Research Article

Reproductive Ecology and Cub Survival of Florida Black Bears

ELINA P. GARRISON,[1,2] *Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville, FL 32611, USA*

J. WALTER MCCOWN, *Florida Fish and Wildlife Conservation Commission, 4005 S. Main Street, Gainesville, FL 32601, USA*

MADAN K. OLI, *Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville, FL 32611, USA*

ABSTRACT We investigated reproductive ecology and cub survival of Florida black bears (*Ursus americanus floridanus*) in Ocala National Forest and the adjacent residential area of Lynne, Florida, USA, 1999–2003. We documented production of 81 cubs from 39 litters. Average litter size was 2.08 ± 0.11 (SE) cubs. The mean age of first reproduction was 3.25 ± 0.27 years. Excluding females that reproduced in consecutive years due to litter loss, interlitter interval was 2.11 ± 0.11 years. The mean annual fecundity rate was 0.57 ± 0.06. We used expandable radiocollars to monitor the fate of 41 bear cubs. The probability of cubs surviving to 9 months of age was 0.46 ± 0.09 and did not differ between cohorts or study locations. The most important causes of cub mortality included infanticide and mortality caused directly or indirectly by collisions with vehicles. Our results indicate that reproductive rates of female black bears in the Ocala study area are comparable to those reported for other black bear populations from eastern United States, but cub survival rates are lower than those reported for most black bear populations. Management of Florida black bears should emphasize strategies to reduce the mortality of cubs. (JOURNAL OF WILDLIFE MANAGEMENT 71(3):720–727; 2007)

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Historically, Florida black bears (*Ursus americanus floridanus*) were found throughout Florida, USA, and in portions of southern Georgia, Alabama, and Mississippi, USA (Brady and Maehr 1985). However, by the mid-1900s, large-scale logging and unregulated hunting in Florida reduced the statewide bear population to fewer than 300 individuals (McDaniel 1974). In 1973, bears were listed as threatened in most counties of Florida. The legal protection of bears and maturation of second-growth forests allowed bear populations to rebound. Nonetheless, their current distribution represents only 17% of the historical range (Wooding et al. 1994), and the extant bear populations occur in several subpopulations with limited gene flow among them (Dixon et al. 2006).

As Florida's human population continues to increase, further loss and fragmentation of bear habitat is inevitable. Long-term persistence of Florida black bears may depend on science-based management plans, which require a better understanding of the population ecology of this subspecies. However, data on population parameters are currently scarce (Brady and Maehr 1985, Wooding and Hardisky 1994, Maehr et al. 2001, Dobey et al. 2005). Available estimates of reproductive parameters are based on visual observations after den emergence (Harlow 1961, Dobey et al. 2005) or examination of reproductive tracts (Wooding and Bukata 1996). Data on survival of cubs are currently unavailable for Florida black bears. Due to the heavy influence of reproductive and cub survival parameters on bear populations (Freedman et al. 2003, Oli and Dobson 2003), rigorous estimates of these parameters are necessary for formulating and implementing management plans for Florida black bears.

Our objectives were to estimate reproductive and cub survival parameters of Florida black bears and to assess factors influencing these parameters. We conducted a 4-year (1999 to 2003) study to estimate age of first reproduction, litter size, interlitter interval, and fecundity rate for bears in Ocala National Forest (ONF) and in an adjacent developed area of Lynne, north-central Florida. We provide the first estimate of survival and cause-specific mortality of cubs of Florida black bears. We also investigated several intrinsic and extrinsic factors that can influence reproductive parameters and cub survival rates.

STUDY AREA

We conducted our study within the ONF and adjacent residential community of Lynne. Ocala National Forest covered >1,740 km^2 in north-central Florida and had the largest and densest (0.24 bears/km^2) black bear population in the state (Simek et al. 2005). Ocala National Forest was bound by the Ocklawaha River to the west and north and St. Johns River to the east. Our study area was centered along State Road 40 (SR 40) and extended approximately 10 km north and south of SR 40 between the Ocklawaha River and State Road 19 (Fig. 1). The study area covered the central portion of ONF and Lynne and encompassed approximately 760 km^2 (240 km^2 in Lynne and 520 km^2 in ONF).

The vegetation in ONF was dominated by a central ridge of sand pine (*Pinus clausa*)–scrub oak (*Quercus myrtifolia*, *Q. geminata*, *Q. chapmanii*) community. Other major vegetation types in ONF included swamps and marshes along the

[1] *E-mail: Elina.Garrison@MyFWC.com*
[2] *Present address: Florida Fish and Wildlife Conservation Commission, 4005 S. Main Street, Gainesville, FL 32601, USA*

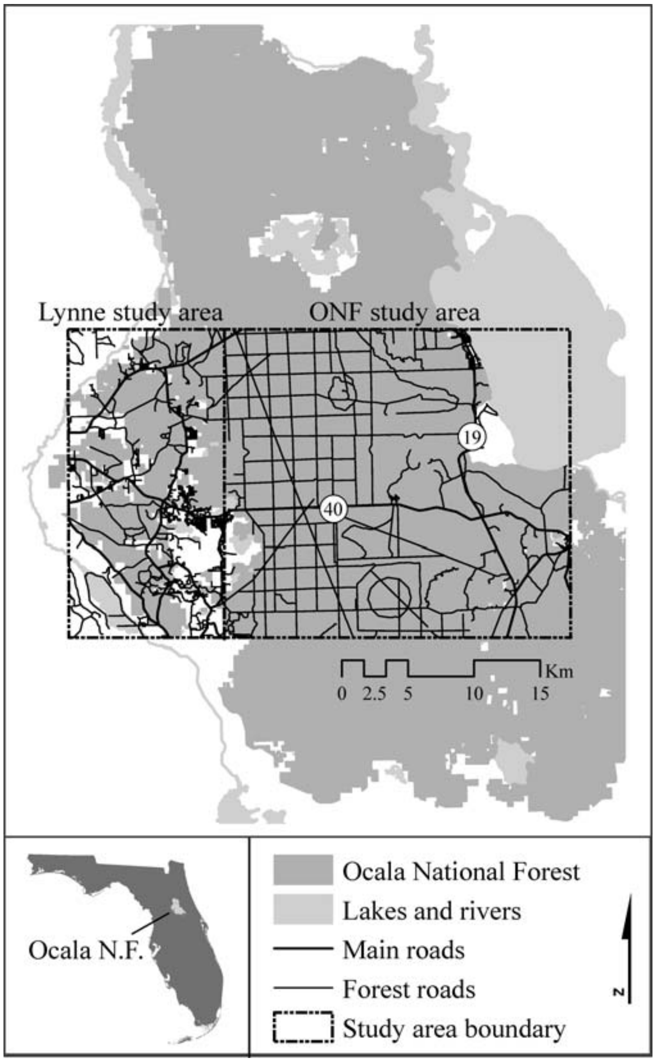

Figure 1. The Ocala National Forest (ONF) and Lynne study areas in north-central Florida, USA, where we studied black bear cub survival, 2000–2003.

Ocklawaha and St. Johns rivers, pine flatwoods between the rivers and central ridge, mixed hardwood swamps and numerous lakes, ponds, and prairies (Aydelott et al. 1975). Slash pine (*P. elliottii*) dominated pine flatwoods with scattered bays such as sweetbay (*Magnolia virginiana*) and loblolly bay (*Gordonia lasianthus*). In addition to the scrub oaks, common shrub species included scrub palmetto (*Sabal etonia*) and rosemary (*Ceratiola ericoides*). In wetter areas, saw palmetto (*Serenoa repens*) and fetterbush (*Lyonia ferruginea*) were common.

Stand age of sand pine–scrub oak ranged from recently harvested clear cuts to mature stands ($\geq$25 yr). In addition to timber, ONF was managed for recreation and wildlife resources. Ocala National Forest received more visitors than any other national forest in Florida. With the exception of 4 designated wilderness areas, ONF contained off-road vehicle roads, forest trails, and an extensive grid of roads maintained by the United States Forest Service.

Lynne habitat consisted of small parcels of slash pine flatwoods under the ownership of ONF, private individuals, and corporations. The habitat was highly fragmented with roads and residential and commercial developments.

METHODS

Reproductive Parameters

From May 1999 through July 2003, we captured bears using Aldrich spring-activated foot snares (Aldrich Snare Co., Clallam Bay, WA). We immobilized bears with a 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®; Fort Dodge Laboratories, Fort Dodge, IA) administered at 3.0–4.5 mg/kg of estimated body weight via remote injection gun. We fit all adult females with a motion-sensitive radiocollar (150–151 MHz; Telonics, Mesa, AZ). Collars had a leather breakaway connector that allowed them to fall off after approximately 2 years. We collected data on body length and chest and neck circumferences. We lip-tattooed and ear-tagged bears for identification and extracted a first upper premolar for age determination (Willey 1974). We examined females for vulval swelling as an indicator of estrus (Jonkel and Cowan 1971). We examined nipples for lactation, length, and color. We used these indicators of reproductive status and subsequent documentation of cub production to estimate age of first reproduction, litter order (first litter: primiparous; subsequent litter: multiparous), interlitter interval, and fecundity.

We estimated age-specific fecundity rate, m_x, as the average number of female cubs (estimated as 0.5× litter size) produced by a radiocollared female of age *x*. We estimated the annual fecundity rate for a given year as the average number of female cubs produced by radiocollared females of reproductive age ($\geq$2 yr) during that year. We defined litter sizes as the number of cubs observed during den visits. We also used remote cameras throughout the study to collect data on the minimum number of cubs accompanying collared females. Remote camera stations consisted of infrared-activated cameras (CamTrakker™, Watkinsville, GA) set 2–3 m from bait of donuts and corn within a female's home range. We assumed young females captured in summer with teat characteristics indicating they had not nursed cubs (teat length <10 mm and no lactation) did not reproduce that year.

We investigated evidence of cub production from late January through February by listening for cub vocalizations near dens of radiocollared females. We visited natal dens from March to April in 2000, 2001, 2002, and 2003. We did not immobilize females; they typically left the den as we approached it. We brought cubs to a nearby area (25–50 m from the den), determined sex and tooth eruption, and collected morphometric data (body mass and length, chest and neck circumference). In most instances, a wildlife veterinarian examined cubs. To identify the cubs, we lip-tattooed them in 2000 and 2001, and we inserted a transponder chip subcutaneously between their shoulder blades in 2002 and 2003. We estimated the age of cubs based on body size, mass, tooth eruption, whether eyes were open or closed, and minimum known age (based on the date we first heard cubs in the den). In 2003, we also measured

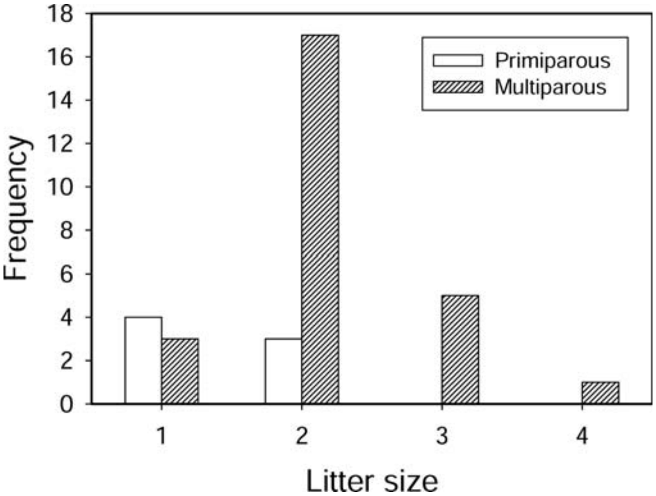

Figure 2. Frequency distribution of litter sizes for primiparous and multiparous Florida black bears in north-central Florida, USA, 2000–2003.

hair and ear lengths to estimate age (Bridges et al. 2002). We returned cubs to the maternal den within 45 minutes and monitored the female with radiotelemetry until she returned to the den site.

We located radiocollared bears from the ground using standard triangulation methods (White and Garrott 1990) and from the air using a Cessna 172 aircraft equipped with wing-mounted antennas. Lone adult bears or those with uncollared cubs were located 1 to 3 times per week; females with radiocollared cubs were located 4 to 7 times per week for the first 3 months (Apr to Jun) and at least twice per week thereafter. This schedule provided intensive monitoring during the period with highest expected cub mortality (Elowe 1987, LeCount 1987).

We used the Kruskal–Wallis test to test the null hypothesis that litter size did not differ among cohorts and that body mass of cubs did not differ among cubs born in litters of various sizes. We used the Spearman's rank correlation to test for correlation of litter size with age, body mass, or measurements of body size (body length, chest circumference, and neck girth) of the mother. We used a chi-square test to test if the sex ratio of cubs deviated from parity. We used the Wilcoxon rank-sum test to compare the litter size and litter mass of cubs from the ONF with those from Lynne and between litters born to primiparous and multiparous females. We also used the Wilcoxon rank-sum test to compare the body mass of male and female cubs and of cubs born to primiparous and multiparous females.

Cub Survival and Causes of Mortality

During den visits in 2002 and 2003, we fit cubs weighing >1.50 kg with lightweight radiocollars. The collars employed a sliding mechanism designed to expand with cub growth (Higgins-Vashon et al. 2003). For added safety, we used a 20-mm piece of elasticized cotton as a breakaway device. The collar weight was $\leq$4% of cub body mass. In 2002, we used a transmitter (55–65 g) with a 12-hour mortality switch (American Wildlife Enterprises, Tallahassee, FL). However, due to numerous transmitter failures in 2002, we switched to a 64-g model with a 2-hour mortality switch (Telonics, Mesa, AZ) in 2003.

We approached cubs immediately if a radiosignal indicated mortality or if a cub was located away from the mother. We determined the cause of cub mortality based on evidence of predation (e.g., visual observation of the predator, predator tracks, scat, blood), carcass characteristics (types of wounds, pattern of consumption; LeCount 1987), and necropsy results.

We used the Kaplan–Meier method with staggered entry design to estimate cub survival (Pollock et al. 1989). The Kaplan–Meier method assumes that survival times are independent among animals; however, survival times of cubs within the same litter may violate this assumption. Violation of this assumption does not bias estimates of survival but will lead to underestimation of the variances (K. H. Pollock, North Carolina State University, personal communication). We also estimated survival rates by using the Cox proportional hazards model (Cox and Oakes 1984) with the family effect (cubs within the same litter) modeled as a random effect.

When the exact date of cub mortality was unknown, we assumed that the cub died at the midpoint between the most recent date we knew the cub to be alive and the date we first detected the mortality signal. We used log-rank tests to test the null hypothesis that survival curves did not differ among cohorts or between ONF and Lynne study sites, between male and female cubs, between cubs born to primiparous and multiparous females, and between lightweight (<2 kg) and heavyweight ($\geq$2 kg) cubs. We used SAS (SAS Institute, Cary, NC) for all statistical analyses, except that we used S-Plus (MathSoft, Seattle, WA) for analysis of cub survival. For all statistical tests, significance was assessed at $\alpha = 0.05$.

RESULTS

Reproductive Parameters

From May 1999 to July 2003, we captured 52 females 67 times. We observed estrus (swelling of the external genitalia) on 29 occasions (43%) in 24 individuals. We documented estrus from 11 May to 26 August, but we observed most females (86%) in estrus between 10 June and 10 August. We determined age of first reproduction for 12 females. Of these, 3 produced first litters as 2-year-olds, 4 as 3-year-olds, 4 as 4-year-olds, and one as a 5-year-old. Mean ($\pm$ SE) age of primiparity was 3.25 $\pm$ 0.27 years.

We obtained data on 12 interlitter intervals from 11 females. Of these, 3 litters were produced at 1-year intervals, 8 at 2-year intervals, and one at a 3-year interval. Only those females that experienced a complete loss of litters prior to the breeding season produced litters in consecutive years. Overall, the mean interlitter interval was 1.83 $\pm$ 0.17 years; excluding the females that reproduced in consecutive years, the mean interlitter interval was 2.11 $\pm$ 0.11 years.

The mean litter size observed in 39 natal dens was 2.08 $\pm$ 0.11, and the modal litter size was 2 (Fig. 2). Litter size did not differ among cohorts (Kruskal–Wallis test; $\chi^2 = 2.58$, df

Table 1. Mean, standard error, and range of litter size of radiocollared female Florida black bears in north-central Florida, USA, 2000–2003.[a]

Variable	n	$\bar{x}$	Sex ratio (M:F)	SE	Range
Yr					
2000	9	1.89	10:7	0.20	1–3
2001	10	2.30	11:12	0.15	2–3
2002	12	2.17	12:14	0.24	1–4
2003	8	1.88	6:9	0.30	1–3
Study area					
ONF	29	2.03	28:31	0.13	1–4
Lynne	10	2.20	11:11	0.25	1–3
Experience					
Primiparous	7	1.43	4:6	0.20	1–2
Multiparous	26	2.15	27:29	0.13	1–4

[a] We grouped cubs based on the following variables: cohort (2002, 2003), study area (Ocala National Forest [ONF], Lynne), and maternal reproductive experience (primiparous, multiparous).

= 3, $P = 0.461$) or between ONF and Lynne study sites ($Z = 0.78$, $P = 0.434$). However, litters born to primiparous females were smaller than those born to multiparous females ($Z = 2.52$, $P = 0.012$; Table 1). When all the females were analyzed together, litter size was correlated with litter order ($r_s = 0.449$, $n = 33$, $P = 0.008$) and the age ($r_s = 0.334$, $n = 38$, $P = 0.040$), body mass ($r_s = 0.411$, $n = 29$, $P = 0.027$), and chest circumference ($r_s = 0.499$, $n = 28$, $P = 0.007$) of the mother. When primiparous and multiparous females were analyzed separately, only the chest circumference of multiparous females was correlated with litter size ($r_s = 0.483$, $n = 18$, $P = 0.043$).

The overall fecundity rate was 0.57 ± 0.06 and ranged across years from 0.45 to 0.70 (Table 2). Age-specific fecundity rate ranged from 0.25 for 2-year-olds and 3-year-olds to 0.79 for 6-year-olds (Table 3).

The sex ratio of 81 cubs (39 M, 42 F) born in 39 litters did not deviate from parity ($\chi^2 = 0.111$, df = 1, $P = 0.739$). The mean mass of cubs in natal dens was 2.02 ± 0.06 kg and ranged from 0.53 kg to 2.92 kg ($n = 81$). The mass of male cubs (2.06 ± 0.08 kg) did not differ from that of female cubs (1.98 ± 0.09 kg; $Z = 0.40$, $P = 0.687$). There was no difference between mass of cubs born to primiparous ($n = 10$) and multiparous females ($n = 56$; $Z = -0.765$, $P = 0.480$). Overall, mean litter mass was 4.19 ± 0.25 kg. Cub birth dates ranged from 15 January to 13 March, and the estimated median birth date was 28 January. Most litters (92%, $n = 36$) were born between 15 January and 8 February.

Table 2. The average fecundity rate (m) of radiocollared female Florida black bears in north-central Florida, USA, 2000–2003.

Yr	No. F[a]	No. cubs[b]	m[c]
2000	17	22	0.65
2001	24	23	0.48
2002	23	32	0.70
2003	19	17	0.45

[a] Number of radiocollared F of reproductive age (≥2 yr).
[b] Total no. of cubs (M and F) born to radiocollared ad F.
[c] Calculated as the no. of F cubs (no. cubs/2) divided by the no. of radiocollared ad F.

Table 3. Age-specific fecundity rates (m_x) of radiocollared female black bears in north-central Florida, USA, 2000–2003.

Age class, yr x	No. F[a]	No. cubs[b]	m_x[c]
2	6	3	0.25
3	8	4	0.25
4	9	6	0.33
5	11	15	0.68
6	14	22	0.79
7	7	6	0.43
≥8	27	37	0.69

[a] Total no. of radiocollared F of age x.
[b] Total no. of cubs (M and F) born to radiocollared F of age x.
[c] Calculated as the no. of F cubs (no. cubs/2) divided by the no. of radiocollared ad F of age x.

Fifty-two of 81 cubs (64%) evaluated during den visits were judged to be in excellent or good condition, and 29 (36%) were in fair or poor condition. During den visits, we observed one female cub from a litter of 2 with a skeletal deformity. She had a domed cranium (possible hydrocephalus), shortened upper jaw, and 8 teats. She weighed 1.29 kg less than her male littermate (1.37 kg vs. 2.66 kg) and was noticeably weak.

Cub Survival and Causes of Mortality

During 2002 and 2003, we monitored 41 cubs. Twenty cubs died, and the overall probability of survival to 9 months of age was 0.458 (95% CI: 0.32 to 0.67; Fig. 3). Four mortalities occurred in the den and 6 mortalities occurred within the first 2 weeks of leaving the den. Ten mortalities occurred later in the year; the last documented mortality occurred on 10 October due to vehicle collision. Overall, 68% of the cub mortality occurred during April to June.

Cub survival did not differ between cohorts ($\chi^2 = 0.59$, df = 1, $P = 0.444$), between ONF and Lynne study sites ($\chi^2 = 1.00$, df = 1, $P = 0.316$), or between male and female cubs

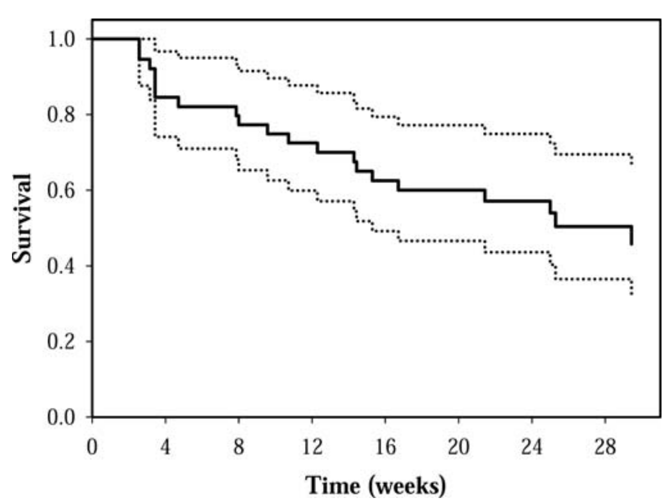

Figure 3. Kaplan–Meier survival curve for Florida black bear cubs in north-central Florida, USA, illustrating survival in 2002 and 2003 combined. We give time in weeks, beginning the week of radiocollaring (last week in Mar). The dashed lines indicate upper and lower 95% confidence intervals.

Table 4. Kaplan–Meier survival rates for radiocollared Florida black bear cubs in north-central Florida, USA, 2002 and 2003.[a]

Variable	No. cubs	Exposure weeks[b]	Survival rate	95% CI
Cohort				
2002	26	29.4	0.42	0.26–0.69
2003	15	25.3	0.56	0.34–0.92
Study area				
ONF	26	29.4	0.43	0.27–0.69
Lynne	15	25.3	0.45	0.21–0.94
Sex				
M	18	29.4	0.45	0.24–0.84
F	23	25.0	0.46	0.29–0.73
Experience				
Primiparous	4	9.57	0.25	0.05–1.00
Multiparous	34	29.4	0.51	0.35–0.74

[a] We grouped cubs based on the following variables: cohort (2002, 2003), study area (Ocala National Forest [ONF], Lynne), sex (M, F), and maternal reproductive experience (primiparous, multiparous).

[b] Number of weeks cubs were radiocollared.

($\chi^2 = 0.31$, df $= 1$, $P = 0.578$; Table 4). Survival function of cubs born to primiparous females was not different from that of cubs born to multiparous females ($\chi^2 = 3.01$, df $= 1$, $P = 0.083$). Although mortality occurrences tended to correlate within families, inclusion of family effects did not change the results of survival analyses.

Of the 20 cubs that died from 2002 and 2003 cohorts, 8 were males and 12 were females. Causes of mortality included infanticide ($n = 7$), anthropogenic sources ($n = 4$) (direct and indirect vehicle-related mortality), malnutrition ($n = 2$), abandonment ($n = 2$), trauma ($n = 1$), and unknown ($n = 4$).

We were able to determine the fate of 20 of the 40 (21 M, 19 F) noncollared cubs from 2000 and 2001 cohorts. We documented 8 (3 M, 5 F) mortalities and verified that 12 cubs (8 M, 4 F) survived 7–13 months. Of the 8 mortalities documented, 7 represented a complete loss of the litter. Cause of death was known for 4 cubs: 2 were due to infanticide, one was due to vehicle-related mortality, and one was due to disease.

DISCUSSION

Reproductive Parameters

The mean age of first reproduction and interlitter interval observed in our study population were similar to those reported for other eastern black bear populations (Hellgren and Vaughan 1994, Maddrey 1995, Kasbohm et al. 1996, Freedman et al. 2003). Because complete loss of litter was observed in our study population, the interlitter interval calculated by including the 1-year intervals might be a better estimate of the average interlitter interval (McLaughlin et al. 1994), although most estimates omit the 1-year intervals resulting from litter loss (LeCount 1987, Beck 1991, Schwartz and Franzmann 1991). Interlitter intervals >2 years have been attributed to food shortages (Rogers 1976, Eiler et al. 1989, McLaughlin et al. 1994, Miller 1994). In the Okefenokee Florida black bear population, only 1 of 15 solitary females produced cubs following a low black gum (*Nyssa sylvatica*) production (Dobey et al. 2005). However, in the Ocala bear population, interlitter intervals >2 years were rare and appeared to be unrelated to food resources. For example, following a mast failure in the fall of 2000 (McCown et al. 2004), only 1 of 11 solitary females failed to reproduce. In addition, the mean litter size for cohort 2001 was the highest recorded in the 4-year study. Bears may have the ability to shift to alternative foods and to locate small, isolated mast-producing areas, an observation supported by our radiotelemetry data. Behavioral plasticity of black bears, specifically the use of alternative food sources in years of hard mast failures has been reported in Tennessee (Eiler et al. 1989), Virginia (Kasbohm et al. 1996), and Maine (McLaughlin et al. 1994).

Overall, the mean litter size observed in this study was similar to the mean litter size of 2.10 reported by Dobey et al. (2005) but slightly smaller than the statewide estimate of 2.60 (Wooding and Bukata 1996) and 2.56 for eastern bear populations (McDonald and Fuller 2001). The statewide estimate was derived from corpora lutea counts. Although corpora lutea counts closely approximate litter size, they represent the maximum reproductive potential (Wooding and Bukata 1996). Fluctuating food abundance, maternal condition, age, and body size have been suggested as factors affecting litter size in black bear and other carnivore populations (Brand and Keith 1979, Elowe 1987, Alt 1989). However, some studies have indicated that litter size is relatively insensitive to maternal condition and that litter order is the most important factor (Noyce and Garshelis 1994, McDonald and Fuller 2001). In our study, litter order influenced the litter size, with first litters being smaller than subsequent litters, indicating that maternal experience is an important influence on litter size.

Our estimates of age-specific fecundity rates are similar to those reported by McLean and Pelton (1994) for black bears in Great Smoky Mountains National Park but slightly lower than those reported by Powell et al. (1996) for North Carolina black bears. The latter study estimated the fecundity from data on reproductive tracts of harvested bears. Therefore, some of the differences between our estimates of fecundity rate and those of Powell et al. (1996) may have been due to methodological differences.

Cub Survival and Causes of Mortality

Our estimates of cub survival were substantially lower than those reported for other black bear populations. Most studies have reported first-year survival of black bear cubs to be ≥55% (Table 5; see also Bunnell and Tait 1981, Freedman et al. 2003). We were unable to monitor cubs beyond 9 months because either radiocollars dropped off or transmitters failed.

The most common cause of cub mortality in our study population was intraspecific predation, or infanticide. Potential explanations for infanticide in many species include nutritional gain, elimination of competitors for a resource, sexual selection, parental manipulation of progeny,

Table 5. Estimates of first-year survival of black bear cubs in North America and respective references.

Study area	Survival (%)[a]	No. cubs	Reference
Wildland, NV	100	6	Beckmann and Berger 2003
Dry Creek, AR	90	20	Clark 1991
PA	86	111	Alt 1982
Shenandoah National Park, VA	73	40	Kashbohm 1996
Great Smoky Mountains National Park, TN	62	29	Eiler et al. 1989
Western MA	59	41	Elowe and Dodge 1989[b]
West-central CO	56	39	Beck 1991
NM	55	148	Costello et al. 2003
Sutsina, AK	54	73	Miller 1994
East-central ON	53	32	Kolenosky 1990
North-central AZ	48	25	LeCount 1987[b]
North-central FL	35[c]	41	This study[b]
White Rock, AR	31	13	Clark 1991
Urban interface, NV	17	18	Beckmann and Berger 2003

[a] Unless otherwise noted, we estimated survival rates by comparing the no. of cubs counted in natal dens of individual F to the no. of yearling in dens with same F the following winter. All values are finite annual survival rates.
[b] We estimated survival rates from telemetry data.
[c] Survival to 9 months converted to annual rate using methods of Krebs (1999).

and sociopathology (Fox 1975, Hrdy 1979, Polis 1981). The causes and consequences of infanticide in bear populations are poorly understood and are a subject of continued controversy (LeCount 1987, Derocher and Wiig 1999, Swenson et al. 2001, Miller et al. 2003). Based on evidence that male bears kill cubs, an inverse relationship between male abundance and cub survivorship has been suggested (McCullough 1981). However, recent reviews found no evidence for the suggested relationship between abundance of adult males and cub survival (Garshelis 1994, Sargeant and Ruff 2001, Miller et al. 2003), and studies in Scandinavia reported that removal of males resulted in lower cub survivorship (Swenson et al. 2001).

In our study, infanticide appeared to be a response to the presence of vulnerable individuals, and the benefit gained most likely was nutrition. Mating opportunity did not appear to be the motivation because most attacks did not result in complete loss of the litter, and the females did not breed the following year. Infanticide cases that resulted in a complete litter loss occurred in or near dens, and in 2 of 3 instances the mother was also killed and thus was not available for mating. One of the sites showed evidence of fighting and the female likely was killed while defending the cubs, as has been documented in other black bear and brown bear studies (Garshelis 1994, McLean and Pelton 1994, Swenson et al. 2001). We found most females with young used ground dens and were inactive throughout the denning period (Garrison 2004), whereas males typically remained active throughout the year (Wooding and Hardisky 1992, Garrison 2004). Thus, the physical state of denning females and den-site characteristics may influence vulnerability to cannibalistic males. Although there likely are multiple factors contributing to infanticide, it seems reasonable to assume that an increased density of bears may increase intraspecific encounters. Long-term monitoring (e.g., nuisance bear reports, vehicular mortality data) in our study area indicates that the Ocala bear population has increased in the past decade.

In most instances where we suspected or confidently identified the predator, it was an adult male bear. This observation is consistent with other reports that adult males are most often the predators (Bunnell and Tait 1981), although females occasionally kill unrelated cubs (Garshelis 1994). In one instance in our study, an abandoned cub attempted to associate with another family group (F with 2 cubs) but was killed and consumed by the group within a few days. Other potential predators of bear cubs in our study area included bobcats (*Felis rufus*), coyote (*Canis latrans*), and dogs (*C. familiaris*). However, we did not find any evidence (e.g., tracks, scats, caching) of these predators near the cub mortality sites.

Anthropogenic factors also contributed to cub mortality, particularly in Lynne. Cubs were killed directly by vehicle collisions or died of malnutrition after their mother was killed. In Lynne, 37.6% of the radiocollared adult females ($n = 13$) were killed during 2000–2002 (McCown et al. 2004), exposing cubs to a higher risk of mortality. Age of orphaned cubs influenced survival. For example, a 5.5-month-old (presumed age of self-sufficiency; Erickson 1959) survived after orphaning. As in other studies where cubs were followed with radiotelemetry (LeCount 1987, Elowe and Dodge 1989, Higgins-Vashon et al. 2003), we found that mortality of black bear cubs due to disease, abnormalities, or natural accidents was low. The cub with the skeletal deformities died 2 months after radiocollaring. Cause of her death was unknown; her body was almost completely consumed by a bear, however, it was unclear whether she was killed by a bear or whether a bear(s) consumed her after her death.

MANAGEMENT IMPLICATIONS

We provide estimates of age of first reproduction, interlitter interval, litter size, and fecundity useful for the development of demographic models for Florida black bears, helping guide future management plans. Moreover, because we found cub survival in our study area to be relatively low with most of the mortalities due to infanticide and we documented cannibalism of adult bears, we suggest the current practice of translocating nuisance bears to ONF be reevaluated. Although several factors can influence intraspecific aggression, relatively high density of bears in Ocala (Simek et al. 2005) may be a contributing factor. Translocation of nuisance bears to ONF, which harbors one of the densest populations of the Florida black bear (Simek et al. 2005), may exacerbate the potential effects of population density (Polis 1981). In addition, because survival of cubs depends heavily on survival of mothers, measures to reduce mortality of adult females due to anthropogenic causes (e.g., vehicular collision) could also enhance survival of cubs. Consequently, we recommend underpasses on highways in human-dominated landscapes.

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