

# Determinants of male reproductive success in American black bears

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**Abstract** We determined annual male reproductive success in black bears (*Ursus americanus*) using DNA and field data from two populations in New Mexico. We identified the likely father for 78 of 120 genotyped cubs born during 1994–2000 and calculated reproductive success for 102 males known or presumed present within designated mating regions. Age was a strong determinant of reproductive success. The observed peak in reproductive success occurred at roughly the same intermediate age (10 years) as milder peaks in body size characteristics (11–12 years) and frequency of bear-inflicted wounds (13 years), suggesting body size and fighting might be important for mating. Success was negatively associated with the distance between home range centers of males and mothers. Success of young males (<7 years old) was also negatively associated with mature male ( $\geq 7$  years old) density, and increasing density shifted the peak age of reproduction higher. The dispersed distribution of females likely limited the capacity of large mature males to

dominate reproduction; therefore, success was determined by a complex set of variables.

**Keywords** Age · Body size · Density · DNA · Paternity · *Ursus americanus*

## 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, 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 (Coltman et al. 2001).

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) 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).

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Similarly, a pronounced skew in mating success was observed at high male density in European sousliks (*Spermophilus citellus*), but a normal distribution was observed at low male density (Millesi et al. 2004). Counter to these studies, sneaked fertilizations increased with increasing male density of European bitterlings (*Rhodeus sericeus*) 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).

Using DNA microsatellite analyses and field data, we examined 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 consistent with intense sexual selection. They display considerable sexual size dimorphism, with males weighing 1.2–2.2 times more than females (Alt 1980; Noyce and Garshelis 1994). Offspring stay with their mother for over one year and females exhibit asynchronous estruses occurring from about May to August (Erickson et al. 1964; Garshelis and Hellgren 1994), combining to create a male-biased OSR. The dispersed spatial distribution of female bears likely limits the ability of any male to monopolize breeding. 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; Costello 2008). Nonetheless, it is possible that males exhibit space-related dominance and hinder other males from mating with females residing near the center of their home range. Alternatively, males may simply search widely for females and rely on scramble competition for success (Schwagmeyer and Wootner 1986).

In black and brown bears (*Ursus arctos*), it has long been presumed that older, larger males are more reproductively successful. Hornocker (1962) established the promiscuous nature of the brown bear mating system and not only indicated that larger, dominant bears had greater access to females but also showed that smaller subordinate males obtained breeding opportunities, even in the presence of larger males. Later observations proved similar for black bears (Barber and Lindzey 1983; Rogers 1987). Higher success of large males has recently been substantiated with DNA evidence in both species (Craighead et al. 1995; Kovach and Powell 2003; Zedrosser et al. 2007). Although these papers discussed factors affecting the skew in age- or size-related reproductive success, ours is the first paper to examine how observed demographic changes in population parameters modify this skew.

The aim of this paper 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 (e.g., McElligott et al. 2002). Second, due to the dispersed distribution of females, we hypothesized the capacity of older, larger males to dominate reproduction would be affected by spatial or temporal variation in demography. We predicted that young males, dispersing or newly resident, would rarely father offspring but would be more successful (1) when density of older, larger males is low and (2) when many females are in estrus at the same time (i.e., the OSR becomes more even). Third, we hypothesized that males would have higher success with females residing within their home range due to space-related dominance or higher encounter rates. Thus, we predicted that male reproductive success would increase with proximity to individual females.

## Materials and methods

This paper draws from a larger study primarily designed to investigate natality and survival (Costello et al. 2001). Capturing, radio-telemetry monitoring, and den investigations were our primary means of obtaining data on individually known bears. Collection and subsequent analyses of DNA samples allowed us to conduct post hoc investigations of parentage, relatedness, and social structure (Costello et al. 2008).

### Study areas

The 310 km<sup>2</sup> northern study area (NSA) was located in the Sangre de Cristo Mountains of northern New Mexico. The 420 km<sup>2</sup> southern study area (SSA) was located in the Mogollon Mountains of west-central New Mexico. These two areas were separated by ~475 km and tracts of unsuitable habitat; hence, genetic exchange was absent. Dominant habitat types in both areas included pinon–juniper (*Pinus edulis*–*Juniperus* spp.) woodlands, oak–mountain mahogany (*Quercus* spp.–*Cercocarpus* spp.) scrub, and conifer forests (*Pinus ponderos*, *Pseudotsuga menziesii*, *Abies concolor*, *Picea engelmannii*, and *Abies lasiocarpa*). Elevations ranged from 2,070 to 3,793 m in the NSA and 1,750 to 3,035 m in the SSA. Climate varied with elevation, with slightly warmer and drier conditions in the SSA. The NSA encompassed private and state lands where recreation and cattle ranching were the primary land uses and was closed to bear hunting for study purposes during 1992–1998. The more remote SSA was within Gila National Forest where livestock grazing and timber harvest were primary land uses and was open to bear hunting throughout the study period. More detailed study area descriptions were reported in Costello et al. (2001, 2008).

## Capture and telemetry

We marked or uniquely identified 515 individual bears (198 females, 289 males, and 28 unknown) between September 1992 and June 2000, by means of trapping and den investigations detailed in Costello et al. (2001) and Inman et al. (2007). Among these bears, 297 (101 females, 192 males, and two unknown sex) were first encountered during trapping; individuals were captured one to nine times for a total of 517 captures. The male bias was due to the larger home ranges of males (Costello et al. 2001). Bears were chemically immobilized, sexed, and marked with ear-tags and lip tattoos. We field-estimated age and extracted a premolar tooth from most bears ( $n=292$ ) for cementum aging (Willey 1974). We obtained scale body mass, chest girth, and neck circumference. Nearly all females captured ( $n=99$ ) were radio-marked with collars or ear-tag transmitters to monitor reproduction and survival, but males were radio-marked as needed to maintain a sample of about ten individuals each year ( $n=53$ ). Initially, we radio-marked some captured 2- to 4-year-old bears ( $n=29$ ), but this practice was terminated after 1994 due to the difficulty and costs of tracking dispersers. We first handled or observed the other 218 (97 females, 95 males, and 26 unknown sex) bears as cubs or yearlings accompanying their radio-marked mothers in winter dens, but sex of all offspring could not be verified due to inaccessibility. Yearling females ( $n=28$ ) and males ( $n=30$ ) were radio-marked in the den when accessible. All 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 grid coordinates to the nearest 0.1 km on US Geological Survey 7.5-min maps. We obtained 5,723 radio-telemetry locations.

## Microsatellite DNA and paternity analysis

We collected samples (tissue, blood, or hair) from 430 bears and obtained genotypes for 407 bears (79% of individuals identified; Costello et al. 2008). Genotypes were based on 11 microsatellite loci: 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). We calculated a genotyping error rate of 0.01 errors per allele based on paired samples from the same bears (Costello et al. 2008) and a rate of 0.002 errors per locus based on known mother–offspring pairs. We observed no significant deviations from the Hardy–Weinberg equilibrium for any of the 11 loci ( $P>0.05$ ; Costello et al. 2008).

We analyzed paternity (and maternity, when necessary) using Cervus 3.0 software (Marshall et al. 1998; Kalinowski et al. 2007). Potential parents were any bear  $\geq 2$  years old not

known to be dead during the mating season (den emergence to 20 July) when the offspring was conceived. Potential parents included 183 males and 72 females. 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; Costello et al. 2008; Costello 2009). We ran alternate simulations with lower estimates for the proportion of candidates sampled (i.e., 0.50 or 0.15), for 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

Once paternities were determined, we wished to quantify reproductive success and the factors related to it. It was critical to spatially and temporally limit our analyses to those genotyped offspring for whom we could correctly identify the set of males that were likely present to mate with those mothers that produced cubs. In many studies of male reproductive success, researchers directly observe social units, such as African lion (*Panthera leo*) prides, red deer (*Cervus elaphus*) herds, and elephant seals (*Mirounga angustirostris*) breeding colonies (see Clutton-Brock 1988); thus, identifying the set of potential fathers is relatively straightforward. In contrast, black bears exist in dispersed, non-social populations offering limited opportunities for encounters with each individual. Thus, we used information about space use, dispersal, and survival to develop criteria for defining the set of males present for mating each year.

We used location data to roughly define a core home range and center for all males and each mother of genotyped offspring. For individuals with  $\geq 30$  locations ( $n=17$  males and  $n=43$  females), we defined the core home range as a 50% fixed kernel (Costello 2008) using the Animal Movements 2.04 extension (Hooge and Eichenlaub 2000) developed for ArcView 3.3 software (Environmental Systems Research Institute, Redlands, California). For individuals with  $< 30$  locations ( $n=113$  males and  $n=11$  females), 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 (Costello 2008). The home range center was defined as the centroid of a fixed 50% kernel contour ( $n=75$  males and  $n=54$  females) or the

arithmetic mean of the  $x$  and  $y$  coordinates when  $\leq 3$  locations were obtained ( $n=55$  males).

We defined our restricted offspring sample by limiting our analyses to those genotyped offspring conceived during years when we were actively sampling males through trapping and radio-telemetry monitoring (1993–1999), corresponding to birth years when we were actively sampling cubs through den investigations (1994–2000). We further restricted the sample to offspring of females whose core home range overlapped the effective sampling region ( $n=120$  cubs in 76 litters) defined by buffering mating season trapsites by 4.0 km, the median distance between each location, and the home range center for radio-marked males (Costello 2008).

We spatially defined a mating region for each year by merging the core home ranges of these mothers. We then identified the sets of males that were likely present within these mating regions during relevant years. Space use analyses indicated that bears typically remained within or near their core home range during the mating season but traveled more widely in search of acorns and other mast during fall hyperphagia (Costello 2008). Thus, we compiled records of males known to be present within the effective sampling regions during the mating season of each year, yielding a sample of 129 males present during 252 bear years.

We developed age-specific criteria to infer the likelihood that these individuals were present during other years, based on dispersal and survival analyses. Dispersal analyses indicated that 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 (Costello 2009). Hunting and depredation mortality was known, and mortality from other sources was rare ( $\leq 0.06$ /year; Costello et al. 2001). Thus, males known to be present when  $\geq 5$  years old were presumed present in prior years back to age 4 years. Males known to be present when  $\geq 4$  years old were presumed present in subsequent years until the end of the study or until they were known to have died. Males known to be present only as 2- or 3-year-olds were not presumed present during other years. Males captured only during the mast season were not presumed present during the mating season of any year. This process increased the sample to 483 bear years for the same 129 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 119 bears in 452 bear years.

We then limited the set to those males whose home range overlapped the annual mating region or were located at least once within the region during the mating season of that year. This reduced the sample to 103 individuals known or presumed present during 333 bear years. We

merged paternity data with male presence data and found that a few of the assigned fathers were not presumed present within mating regions. These included one male whose home range overlapped the effective sampling region but not the mating region, one male captured only during the mast season, three males captured as 2- or 3-year-olds and not forward-dated to their eventual age of reproduction, and one male captured as an 8-year-old and not back-dated to age 3 years when he reproduced. Because DNA analysis confirmed their presence in some years, we revised their presence for other years using the same criteria explained above. This added 23 bear years to the sample, making it 105 males presumed present during 356 bear years.

### Statistical analyses

Using our restricted sample, we aspired to relate male reproductive success to several covariates. To accommodate model comparison, we used data from birth years 1995–2000 because some covariates were unknown for birth year 1994. This final sample included 102 males during 334 bear years. Annual estimates of the number of cubs fathered by individual males ranged from 0 to 4, with a high proportion of 0 values (86%). This skewed distribution was not appropriate for use in linear regression models; therefore, we applied 1 to males that fathered genotyped cubs and 0 to males that did not father genotyped cubs and used logistic regression models to predict the probability that a male fathered offspring (SPSS 11.5.0, Chicago, IL, USA). We used Akaike Information Criteria (AIC) to compare models (Burnham and Anderson 2002). We included repeated measures in the data set by treating annual estimates of reproduction for the same male as independent observations. We believe that this was justified given that observed year-to-year variation in reproduction by individuals was as great as variation among individuals. The number of observations/male ranged from 1 to 6 with a mean of 3.3 (SE=1.9).

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 sample. 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 body mass or size. To 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 body mass, chest girth, and neck circumference. We also used logistic regression to examine the relationship between age and frequency of bear-inflicted wounds. For these models, as well as models for reproductive success, we entered age as a quadratic function, allowing for an asymptote and

possible decline associated with senescence. We centered age on 8 years to reduce the correlation between age and age<sup>2</sup>. The age model served as the basis for subsequent models predicting the probability of male reproduction.

We estimated density of mature ( $\geq 7$ -year-old) males and proportion of females in estrus and added these covariates to the age model with interactions to determine if these factors affected the age-related skew. We calculated proportion of females in estrus each year based on their reproductive status during den visits the following year (Costello et al. 2003) as  $1 - P_y$ , where  $P_y$  = the proportion of adult ( $\geq 5$ -year-old) females with yearlings. In other words, any adult female that did not have surviving cubs was presumed available for breeding. We did not use the proportion of females observed with cubs during the den season immediately before mating for two reasons. First, cub survival was only 55% and many females came into estrus after losing cubs and produced cubs the following winter. Second, cub production was affected by fall acorn abundance (Costello et al. 2003); therefore, the absence of cubs was not necessarily indicative of a lack of estrus. To obtain a density estimate for year, we summed the number of mature males known or presumed present within sampling regions and divided the sum by the area of the sampling regions.

We measured the distance between the home range center of each male present within the mating region and each female with genotyped cubs and scaled it in units of male home range radii (5.3 km). By necessity, models with this distance covariate required an observation for each male–female pair; therefore, the sample was enlarged to  $n = 1,645$ . Using this enlarged sample, we compared a set of models including age, density, estrus, and distance to determine if male reproductive success was determined by a simple or more complex set of variables.

## Results

### Paternity analysis

Among the full set of 407 bears with estimated birth years 1973–2001, we identified a single likely father for 106

bears (26%; Table 1). We did not identify the father of any bear born prior to 1990. As expected, paternity assignment was substantially higher among the restricted sample (i.e., cubs born of known mothers within the sampling regions during 1994–2000), where we assigned fathers for 78 of 120 genotyped bears (65%). This set represented 45% of offspring identified in the field within our sampling regions 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 assign a father for the other 23%.

We identified 36 fathers. Within years, these males fathered cubs with one to three different females ( $x = 1.2$ ,  $SE = 0.4$ ) and produced one to four cubs ( $x = 1.6$ ,  $SE = 0.7$ ). Among all years, these males fathered offspring with one to eight females ( $x = 1.9$ ,  $SE = 1.4$ ) and produced a total of one to 16 cubs ( $x = 2.9$ ,  $SE = 2.9$ ). Age of fathers at the time of breeding ranged from 3 to 21 years ( $x = 8.4$ ,  $SE = 3.2$ ). Nineteen of 36 (53%) fathers bred more than once; the time between their first and last detected litter ranged from 0 to 9 years ( $x = 3.3$ ,  $SE = 2.6$ ). Among fully sampled, multi-cub litters with at least one father assigned, multiple paternities were apparent in nine of 32 litters (28%).

### Patterns in reproductive success

Using our restricted sample, we documented reproduction by 14% of males known or presumed present within mating regions each year and our estimate of reproductive success was 0.23 offspring per male per year. The quadratic age function was a significant predictor of the proportion of males fathering cubs (Table 2). The age model indicated reproductive success peaked at about 10 years of age (Fig. 1). Even among the most successful age classes, fewer than 20% of bears were predicted to produce offspring annually.

A more complex model including age, density, and distance to females was superior to simpler models according to AIC (Tables 2 and 3). As predicted, decreasing density of mature males shifted the peak age of reproduction toward a lower age. Young ( $< 7$ -year-old) males had

**Table 1** Microsatellite DNA paternity assignment success for black bears within the full sample (all genotyped bears born 1973–2001) and the restricted sample (genotyped offspring born within sampling regions during 1994–2000)

Sample	Subsample	<i>n</i>	Paternity assigned (%)
Full		407	26
	Mother known	144	56
	Mother assigned using DNA	25	68
	Mother unknown	238	4
Restricted		120	65
	Mother known	115	65
	Mother assigned using DNA	5	60

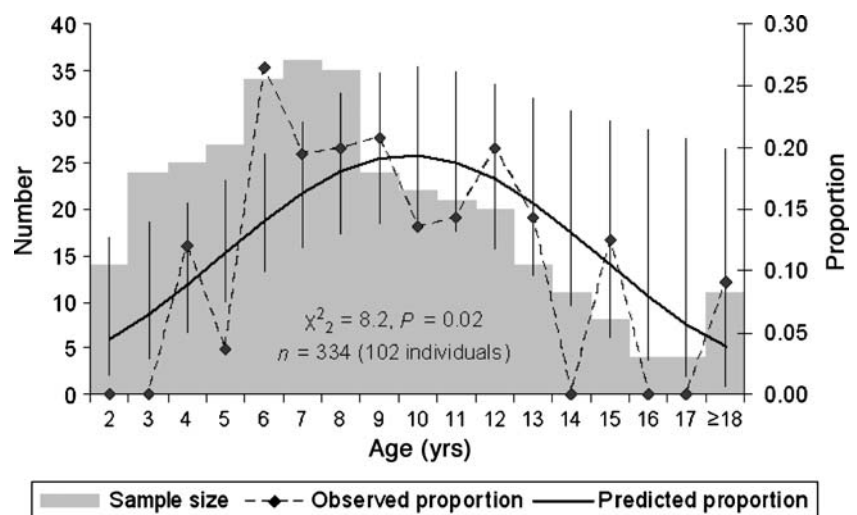
**Table 2** Results of AIC model selection and Hosmer Lemeshow goodness of fit tests for logistic regression models predicting probability that a male black bear fathered offspring

Model	Model selection					Goodness of fit		
	<i>n</i>	<i>k</i>	AIC	ΔAIC	Model weight	$\chi^2$	df	<i>P</i>
Age+age <sup>2</sup> +density+density×age	334	5	254.1	0.0	0.95	6.6	8	0.59
Age+age <sup>2</sup>	334	3	265.6	11.5	<0.01	10.6	8	0.22
Age+age <sup>2</sup> +density+estrus+density×estrus+density×estrus×age	334	7	266.2	12.1	<0.01	2.1	8	0.98
Age+age <sup>2</sup> +estrus+estrus×age	334	5	268.3	14.2	<0.01	9.6	8	0.30
Age+age <sup>2</sup> +distance+density+density×age	1,645	6	436.4	0.0	0.78	6.0	8	0.65
Age+age <sup>2</sup> +distance	1,645	4	440.1	3.7	0.12	7.5	8	0.48
Age+age <sup>2</sup> +distance+density+estrus+density×estrus+density×distance×age	1,645	8	441.1	4.7	0.07	8.8	8	0.42
Age+age <sup>2</sup> +distance+estrus+estrus×age	1,645	6	444.0	7.6	0.02	9.7	8	0.29
Age+age <sup>2</sup>	1,645	3	469.5	33.2	<0.01	9.5	7	0.22

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

higher reproductive success when densities of mature males were lower. At lower mature male densities (2.6–3.3 males/100 km<sup>2</sup>), 44% (*n*=52) of cubs were fathered by young males, while no cubs (*n*=24) were fathered by young males when mature male densities were higher (4.9–5.5 males/100 km<sup>2</sup>). Distance was negatively associated with reproductive success by age (Table 2). Fifty-six percent of fathers resided within one home range radius from the mother, 31% resided between one and two radii from the mother, and 11% resided between two and three radii from the mother. The longest distance observed between a mating pair was 17.8 km or 3.4 radii. Only 18% of fathers were the male residing closest to the female, and half of those were young males that may not have established a permanent home range. Contrary to our prediction, the proportion of females in estrus did not influence the age-related skew in reproduction. This covariate had little support according to AIC (Table 2).

**Fig. 1** Observed and model-predicted proportion ( $\pm 95\%$  CI) of male black bears that fathered genotyped cubs as a quadratic function of age. The sample included repeated measures of individual males across years and sample size is shown in bear years



We observed a positive asymptotic relationship between age and breeding season body mass, chest girth, and neck circumference (Fig. 2). All body measurements peaked at approximately 11–12 years of age. Observations of wounds, apparently inflicted by other bears, were more common during the mating season than the mast season ( $\chi^2_1=7.7$ ,  $P=0.005$ ), and their frequency increased asymptotically with age, with a mild peak at roughly 13 years of age (Fig. 3).

## Discussion

All lines of evidence indicated that male–male competition was intense. Reproductive success of males was determined by a complex set of variables, including age, their proximity to estrous females, and the number of other males competing for breeding opportunities. Of 56 males

**Table 3** Parameter estimates for top AIC-ranked logistic regression model predicting probability that a male black bear fathered offspring

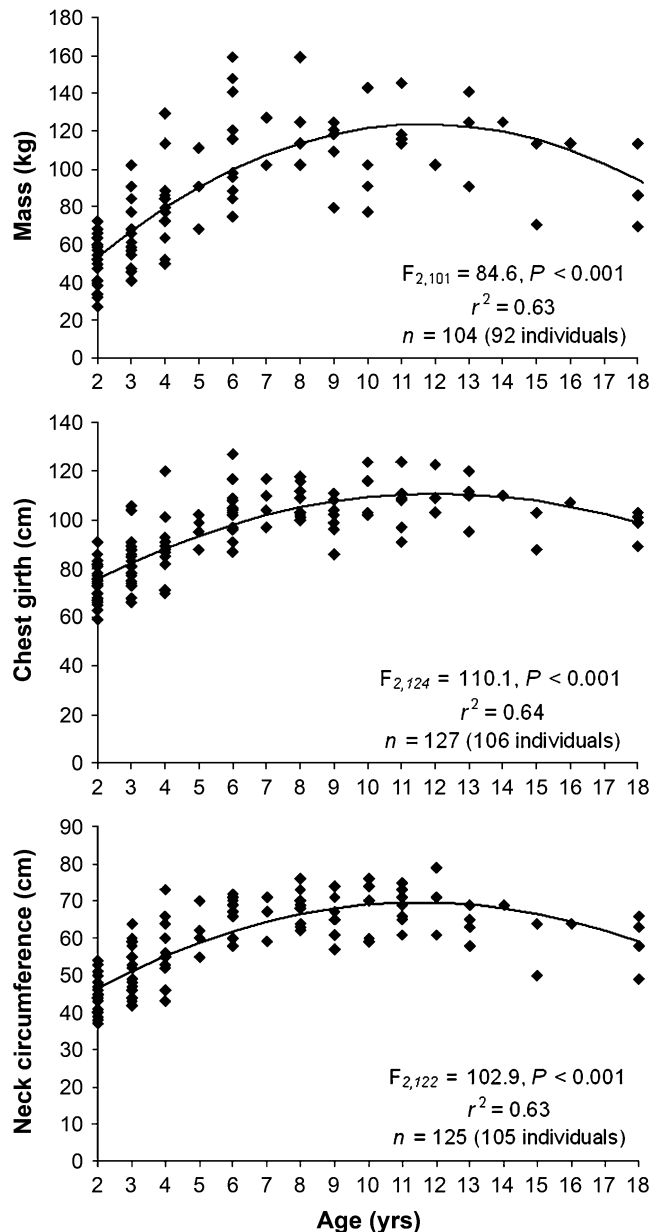
Parameter	$\beta$	SE	Wald	df	p value
Intercept	-0.73	0.73	1.0	1	0.32
Age	-0.47	0.24	3.7	1	0.05
Age <sup>2</sup>	-0.05	0.02	9.8	1	<0.001
Distance	-1.00	0.20	24.2	1	<0.001
Density	-0.25	0.19	1.8	1	0.18
Density×age	0.17	0.07	5.9	1	0.02

present within mating regions between the ages of 8 and 13 years, only 33% were known to sire offspring. Our estimates of reproductive success were biased low because we did not obtain genotypes for all cubs born within sampling regions, much less within home ranges of all males present within these regions. However, we did obtain genotypes for over two thirds of cubs known to be born within study areas during 1994–2000, and this sample was likely unbiased relative to our covariates.

The dispersed distribution of females and asynchronous estruses necessitate a substantial search effort for receptive females by males. Our results suggest a strategy of staying home and guarding females within a home range is less effective than roaming. Resident males appeared incapable of excluding other males from their home range or its resident females, as observed in territorial solitary carnivores, such as cougars (*Puma concolor*; Murphy 1998), or territorial social carnivores, such as dwarf mongooses (*Helogale parvula*; Keane et al. 1994). Instead, it appears that encountering and courting a female before rivals arrive may be an important aspect of success. 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. 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 (Costello 2008). In addition, distance between successive locations was highest during the mating season, suggesting that males were actively searching for mates, both inside and outside of their core home range. It also appears that roaming strategies do not differ between young and mature bears, as distribution and mean values for 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 receptive females, indicating superior ability to locate estrous females and to repel other bears from her vicinity. Bellemain et al. (2006) found proximity was a significant

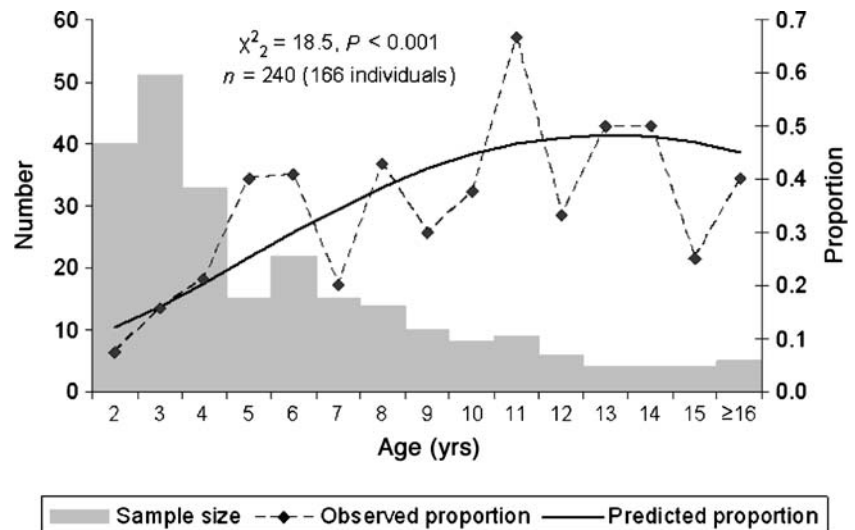
determinant of paternity of brown bears but attributed it to mate choice by female brown bears as a counter-strategy to infanticide.

Although encountering a female first may provide an unencumbered opportunity for breeding, the appearance of rivals (more common 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



**Fig. 2** Observed and predicted values for linear regression models predicting body mass (*top*), chest girth (*center*), and neck circumference (*bottom*) as a quadratic function of age. The sample included repeated measures of individual bears across years and sample size is reported in bear years

**Fig. 3** Observed and predicted values for logistic regression model predicting presence of wounds (apparently inflicted during fights with other bears) as a quadratic function of age. The sample included repeated measures of individual males and sample size is shown in bear years



displays, as well as fighting to exert dominance over conspecifics (Hornocker 1962; Stonorov and Stokes 1972; Herrero 1983). Age was a strong determinant of reproductive success and intermediate-aged bears appeared to have a substantial advantage. The observed peak in reproductive success occurred at roughly the same intermediate age (10 years) as milder peaks in body size characteristics (11–12 years) and frequency of bear-inflicted wounds (13 years), suggesting that body size and fighting might be important for mating. 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 black 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.

Factors other than body size might explain the success of intermediate-aged bears. Sperm competition is assumed to be an important determinant in reproductive success of male bears (Kovach and Powell 2003; Zedrosser et al. 2007). Or perhaps female show a preference for intermediate-aged individuals, as has been observed in lekking sandflies (*Lutzomyia longipalpis*; Jones et al. 2000). Females may prefer males that have demonstrated genetic quality merely by surviving to an intermediate age (Manning 1985; Brooks and Kemp 2001; Proulx et al. 2002) but select against older males that may be compromised by lower fertility or an accumulation of mutations (Brooks and Kemp 2001). This pattern would be consistent with the high adult survival and low juvenile survival observed in bears (Beck and Powell 2000).

Higher density of 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 that small males directly challenged older males as much as three times their size. Given the relatively high survival of adult males, it is unlikely that 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). The relationship with density suggests that 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.

Mature 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, Taylor (1994) argued that 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 that 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% (Costello 2008). Results from this study indicate that 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 support.

Instead, our results suggest an indirect, and less lethal, mechanism by which the presence of mature males might influence local population density and composition, con-

tingent on immigration of dispersing males. This idea was also proposed by Rogers (1987). Dispersal from natal areas is high for male bears, and dispersing males are known to travel approximately 20–60 km before settling in a more permanent home range (Costello 2009). Besides selecting for areas with adequate food and cover, young males also likely select for sites based on opportunities for reproduction. Our results indicated that higher densities of mature males reduced the immediate chances of mating for young males, making areas with low male density more appealing 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. At the wildlife–human interface, the presence of large numbers of young male bears is undesirable because of their higher tendency to exploit sources of anthropogenic foods and cause bear–human conflict (Rogers 1976). We propose that 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 contribute to the reduction of bear–human conflict. Of course, this strategy would require concurrent efforts to reduce availability of anthropogenic foods to bears, to ensure that mature bears were not removed as a result of nuisance behavior.

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