds (Greenwood 1980). Logically, sex-biased dispersal is expected to generate a non-random pattern of relatedness among adult cohorts residing in close proximity. Avoidance of inbreeding is one among several hypotheses put forth to explain sex-biased dispersal. Greenwood (1980) proposed that the direction of the sex bias is a consequence of the mating system and resource competition. In mammals, selection would favor philopatry in females, because they bear the burden of raising offspring (Greenwood 1980). Building on this connection between breeding system and dispersal, Wolff (1993, 1994) further developed the inbreeding avoidance hypothesis for mammals. He contended that daughters typically grow up in the absence of their father due to polygyny and the short breeding tenure characteristic of most male mammals. Thus, females would not have to disperse to avoid inbreeding. As a consequence of female philopatry, most males would be compelled to disperse to avoid inbreeding with their mothers or other female kin. As originally formulated, this argument does not explicitly address the point that costs of inbreeding accrue not only to the male, but also to the female relative with whom he mates. Nonetheless, in experimental and observational studies, inbreeding avoidance has been found to be a proximate, and some argue, an ultimate cause of sex-biased dispersal in mammals (Dobson 1979, Cockburn et al. 1985, Keane 1990, Wolff 1992, Loison et al. 1999).

We investigated the genetic structure of two American black bear populations in New Mexico from 1993–2000 to examine the possible relationship between dispersal and inbreeding avoidance. Black bears are solitary omnivores exhibiting overlapping home ranges (Amstrup and Beecham 1976, Garshelis and Pelton 1981, Horner and Powell 1990) and a promiscuous mating system (Schenk and Kovacs 1995, Kovach and Powell 2003, Onorato et al. 2004). A pronounced sex bias in dispersal has been observed (Rogers 1987b, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Beck 1991), though observations have been limited in some potentially important ways. First, attempts to document black bear dispersal have been rare, probably owing to reluctance to radio-mark juvenile males due to the difficulty and expense of maintaining contact during a period of wide-ranging movements, as well as the potential for collar injuries resulting from rapid growth. Second, most studies of black bear dispersal have successfully documented emigration from natal ranges, but settlement in breeding ranges has rarely been observed due to mortalities, shed transmitters, and loss of contact. Data available, however, show such a high frequency of emigration by male bears as to suggest the behavior may be nearly universal. In contrast, few cases of female dispersal have been reported. Summarizing published data, only 6% of 79 juvenile females emigrated from their natal range (Rogers 1987b, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Beck 1991). Radio-telemetry results from New Mexico corroborated these findings (Costello 2008). Mean distance between the center of the natal home range and the most recent annual range ($\geq$3 years old) was 34.0 km for males, but only 2.9 km for females.

The purpose of this study was to quantify the effect of this sex-biased dispersal on the genetic structure of the populations and the potential for close inbreeding. Our working hypothesis was that male-biased dispersal reduces close inbreeding by limiting the spatial overlap of opposite-sex pairs of close relatives. We further hypothesized that the resulting spatial genetic structure would minimize for the need for active inbreeding avoidance (via kin recognition) among potential mates residing near one another. Based on these hypotheses, we made the following specific predictions: (1) relatedness among female pairs would decrease with distance, but relatedness among male pairs and opposite-sex pairs would not differ with distance (or would be less correlated with distance), (2) closely related opposite-sex pairs would rarely live in close proximity to each other, and (3) as a consequence of predictions (1) and (2), opposite-sex pairs residing near one another would mate at random relative to relatedness.

Methods

To examine genetic structure, we estimated relatedness and distance between each pair of adult bears that lived in the same study area at the same time. As our focus was spatial genetic structure in the population of post-dispersal, potentially breeding individuals, we restricted our analyses to pairs of bears that were both ≥4 years old. Previous analyses indicated that most bears settled into their adult home range by four years of age (Chapter 3), similar to another study (Rogers 1987a). The youngest documented breeding age was three for both males and females (Costello et al. 2003, Chapter 4), but successful breeding at this age was rare (i.e., four of 46 [9%] females, one of 27 [4%] males). Our unbiased estimate

(Garshelis et al. 1998) of mean age of first breeding was 4.7 years for females (Costello et al. 2003) and 6.5 years for males (Chapter 4). We further restricted analyses to those dyads that were known or presumed to occupy their home ranges during the same year. We presumed that bears captured as adults were present within their home range from age four until the end of the study, unless they were known to have died. This assumption is justified because human-caused mortality was well-documented (i.e., known) and mortality from other sources was rare (≤0.06/year; Costello et al. 2001). Finally, we restricted analysis to bears located at least once during the period between den emergence and 20 July (pre-mast season), when bears typically stay within or close to their established home range. It was not possible to ascertain whether bears captured after this date had breeding ranges within the study area, because bears travel widely in search of food during fall hyperphagia (mast season). We characterized each dyad by sex: female-female, male-male, or female-male. This yielded a sample of 5,858 dyads (2473 NSA and 3385 SSA) comprised of 161 individuals (80 F and 81 M; 74 NSA and 87 SSA). Of these dyads, 25% were female-female, 26% were male-male, and 49% were female-male.

We estimated a home range center for each bear and determined the distance between home range centers for each dyad of bears. Incremental analysis, to determine change in the estimated home range center with sample size, indicated a minimal sample of pre-mast locations was needed to estimate the home range center. For most bears (125 of 161 [78%]), we calculated a 50% kernel home range (Silverman 1986) fit with a smoothing parameter of 3800 m for males and 1800 m for females, based on 6–100 locations ($\bar{x} = 37.5 \pm 24.1$ SE). These values were the rounded mean of h_{ref} for bears with ≥30 locations (see Chapter 2).

Most of these ranges were represented by a single contour. When ranges were represented by two, or more rarely three contours, one contour typically contained predominantly pre-mast season locations, while the other(s) typically contained mast season locations. The home range center was estimated as the center coordinates of the kernel contour dominated by pre-mast season locations. For animals known to have dispersed (i.e., those that moved to a new home range ≥20 km from their natal range; Costello 2008), we used contours containing post-dispersal locations. These analyses were conducted using the Animal Movements 2.0 extension (Hooge and Eichenlaub 2000) developed for ArcView 3.3 software (Environmental Systems Research Institute, Redlands, California). For the remaining 36 (22%) bears, we had limited location data (only 1–3 locations), either because they were not radio-marked or they shed their radio-transmitter prematurely. We estimated their home range center as the arithmetic mean of their locations. Patterns in relatedness versus distance were very similar regardless of whether we included the bears with limited data. However, we chose to include these bears, because it allowed us to boost the overall sample size (which was important when distance was small) and to balance the number of observations between the sexes (since fewer males were radio-marked).

We used ML-Relate (Kalinowski et al. 2006) to obtain a maximum likelihood estimate of the coefficient of relatedness, r, for each dyad. In addition, we also identified the most likely relationship between bears in each dyad. Within this sample of mature bears, we had 32 dyads with verified relationships: six mother-offspring pairs known from field observations; and 10 mother-offspring, 11 father-offspring, one full sibling, and four half sibling relationships determined by parentage analysis using CERVUS 3.0 software

(Marshall et al. 1998, Kalinowski et al. 2007, Chapter 4). Although parentage analysis

allowed us to identify parent-offspring relationships with 95% confidence, it did not allow us

to identify full or half sibling relationships unless the parents were included in our sample

(which was unlikely for many of the older bears). Using maximum likelihood, ML-Relate

determines a single "most likely" relationship for each dyad among four categories: parent-

offspring (PO), full sibling (FS), half sibling (HS), or unrelated (U [i.e., all relationships with

relatedness lower than half siblings]). Unfortunately, the likelihood obtained for the most

likely relationship was often not much higher than the likelihood(s) obtained for other

categories. ML-Relate provides a simulation method to determine which of the four

relationship categories were consistent with genetic data for $\alpha = 0.05$. We ran this analysis

(using 50 randomizations) and found 85% of dyads had >1 relationship consistent with the

data. Consequently, we used this output to estimate the "most distant" relationship consistent

with the data. Neither the most likely nor the most distant categorization appeared to be

completely accurate for assessing the true relationship for all dyads. Using the most likely

relationship, 78% of our verified relationships were correctly identified, but another 225

dyads were also identified as PO. It was quite unlikely that we failed to identify this many

PO relationships using CERVUS, suggesting the most likely relationship was biased toward

relationships closer than reality (similar to other estimators; Van Horn et al. 2008). Only 3%

of our verified relationships were correctly identified using the most distant relationship,

suggesting it was biased toward relationships more distant than reality (as expected).

Consequently, we examined relationship frequencies among dyads using both the most likely

and the most distant relationships, and presumed the true relationship frequencies fell

somewhere between them. This dual analysis allowed us to explicitly test the sensitivity of

our inferences to uncertainties inherent in all current methods of estimating relationships.

Finally, where relationships were known from other data, we substituted these known

relationships into both categories (most likely and most distant). This methodology was

consistent with the suggestions of Van Horn et al. (2008), who recommended assigning

ranges of possible kinship derived from a combination of pedigree data and pairwise genetic

estimators of relatedness, to overcome the limitations in accuracy and precision of current

methods.

We tested for relationships between distance and relatedness by estimating the

correlation coefficient between distance and *r* for each sex category. We used a

randomization method akin to the Mantel test (Mantel 1967) to obtain a significance level,

which accounts for the unavoidable lack of independence in dyadic data (i.e., many dyads

shared one bear in common). The *r* column was subjected to 10,000 random permutations, a

distribution of correlation coefficients was obtained for the randomized data, and the

proportion of values more extreme than the observed value was determined (i.e., the p-

value). Second, we examined mean *r* and relationship frequencies for dyads within three

distance categories: 3 km, 6 km, and 35 km. Three km was the rounded mean distance

between an adult female and her mother (i.e., female natal dispersal distance). Six km was

the rounded mean distance between mating pairs (i.e., mating distance) as determined by

parentage analysis. Forty km was the rounded mean distance between male offspring and

their mother (i.e., male natal dispersal distance). We calculated mean and 95% confidence

intervals for *r* within these distance categories to compare across sexes and study areas. We

determined frequencies of relationships within these distance categories and used the χ^2 statistic to test for differences by sex and study area. To determine whether bears selected mates according to relatedness within the pool of spatially available mates, mean r and relationship frequencies observed for actual mating pairs (determined by parentage analysis) were compared to those expected from opposite-sex dyads occurring within the mean mating distance. Analyses were conducted using SPSS 11.5 (Chicago, Illinois, USA) and the PopTools 2.7 add-in (Hood 2006) for Microsoft Excel 2000 (Redmond, Washington, USA).

All analyses were run separately for each study area and then with data pooled from both areas. In this context, 'pooled' does not mean we considered dyads with one bear from the NSA and one bear from the SSA. It means data from the two sites were combined after within-site analyses. Where patterns were the same on both study areas, we report only the pooled result.

Results

Our full microsatellite data set consisted of 8–11 loci typed for 407 bears; 212 bears from the NSA and 195 bears from the SSA (Table 5.1). This represented 79% of bears identified during the study and 95% of bears from whom samples were collected. We failed to obtain genotypes for 15 bears and misplaced samples for 8 bears. No significant deviations from Hardy-Weinberg equilibrium were observed for any of the 11 loci ($P > 0.05$). Among our sample of ≥4-years-old bears, we obtained r coefficients for pairs ranging from 0.0 to 0.79, with a mean of 0.080 in the NSA and 0.089 in the SSA. The most likely

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Table 5.1. Number of alleles (*k*), number of individuals typed (*n*), observed heterozygosity (*H$_o$*), and expected heterozygosity (*H$_e$*) for 11 microsatellite loci sampled from black bears in the Northern Study Area (NSA) and Southern Study Area (SSA), New Mexico. No significant deviations from Hardy-Weinberg equilibrium were observed (*P* > 0.05 for χ2 tests at all loci).

Locus	NSA				SSA			
	k	*n*	*H$_o$*	*H$_e$*	*k*	*n*	*H$_o$*	*H$_e$*
Cxx20	6	201	0.57	0.60	6	189	0.32	0.30
G10J	7	212	0.72	0.72	7	194	0.70	0.71
G10L	8	211	0.84	0.80	8	193	0.80	0.79
G10O	5	209	0.40	0.42	2	193	0.13	0.13
G10P	7	210	0.51	0.50	6	193	0.57	0.55
G1D	6	211	0.80	0.76	6	192	0.76	0.72
Mu05	5	210	0.35	0.41	5	193	0.43	0.42
Mu10	7	210	0.68	0.67	6	194	0.62	0.68
Mu15	4	212	0.58	0.61	3	195	0.44	0.46
Mu23	5	212	0.51	0.51	2	195	0.35	0.36
Mu59	7	212	0.65	0.65	8	195	0.71	0.71

relationships (MLR) were 79% U, 15% HS, and 6% PO/FS, while the most distant

relationships (MDR) were 92% U, 7% HS, and ≤1% PO/FS.

Spatial Genetic Structure

As predicted, relatedness was negatively correlated with distance among female dyads (*r* = -0.03, *P* = 0.03), but was not correlated with distance among male dyads (*r* = 0.001, *P* = 0.41) or among female-male dyads (*r* = -0.0004, *P* = 0.50). Across all distance categories, mean *r* was higher for female dyads than for male dyads or female-male dyads,

although 95% CI overlapped (Figure 5.1). Viewed in more details, these differences were

attributable to a higher frequency of close relationships among female dyads (Figure 5.2).

Whether we classified dyads according to the MLR or the MDR, we detected significantly

more PO/FS relationships among female dyads than either male dyads or female-male dyads

within the same distance (χ^2 $P \leq 0.03$). Understandably, our sample size of dyads increased

with distance category: $n = 367$ within 3 km, $n = 1152$ within 6 km, and $n = 5308$ within 35

km. Within the mean male dispersal distance (i.e., 35 km), the large sample allowed us to

detect statistically significant differences between female dyads and both male dyads and
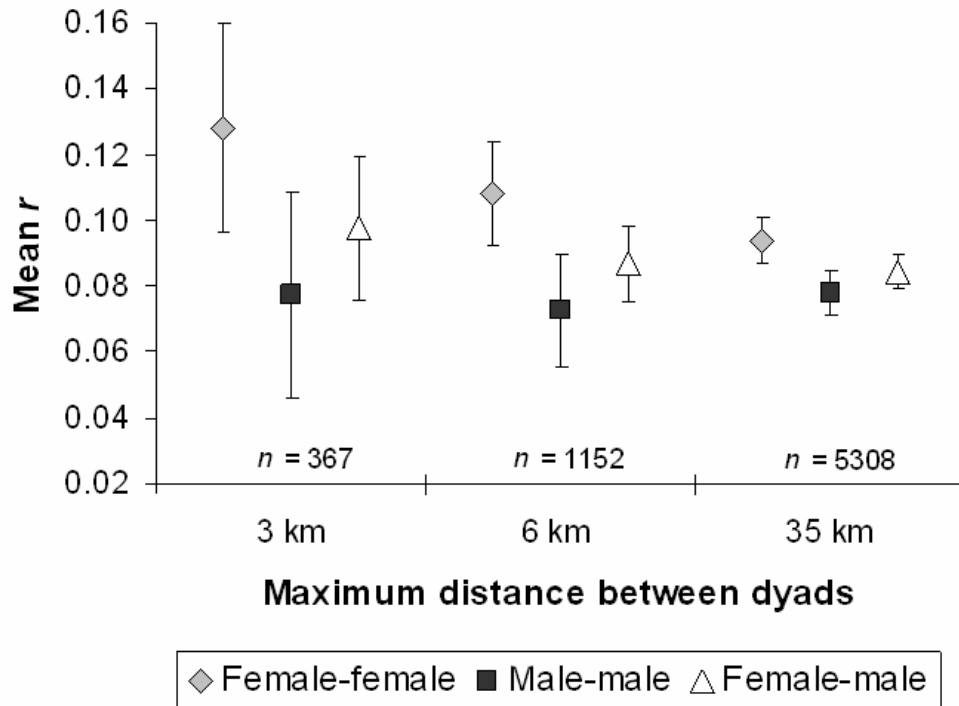
Figure 5.1. Mean (±95% CI) relatedness coefficient (*r*), by distance and sex, among dyads of black bears (≥4 years old). Based on field data and parentage analysis, 3 km was the rounded mean distance between a philopatric adult female and her mother, 6 km was the rounded mean distance between mating pairs, and 35 km was the rounded mean male dispersal distance.
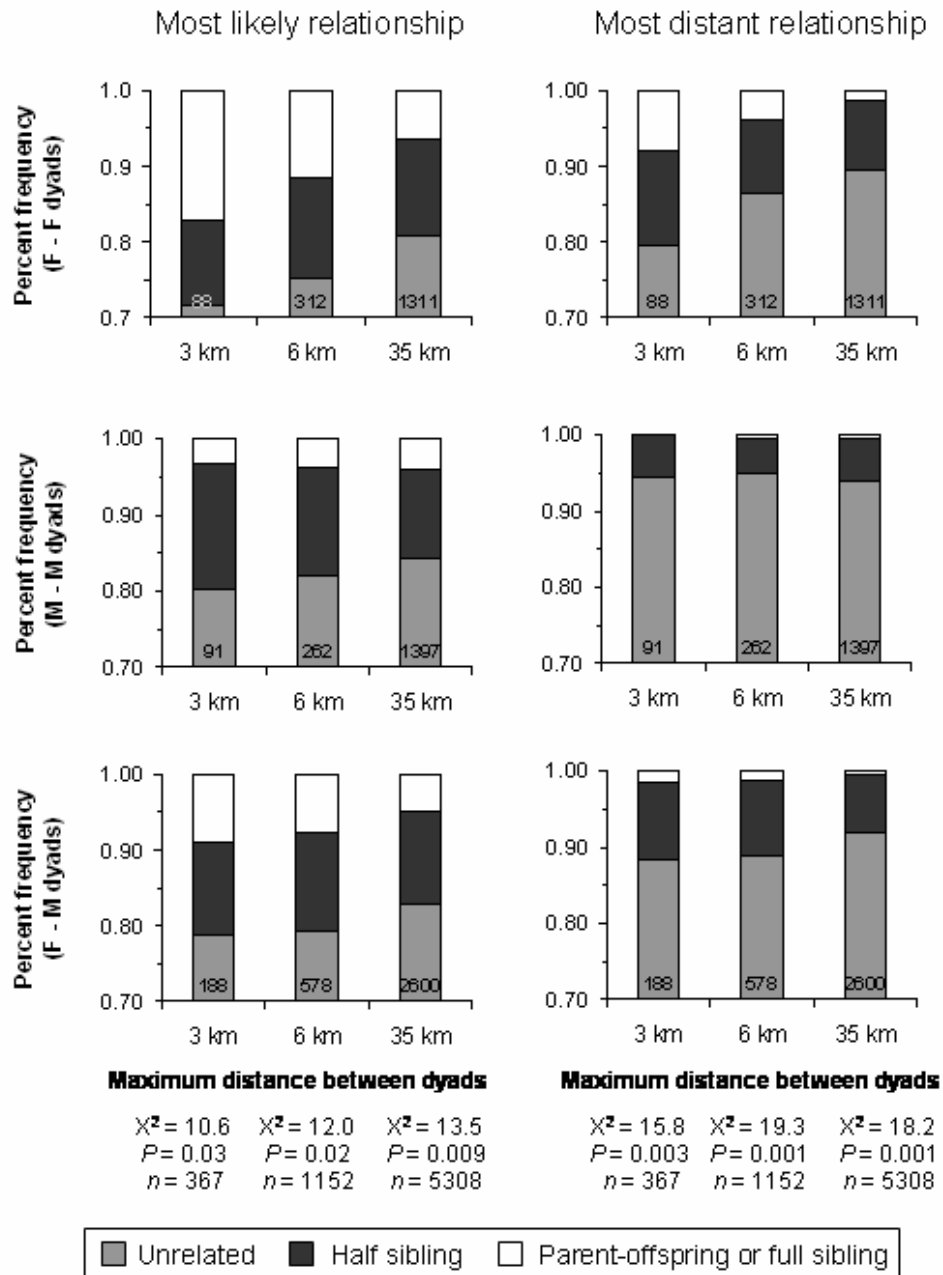
Figure 5.2. Percent frequency of relationships, by distance, among dyads of black bears (≥4 years old): (top) female-female dyads; (center) male-male dyads; and (bottom) female-male dyads. Dyads were classified according to the most likely relationship (left) and the most distant relationship (right). Note the y-axis begins at 0.70 to better illustrate differences among groups. Sample sizes appear within each bar and test statistics refer to vertical comparisons of relationship frequencies among sexes within a distance category.

female-male dyads, however the differences were very small and probably not biologically significant. On an individual basis, a lower proportion of bears had a male relative residing with 6 km than had a female relative residing within that distance (Figure 5.3). However, when study areas were examined separately, the difference was absent or less pronounced in the SSA.

Inbreeding Avoidance

Within the mean mating distance, most opposite-sex dyads were unrelated: 79% based on the MLR or 89% based on the MDR (Figure 5.4). Only 8% (MLR) or 1% (MDR) of these dyads consisted of PO/FS pairs. If we examine bear ages in these dyads and assume an age difference of ≥4 years between parents and their offspring, then father-daughter relationships appeared to be most common (45% using MLR or 88% using MDR), followed by full sibling relationships (39% using MLR or 13% using MDR) and mother-son relationships (15% using MLR).

Among 56 actual mating pairs, mean r was 0.067 and this value did not differ from the mean for all opposite-sex dyads residing with the mean mating distance, 0.087 ($t = 0.51$, $P = 0.61$). As expected if mating within the pool of spatially available mates was random, most of the actual mating pairs were unrelated (84% using MLR or 91% using MDR). Only three dyads (5%) consisted of PO/FS pairs using MLR; none using MDR. Again, if we assume an age difference of ≥4 years between parents and their offspring, then two of these three PO/FS mating pairs appeared to be full sibling relationships and one appeared to be a father-daughter relationship. We observed no mother-son relationships among mating pairs. Relationship frequencies did not differ between mating pairs and opposite-sex dyads residing
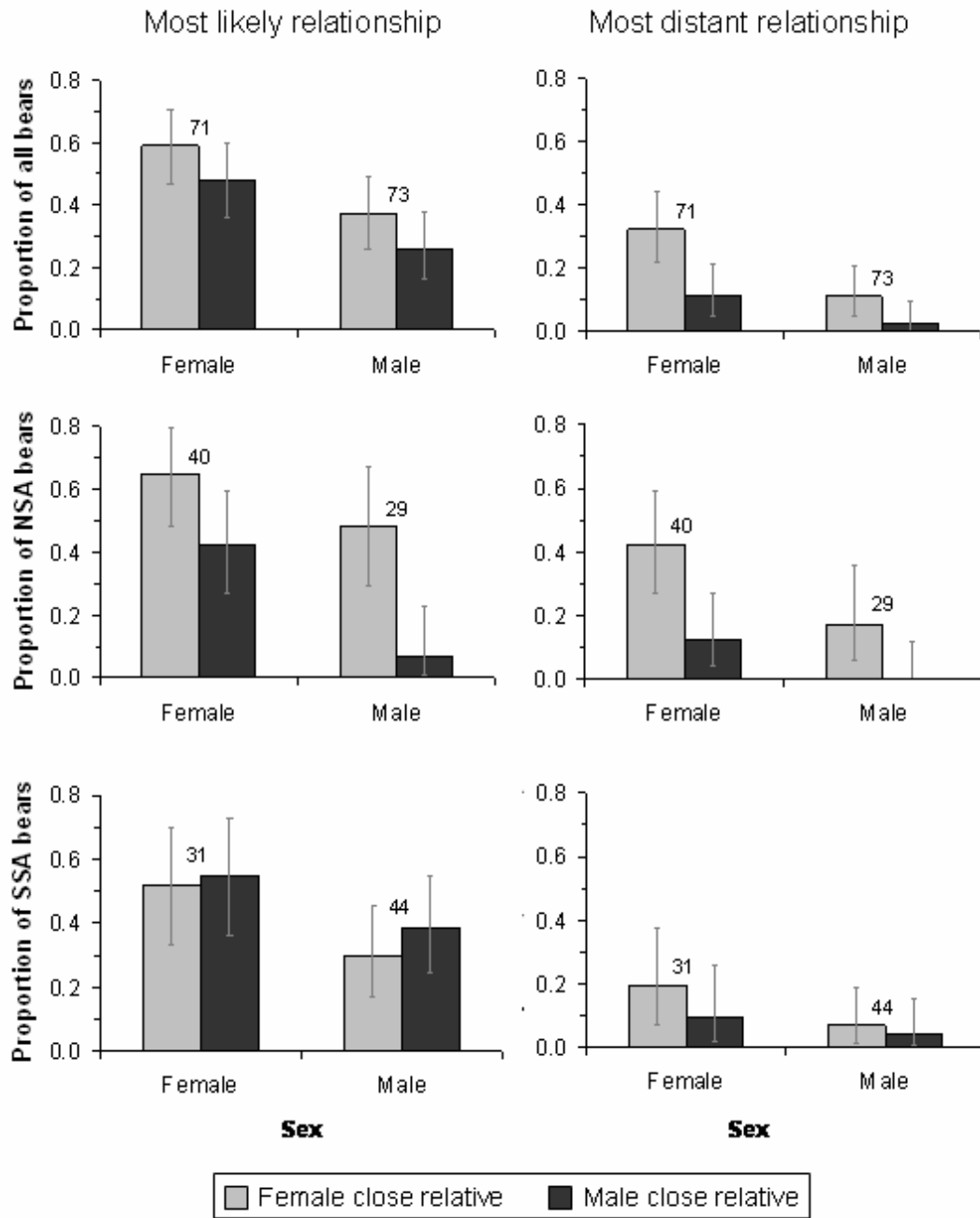
Figure 5.3. Proportion (±95% CI) of black bears (≥4 years old) that had a close relative (parent-offspring or full sibling) residing within the mean mating distance of 6 km: (top) all bears from both study areas; (center) bears from the Northern Study Area (NSA); and (bottom) bears from the Southern Study Area (SSA). Dyads were classified according to the most likely relationship (left) and the most distant relationship (right). Sample sizes appear above bars.
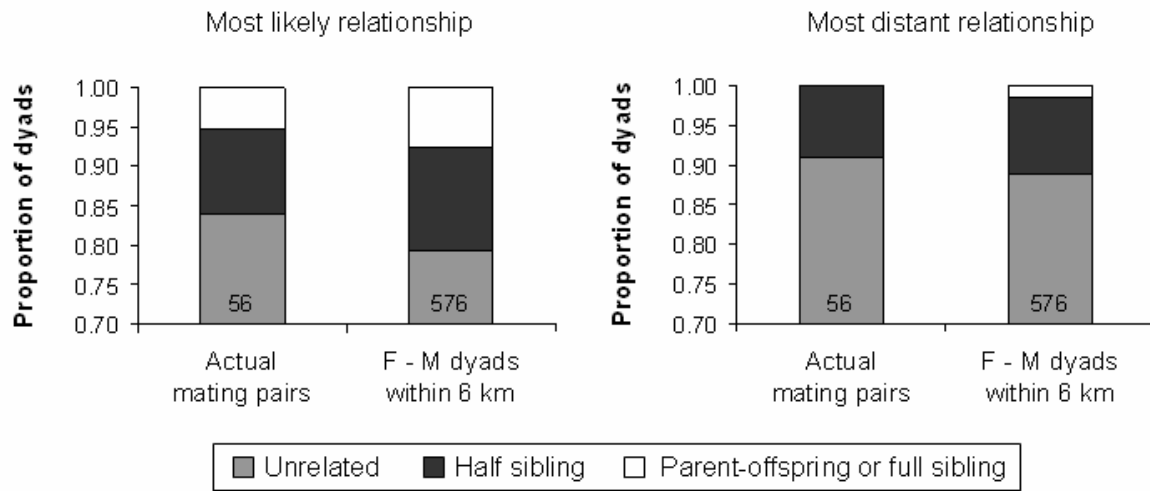
Figure 5.4. Percent frequency of relationships for mating pairs of black bears compared to those for opposite-sex dyads residing within the mean mating distance of 6 km. Dyads were classified according to the most likely relationship (left) and according to the most distant relationship (right). Note the y-axis begins at 0.70 to better illustrate differences among groups. Sample sizes appear within each bar and test statistics refer to horizontal comparisons of relationship frequencies between mating pairs and opposite-sex dyads residing within 6 km.

within the mean mating distance (Figure 5.4), using either criterion for assigning

relationships (χ^2 $P \geq 0.66$).

Discussion

Our analyses revealed sex differences in the spatial genetic structure of the study

populations consistent with male-biased dispersal. As predicted, mean relatedness and

proportion of relatives decreased as a function of distance among female pairs, while little

change was observed with distance among male pairs or opposite-sex pairs. In addition,

females living in close proximity were, on average, more closely related than males living

near one another. These patterns were apparent in both study areas and are consistent with

previous descriptions of black bear ecology and behavior (Rogers 1987ab, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Beck 1991). Nonetheless, these sex differences in genetic structure were smaller than would be expected if male dispersal and female philopatry were nearly absolute, as was observed among our sample of radio-marked offspring ($n = 22$; Chapter 3). If all or nearly all females settled near their natal range, we would expect most females to have a close female relative residing nearby. But examining individual bears, we found only 33–59% of females had another female PO/FS relative within 6 km (Figure 5.3). Thus, the potential for kin-structuring to affect social evolution in female black bears was weaker than one might have previously assumed. Similarly, if all or nearly all males dispersed ≥25 km from their natal range, we would expect few, if any, to have a close male relative residing nearby. But, as much as 26% of males had another male PO/FS relative residing within 6 km. These and other patterns in the proportion of bears with neighboring relatives suggested the sex bias in dispersal was probably not as high as our field results implied. They also suggested the sex bias was less pronounced in the SSA, owing primarily to differences among males.

At first glance, the lower-than-expected proportions of females with close female relatives living nearby suggested some females might have dispersed away from their natal ranges. However, a closer examination showed the estimates were consistent with the relatively low reproductive potential of bears in New Mexico. Mean natality and survival rates (Costello et al. 2001, Costello et al. 2003) indicated that females surviving to the age of four years would recruit only about 1.4 female offspring (also surviving to age four) during an average life span. With this low reproductive potential, it would be unlikely that any

female would have more than a few closely related female neighbors and many females would have none. Both adult female survival and natality were slightly higher in the NSA than in the SSA, apparently due to the hunting closure and more consistent oak production (Costello et al. 2001, Costello et al. 2003). Thus, NSA females would recruit about 1.8 female offspring during their lifetime, while SSA females would recruit about 1.0. This difference in recruitment is a reasonable explanation for the higher proportion of females in the NSA that had closely related female relatives residing within 6 km (43% versus 19% based on MDR, $\chi^2_2 = 4.2$, $P = 0.04$; Figure 5.3).

The substantial proportion of males that had closely related males residing nearby may indicate a lack of dispersal by some males, or at least dispersal distances shorter than those we observed in the field. If inbreeding avoidance were the sole driver of male dispersal, it would be reasonable to assume rates of male dispersal would be density-independent, but our data suggest males in the lower-density SSA dispersed less often or shorter distances than males in the NSA. Higher density has been hypothesized to increase dispersal rates by compelling more individuals to emigrate to reduce resource or mate competition (Greenwood 1980, Dobson 1982, Waser 1985).

Our estimates of density indicated bears were 1.7 to 2.0 times more numerous in the NSA than the SSA (Costello et al. 2001). Estimated densities in both study areas were relatively low (≤ 19 bears/100 km^2) and likely well below carrying capacity; densities of >30 bears/100 km^2 have been estimated for nearby Arizona populations (Waddell and Brown 1984, LeCount 1982). Although slightly higher natality in the NSA (Costello et al. 2003) may account for some of this difference in density, it is likely hunting (before and during the

study period) reduced the SSA population below carrying capacity to a much larger degree than the NSA, where some hunting closures were in effect since the 1960s. We suspect males in the SSA responded to low density by remaining near their natal range. Results of our paternity analysis indicated higher densities and lower turnover of mature males lessened the chances of mating for young males (Chapter 4), probably making areas with low male density more appealing for establishment of a home range by a dispersing male. Higher mortality among both sexes would also reduce the likelihood that philopatric, opposite-sex pairs would simultaneously survive to reproductive age. In heavily-exploited populations, philopatric males may benefit from the scarcity of males near their natal range, without suffering the cost of close inbreeding. Similar to our finding, Ji et al. (2001) found that mean relatedness of male brushtail possums (*Trichosurus vulpecula*) was higher (and more similar to that of females) in populations recovering from intense mortality than in undisturbed populations. They suggested it was explained by the short-distance dispersal of related males into the disturbed area from the edge of the undisturbed area.

Despite some evidence that the sex bias in dispersal was, perhaps, lower than expected, the potential for close inbreeding was still low. We estimated 79–89% of the 578 opposite-sex dyads residing within the mean mating distance were unrelated (meaning their relatedness was lower than that of half siblings). Only between 1% and 7% of these dyads appeared to involve PO/FS relationships. Although some individuals had an opposite-sex close relative residing nearby, unrelated neighbors far outnumbered relatives. We found no evidence that bears were actively avoiding inbreeding in their selection of mates from this nearby pool of relatives and non-relatives. The frequencies of probable relationships among

mating pairs and those among dyads within the mean mating distance were remarkably similar.

Avoidance of close kin, particularly paternal kin, as potential mates would likely require a relatively sophisticated form of kin recognition in bears. In a review of paternal kin discrimination studies, Widdig (2007) focused on two primary mechanisms for kin recognition: familiarity and phenotypic matching. The solitary behavior of bears does not provide a social context in which fathers and their offspring become familiar with each other, nor does it offer much opportunity for siblings born in different litters to gain familiarity. Promiscuous mating by female bears would also reduce a male's ability to ascertain the parentage of offspring produced by a female mate. Therefore, paternal kin recognition in bears would likely require phenotypic matching (to self or familiar kin) by means of a cue, such as odor or appearance. Little is known about the costs or effectiveness of these phenotypic recognition mechanisms. However, Hain and Neff (2006) studied helping behavior among bluegill sunfish (*Lepomis macrochirus*) nest mates and estimated the cost of self-referent kin recognition. They found the cost was high enough that its expression was inhibited among those individuals for whom most other nest mates were full siblings (~80%). In contrast, kin recognition was expressed among those individuals with few full siblings in the nest (~20%), because the cost of misplaced helping behavior was even higher than the cost of kin recognition. Just as the preponderance of close kin alleviated the need for kin recognition in sunfish, the preponderance of non-kin probably alleviated the need for kin recognition in bears. Our results indicated mean r was only 0.087 among opposite sex pairs residing within the average mating distance, and more than 80% of pairs were unrelated.

With this low potential for close inbreeding, presumably a result of sex-biased dispersal, there appeared to be little need for active inbreeding avoidance in bears, especially if mechanisms for distinguishing kin bore substantial fitness costs. Other studies have found that where dispersal minimized inbreeding, inbreeding avoidance through mate choice was weak or absent (Ims and Andreasson 1991, Peters and Michiels 1996, Banks et al. 2005, Hansson et al. 2006).

Among the relatively few closely related (i.e. PO or FS), opposite-sex pairs residing near each other, father-daughter relationships were most common, as expected, given female-biased philopatry. Our paternity analyses indicated male reproductive success was dominated by a fraction of intermediate-aged bears (Chapter 4), indicating most males would have a relatively short reproductive tenure. This short tenure would also minimize the need for kin recognition, as few males would be expected to successfully compete for mates once they reached an age old enough to have fathered a reproductively mature female. Nonetheless, we were able to document individual males fathering litters separated by as many as nine years (Chapter 4), more than enough time for a female offspring to mature. Thus, the individuals most likely to engage in close inbreeding would be the most successful males and their daughters. For these males, secondary dispersal might provide a means to reduce the likelihood of mating with a daughter, such as that observed in swift foxes (*Vulpes velox*; Kamler et al. 2004); however we found no evidence of males abandoning their established home ranges after the age of six years (Chapter 3).

In summary, our results show that high rates of male dispersal and female philopatry combine to create a spatial genetic structure that generates low rates of inbreeding and little

need for kin discrimination among potential mates. Thus, evidence supports the hypothesis that inbreeding avoidance is achieved by means of male-biased dispersal in black bears. Our results also suggest the general pattern of male-biased dispersal is modified by competition for mates or resources.

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APPENDIX A

MODEL COEFFICIENTS

Estimates of coefficients for logistic regression models predicting probability that a male black bear fathered offspring (Chapter 4). The top four models were based on an observation for each male during each year, and the bottom five models were based on an observation for each male-female pair during each year.

Model	Fixed effects			Variance of random effect
	Parameter	$\hat{\beta}$	SE	
age + age^2	intercept	-5.74	1.40	2.51
	age	0.74	0.31	
	age^2	-0.04	0.02	
age + age^2 + estrus	intercept	-6.31	3.74	2.75
	age	0.62	0.52	
	age^2	-0.04	0.02	
	estrus	0.32	3.88	
	age*estrus	0.22	0.44	
age + age^2 + density + age*density	intercept	-3.50	1.75	3.04
	age	0.86	0.34	
	age^2	-0.06	0.02	
	density	-2.37	1.05	
	age*density	0.20	0.11	
age + age^2 + death + age*death	intercept	-10.19	2.91	2.57
	age	1.40	0.50	
	age^2	-0.06	0.02	
	death	3.94	1.96	
	age*death	-0.41	0.20	
age+ age^2	intercept	-5.90	1.00	1.29
	age	0.48	0.22	
	age^2	-0.02	0.01	

	Fixed effects			Variance of random effect
Model	Parameter	$\hat{\beta}$	SE	
age + age^2 + distance	intercept	-4.27	1.06	1.46
	age	0.48	0.23	
	age^2	-0.02	0.01	
	distance	-0.21	0.04	
age + age^2 + distance+ estrus + age*estrus	intercept	-5.01	3.05	1.47
	age	0.53	0.43	
	age^2	-0.02	0.01	
	distance	-0.21	0.04	
	estrus	0.79	3.15	
	age:estrus	-0.04	0.37	
age + age^2 + distance + density +age*density	intercept	-2.40	1.32	1.72
	age	0.45	0.24	
	age^2	-0.04	0.02	
	distance	-0.21	0.04	
	density	-1.70	0.79	
	age:density	0.17	0.08	
age+ age^2 + distance + death + age*death	intercept	-6.54	1.92	1.39
	age	0.82	0.34	
	age^2	-0.03	0.01	
	distance	-0.21	0.04	
	death	2.24	1.35	
	age*death	-0.25	0.14	