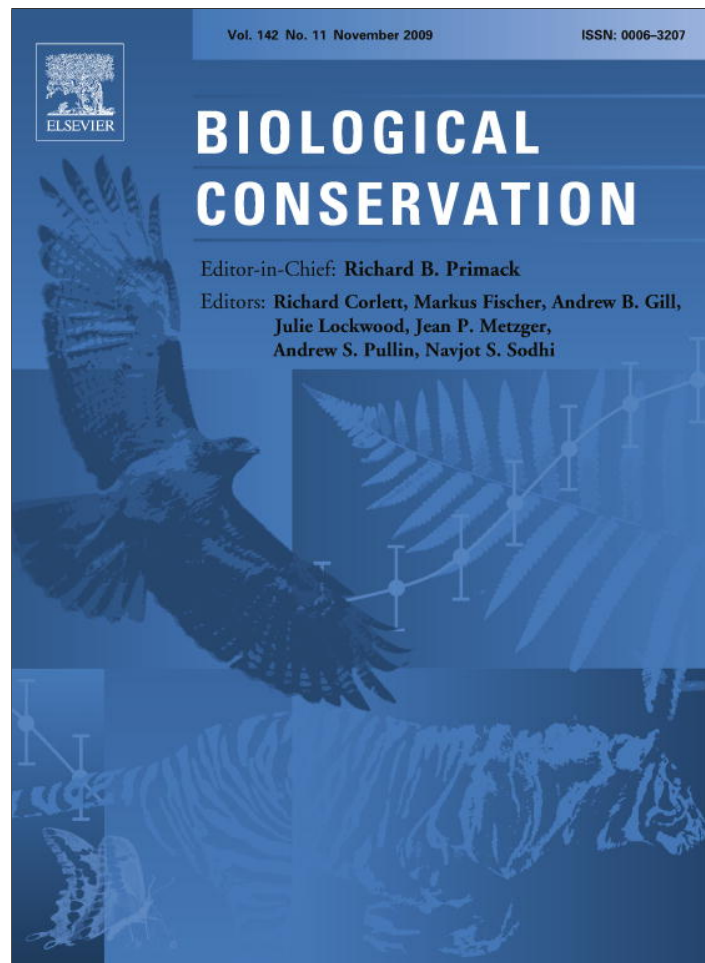


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Demographic consequences of anthropogenic influences: Florida black bears in north-central Florida

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ABSTRACT

Anthropogenic habitat fragmentation poses a serious threat to conservation of large carnivores, due to their extensive movements and potential conflicts with humans. We studied the population ecology of Florida black bears (*Ursus americanus floridanus*) for 6 years in two study areas in north-central Florida: Ocala National Forest (ONF), a contiguous forested habitat, and an adjacent residential community of Lynne, a fragmented habitat with substantial human activities. We estimated age-specific survival and fecundity rates of bears using data from radio-collared bears, and parameterized and analyzed stage-structured matrix population models for the two study sites and also for data pooled from both sites. Annual survival rates of adult females were lower in Lynne (0.776 ± 0.074) than in ONF (0.966 ± 0.023). While cub survival rates were higher in Lynne (0.507 ± 0.135) than in ONF (0.282 ± 0.109), the rates at both sites were substantially lower than those reported for other black bear populations. Age-specific fecundities did not vary between sites. The asymptotic population growth rate for ONF was greater than one, whereas that for Lynne was less than one. Our results suggest that anthropogenic influences (primarily road density and vehicular traffic, through their effect on adult survival) can substantially affect the population dynamics of Florida black bears and other large carnivores with large home ranges. We recommend efforts such as constructing highway underpasses, which could reduce road-related mortalities, to ensure long-term persistence of Florida black bears facing threats from rapidly increasing human influences.

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1. Introduction

The loss and fragmentation of habitat due to human activities is one of the most important factors contributing to loss of biodiversity throughout the world (Diamond, 1989; Lawton and May, 1995; Laurance and Bierregaard, 1997; Young and Clarke, 2000; Fahrig, 2001). Consequently, many species of conservation concern currently occur in fragmented habitats (Young and Clarke, 2000). Habitat fragmentation can disrupt social structure and dispersal patterns, increase mortality, and reduce genetic diversity, reproductive rates, and persistence probabilities of wildlife populations (Goosem, 1997; Jules, 1998; Harrison and Bruna, 1999; Srikwan and Woodruff, 2000; Cale, 2002).

Anthropogenic influences on habitat can include loss, degradation, subdivision, and isolation of habitat; increased edge effects; and other direct and indirect effects of human presence; each of these can affect dynamics and persistence of populations

(Lindenmayer and Fischer, 2006). Among various anthropogenic activities, roads can have especially dramatic effects on wildlife, including direct mortalities, increased air, water, and noise pollution, indirect increase in mortality (e.g., through increased access for hunters), and barriers to or conduits of movement (Trombulak and Frissell, 2000; Forman et al., 2003; Coffin, 2007).

Florida is home to 109 federally listed endangered and threatened plant and animal species (USFWS, 2007), many of which occur in fragmented habitats. Florida's human population is projected to grow by 79% between 2000 and 2030 (US Census Bureau, 2005); this will undoubtedly lead to further loss and fragmentation of remaining wildlife habitat. Understanding how habitat fragmentation influences demography and dynamics of wildlife populations is of paramount importance, because such an understanding will help guide conservation efforts.

The Florida black bear (*Ursus americanus floridanus*) was historically distributed throughout Florida and southern Georgia, Alabama, and Mississippi (Brady and Maehr, 1985). Large scale logging and unregulated hunting greatly reduced their numbers in Florida by the mid-1900s (McDaniel, 1974). Currently, bears

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occupy 17% of their historic range (Wooding et al., 1994) and are listed as threatened in Florida, occurring in several fragmented and geographically isolated populations with limited gene flow between them (Dixon et al., 2006, 2007).

The Ocala National Forest (ONF) harbors one of the largest populations of black bears in Florida (Simek et al., 2005; Dixon et al., 2007). This population, however, also experiences strong anthropogenic influences, such as vehicular mortality and illegal harvest. The human population in the four counties surrounding ONF (Marion, Lake, Putnam, and Volusia counties) is expected to grow by 75% between 2000 and 2030 (Smith and Rayer, 2005). This increase in human population is likely to result in an increase in traffic and traffic-related bear fatalities, which is already substantial (McCown et al., 2009).

Accordingly, an understanding of demographic and population dynamic consequences of anthropogenic effects, and population-level influences of anticipated increases in traffic-related bear fatalities, would help guide management of Florida black bear populations in ONF and other increasingly human-dominated landscapes. Our overall goal was to understand demographic consequences of anthropogenic influences using Florida black bears as a model system. Specifically, we parameterized and analyzed matrix population models for the Florida black bears inhabiting a contiguous forested habitat and an adjacent residential community. We estimated and compared population growth rates, examined the proportional sensitivity (i.e., elasticity) of growth rates to vital demographic parameters, and simulated the effects of increased mortality (perhaps due to an increase in traffic-related mortalities) on Florida black bear population dynamics. We hypothesized that human activity would have no effect on fecundity rates, but that the bears inhabiting the more fragmented habitat would have higher mortality rates, and thus lower population growth rates, than those in the less fragmented habitat. These hypotheses stemmed from previous studies showing substantial demographic effects of habitat fragmentation and other anthropogenic influences, including reduced survival and population growth for a variety of vertebrate species (e.g., Kerley et al., 2002; Kramer-Schadt et al., 2004; Letcher et al., 2007; Ruiz-Gutiérrez et al., 2008).

2. Methods

2.1. Study area

This study was conducted in ONF and the adjacent unincorporated community of Lynne, both located in north-central Florida (Fig. 1). The primary study area consisted of approximately 468 km² of nearly contiguous bear habitat at the center of ONF, bisected by State Road 40 (SR-40), a two-lane paved road with an approximate traffic rate of 5100 vehicle trips per day (Fig. 1; Florida Department of Transportation, 2003). The primary study area was approximately 60% sand pine (*Pinus clausa*)/scrub oak (*Quercus* spp.), 22% slash pine (*P. elliotti*) flatwoods, 10% wetland hardwoods, and 5% prairies (Aydelott et al., 1975; Moyer et al., 2008). The forest is managed for timber, and a variety of recreational activities (camping, hiking, canoeing, swimming, off-road vehicles use, horseback riding, hunting, and fishing). Ages of stands ranged from recent clear cuts (0–2 years) to ≥ 25 years. Bear harvest has not been permitted at ONF since 1971.

The secondary study area consisted of approximately 211 km² in the small residential community of Lynne, which straddles SR-40 3.75 km west of the primary study area. Bear habitat in Lynne consists of small parcels of slash pine flatwoods under ownership of ONF, corporations, and individuals. Bear habitat in Lynne is discontinuous and dispersed in a network of moderate volume roads and residential, industrial, and commercial development.

The study sites were close, and occasional movements of bears between the two sites did occur; thus, we make no claim that these areas represent genetically distinct populations. However, based on our long-term radio-tracking data, we are confident that all females maintained their home ranges within the study area in which they were captured.

2.2. Quantification of habitat fragmentation and anthropogenic influences

Using a Geographic Information System (ESRI ArcMap 9.2), we obtained land cover data for the two study areas from a statewide (30 m resolution) digital layer for Florida (Kautz et al., 2007). Based

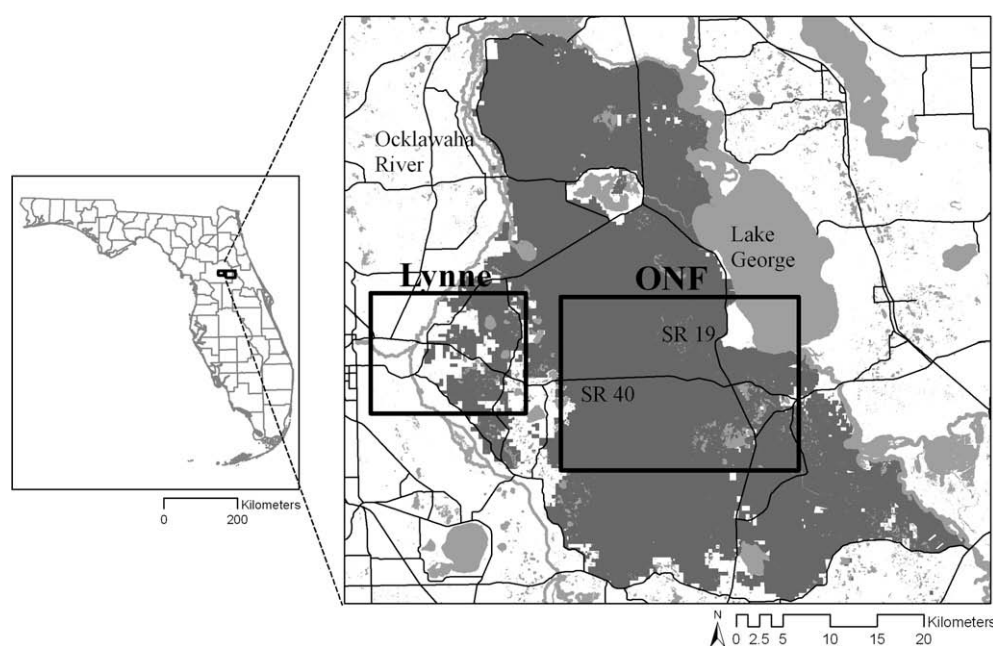


Fig. 1. Map of Ocala National Forest (dark gray) in north-central Florida. The two study areas are ONF (eastward polygon) and Lynne (westward polygon). Other land cover classes within the study areas includes private lands (white), water bodies (light gray), and roads (black lines).

on findings of Moyer et al. (2008) and our long-term radio-telemetry data, we reclassified 24 land cover types into two categories using ArcGIS Spatial Analyst extension (ESRI): suitable habitat (consisting of xeric oak scrub, sand pine scrub, sandhill, dry prairie, mixed pine-hardwood forest, hardwood hammocks and forest, pinelands, freshwater marsh and wet prairie, shrub swamp, bay swamp, cypress swamp, mixed wetland forest, hardwood swamp, shrub and brushland, bare soil/clearcut, and low impact urban), and unsuitable habitat (consisting of high impact urban, improved pasture, unimproved pasture, citrus, row/field crops, other agriculture, and grassland). Gilbert and Stys (2004) provide detailed descriptions of land cover types.

We used four metrics generated by FRAGSTATS 3.3 (McGarigal et al., 2002) to explore landscape fragmentation within the two study areas (contagion (CONTAG), percent land cover (PLAND), patch density (PD), and mean patch area (AREA_MN); see Table 1 for description of fragmentation metrics). Classes consisted of the categories suitable habitat and unsuitable habitat (with open water set as background) and patches were defined using the eight neighbor rule (McGarigal et al., 2002). Finally, we quantified anthropogenic influences using three metrics: (1) the density (km/km²) of major paved roads calculated as length of roads (km) within each study area divided by total size (km²) of the study area (Florida Department of Transportation, 2008); (2) traffic volume (no. of trips/day) along SR-40 within each study area (Florida Department of Transportation, 2003); and (3) resident human population within each study area. Although the road layer consisted of 2008 data, the same major roads (i.e., high impact urban) were present in the 2003 land cover data.

2.3. Telemetry of adult bears

We captured adult bears by modifying standard techniques described by Johnson and Pelton (1980) and by the use of culvert traps. We trapped bears from mid-May to mid-December in 1999–2002 and from June to August in 2005 and 2006. Bears were aged using an extracted premolar tooth (Willey, 1974). All adult females and some adult males captured were fitted with radio collars equipped with mortality beacons that were activated if the collar was motionless for more than 2 h. Capture and telemetry techniques are described in more detail elsewhere (Garrison et al., 2007; McCown et al., 2009).

2.4. Estimation of adult survival

We tracked radio-collared adult females 1–3 times per week, using ground and aerial telemetry, from May 1999 to May 2003 and June 2005 to August 2007. We documented mortalities by ground checking all mortality signals. Whenever possible, we necropsied bears to identify the cause of death. We used the Cox proportional hazard model (with staggered entry) for estimating

survival rates of collared bears, and for testing the effects of site and year on survival (Therneau and Grambsch, 2000).

2.5. Reproductive parameters

We visited natal dens of radio-collared females from March to April in 2000–2003, 2006, and 2007 to count and mark cubs. We obtained the number of cubs from den visits and observations made during capture or tracking of adult females. Field methods were described in detail by Garrison et al. (2007). We estimated age-specific fecundity rates as the average number of daughters (estimated as one-half times the litter size) produced per radio-collared female (including non-breeders) of a given age per year. Thus, some females were included in more than one age class if they produced >1 litter during the study. Females that were captured in summer with no indication of having produced cubs that year (no lactation or evidence of cubs with her, or she produced a litter the following winter) were assumed not to have reproduced that year (Garrison et al., 2007). Age of first reproduction in our study population was as early as 2 years, which is earlier than those reported from other populations (Garrison et al., 2007). We estimated the variance of the age-specific fecundity rates and compared fecundity rates between study sites using the bootstrap method (Efron and Tibshirani, 1994).

2.6. Cub survival

During den visits in 2002, 2003, 2006, and 2007 we fitted cubs weighing more than 1.5 kg with lightweight radio-collars equipped with mortality switches. If a cub did not meet the minimum body weight criterion for radio-collaring, its den was revisited and the cub was collared at a later date. The collars included a sliding mechanism designed to expand with cub growth (Vashon et al., 2003). The collar weight was <5% of cub body-mass.

After the bears emerged from their dens, we located radio-collared females and cubs 4–7 times per week for the first three months (April–June), and at least twice per week thereafter. This schedule provided intensive monitoring during the period with highest expected mortality (Elowe, 1987; LeCount, 1987; Garrison et al., 2007). We approached cubs immediately if a collar transmitted a mortality signal or if a cub was located away from the mother. If the exact date of a cub's death was unknown, we used the midpoint of the interval between the date the cub was last known to be alive and the date the mortality signal was first detected. For more details on cub capture and radio-tracking, see Garrison et al. (2007).

No cubs retained their collars for a full year. We right-censored cubs that lost their collars or had radio failures. Most cubs died or were censored in the first six months, and the last cub was censored 11 months after the first cub was radio-tagged that year. We used parametric survival analyses (Klein and Moeschberger, 2003) to identify appropriate survival functions and

Table 1
Quantification of area and configuration of land cover within the two study sites, Lynne and ONF. The first five variables starting from the left correspond to the entire landscape, whereas the next three variables describe suitable habitat only. FRAGSTATS^a metrics are those represented by all capital letters.

Study area	Landscape area (km ²)	Road density (km/km ²)	Traffic volume (trips/day) ^b	Resident human population ^c	CONTAG	Suitable habitat		
						PLAND	PD	AREA_MN
ONF	467.7	0.12	5100	0	92.0	89.3	0.15	5.8
Lynne	210.8	0.30	14,700–16,700	3760	64.4	87.3	1.33	0.7

^a CONTAG (contagion) = aggregation and interspersions of class types in the landscape (ranges from 0% to 100%); PLAND (% land cover) = sum of class area divided by total landscape area; PD (patch density) = the number of patches divided by landscape area; AREA_MN (mean patch area (km²)) = sum of class area divided by the number of patches.

^b Traffic volume is for SR-40 only, from 2003 (Florida Department of Transportation, 2003).

^c The resident population for Lynne (Moyer et al., 2007) is for the town as a whole instead of the study area.

project survival to a full year. This approach allowed us to estimate annual survival rates with the available data that spanned less than a year. We used the date each cub was captured as the beginning of the study (time 0) for that cub; this approach is commonly used in medical studies and also was appropriate for our study (Klein and Moeschberger, 2003). Unlike non-parametric (e.g., Kaplan–Meier) and semi-parametric (e.g., Cox proportional-hazard) methods, parametric survival analyses presuppose a functional form to the hazard distribution. Because we had no strong *a priori* beliefs about the changes in hazard over the first year of life for bear cubs, we tested several commonly used survival distributions: exponential, Weibull, generalized gamma, lognormal, and log-logistic (Allison, 1995). We used Akaike's Information Criterion (AIC; Burnham and Anderson, 2002) to compare survival distributions, each with and without study site as a covariate. We model-averaged the annual survival estimates from the models that converged successfully (Burnham and Anderson, 2002). The model averaged estimates for each study site were averaged over all models (models without a study site effect were included as having the same survival for both sites), whereas the overall model average estimated only includes models with no study site effect.

2.7. Construction and analysis of population models

We developed stage-structured matrix population models (Caswell, 2001) based on a post-breeding census for females in ONF, Lynne, and the combined population (i.e., data pooled from both sites). We used a one year projection interval and five stages, the first four of which represented age classes 1–4 and the last of which represented bears ≥ 4 year of age. We used the estimate of annual survival rate obtained from the parametric survival analysis for the survival of the cubs (age class 1). The survival of the adult age classes (2-years old and older) were estimated from the analysis of radio-telemetry data as described previously. When data from ONF and Lynne were pooled and treated as one population, we had sufficient data for separate survival estimates for 2-year old and ≥ 3 -year old bears. When each site was considered separately, however, data were insufficient for estimation of survival for two adult age classes; thus, we used a single estimate of survival for females aged 2 and older. We only were able to radio-collar two yearling females in this study. Therefore, for the survival of second age class (1–2 years) we used a range of values between the annual survival rates of cubs and adult bears. We estimated the fertility rate for each age class using the post-breeding census formulation (Caswell, 2001) as the product of the survival and fecundity rates of that age class. To estimate the variances of the fertilities, we used Goodman's (1960) exact method for the variance of products of random variables.

Using these population projection matrices, we calculated the asymptotic population growth rates (λ), and elasticity of λ to matrix entry and lower-level parameters (Supplementary material) using methods described by Caswell (2001). We estimated the variance of λ using the delta method (assuming no covariation among vital demographic rates), and constructed approximate confidence intervals on λ assuming normal distribution (Caswell, 2001).

2.8. Simulation of increased mortality

To examine the potential effects of increased mortality in the future (e.g., due to increased traffic fatalities, removal of nuisance bears, harvest, or other causes) on population dynamics and to evaluate a sustainable level of increased mortality, we added a removal term to all matrix models with $\lambda > 1$ (removal in a population with $\lambda \leq 1$ could not be sustainable) as follows:

$$\mathbf{A} = \begin{bmatrix} 0 & P_2(1-h)m_2 & P_3(1-h)m_3 & P_4(1-h)m_4 & P_{5+}(1-h)m_{5+} \\ P_1 & 0 & 0 & 0 & 0 \\ 0 & P_2(1-h) & 0 & 0 & 0 \\ 0 & 0 & P_3(1-h) & 0 & 0 \\ 0 & 0 & 0 & P_4(1-h) & P_{5+}(1-h) \end{bmatrix}$$

where \mathbf{A} is the population projection matrix, P_i is the survival rate of age class i , m_i is the fecundity of age class i , and h is the removal rate (i.e., proportion of adults and yearlings removed each year). Incorporating removal into fertility (survival times fecundity) terms is appropriate when removal precedes reproduction (Caswell, 2001, pp. 640–641), as is the case for any post-breeding census model, because adults may be removed before they can reproduce.

We simulated a range of removal levels between 0 and 0.15. Because yearling survival was also unknown, we varied removal and yearling survival rates simultaneously and examined the effects on the population growth rate and lower level elasticities. Specifically, we looked at what combinations of removal and yearling survival would lead to $\lambda = 1$.

3. Results

3.1. Fragmentation and anthropogenic influences

Although the two study areas contained similar proportions of suitable habitat, fragmentation metrics revealed a more fragmented landscape with patchily distributed habitat in Lynne compared to ONF (Table 1). The mean patch size was much smaller in Lynne, and 94% ($N = 281$) of patches were ≤ 0.01 km²; in ONF, only 83% ($N = 72$) of patches were ≤ 0.01 km². Furthermore, contagion was lower in Lynne than ONF, indicating habitat classes in Lynne were less aggregated and more dispersed. The density of paved roads and traffic volume in the Lynne study area were each more than double that in ONF study area. Finally, Lynne contained a resident human population of 3760, whereas there was no resident human population in ONF (Supplementary Table 1).

3.2. Demographic variables

We placed radio collars on 39 adult females in ONF and 18 adult females in Lynne, and monitored them for a total of 58,382 radio-days. We documented two mortalities of radio-collared females in ONF (from intraspecific aggression) and seven among radio-collared females in Lynne (from vehicular accident and illegal hunting) (Appendix B).

The Cox proportional-hazard analysis indicated that the survival curves for Lynne and ONF females differed significantly (Fig. 2), but there was no evidence for temporal variation in survival in either site. The annual survival rate for radio-collared adult females was 0.966 (95% CI = 0.921–1) in ONF and 0.776 (95% CI = 0.644–0.936) in Lynne (Table 2). The annual survival rate estimated for the combined population (i.e., data pooled from both sites) was 0.744 (95% CI = 0.484–1.0) for 2-year old females and 0.914 (95% CI = 0.855–0.977) for older females (Table 3).

Reproductive data were collected from 47 radio-tagged adult females of known age that were monitored from 2000 to 2003, 2006, and 2007, for a total of 94 bear-reproductive seasons. Over that period, they produced 105 cubs. The age-specific fecundity rates ranged from 0.25 for 2 and 3-year olds to 0.669 for females 5-years and older (Table 2). Fecundity rates for the two sites were similar (overall fecundity at ONF = 0.565 and at Lynne = 0.547; $p = 0.444$; differences between sites by age class were also non-significant).

We placed radio collars on 26 cubs in ONF and 24 cubs in Lynne in 2002, 2003, 2006 and 2007. We monitored these cubs for a total

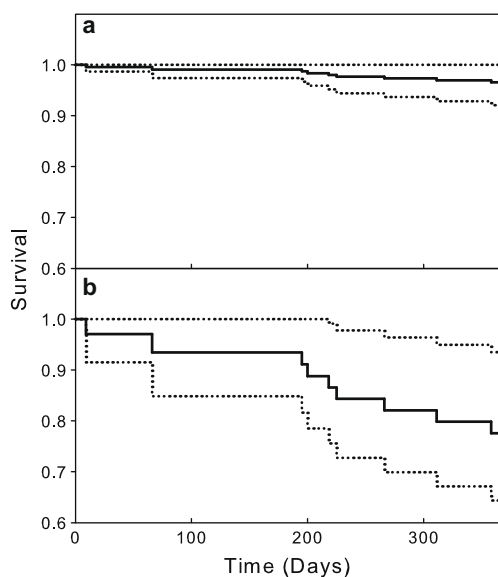


Fig. 2. Cox-proportional hazard survival curves for adult females in (a) Ocala National Forest and (b) Lynne study sites. Time is given in day of the year, beginning on March 31. The dotted lines represent the 95% confidence intervals.

Table 2

Age- and site-specific fecundity (m_i) and survival (P_i) rates used in the population models. P_i represents the survival rate between ages $i - 1$ and i and m_i represents the fecundity at age i . A range of values between the cub survival rate and survival rate of age class three were used for yearling survival rates.

Study area	Age class	m_i	SE	P_i	SE
Ocala	1	–	–	0.282	0.109
	2	0.250	0.157	0.28–0.97	–
	3	0.250	0.106	0.966	0.023
	4	0.300	0.127	0.966	0.023
	5+	0.669	0.071	0.966	0.023
Lynne	1	–	–	0.507	0.135
	2	0.250	0.157	0.50–0.78	–
	3	0.250	0.106	0.776	0.074
	4	0.300	0.127	0.776	0.074
	5+	0.669	0.071	0.776	0.074
Combined	1	–	–	0.382	0.107
	2	0.250	0.157	0.38–0.75	–
	3	0.250	0.106	0.744	0.164
	4	0.300	0.127	0.914	0.031
	5+	0.669	0.071	0.914	0.031

Table 3

Model selection results for parametric survival analysis for black bear cubs in north-central Florida. Shown are the survival distributions tested, whether study site (ONF or Lynne) was used as a covariate in each model (Site), the number of parameters for each model, the difference in Akaike's Information Criterion between each model and the best model (Δ AIC), the AIC weights, the intercept, scale, and site effect (parameters for the survival distributions, estimated by maximum likelihood methods), and the predicted annual survival rates (SE in parentheses) for each site (or for the sites combined). A site effect >0 indicates a decline in hazard (or increase in survival) for Lynne compared to ONF. The bottom row shows the model-averaged annual survival rates. The value of the shape parameter for the gamma distribution is -0.660 .

Distribution	Site	Par.	Δ AIC	AIC Weight	Inter.	Scale	Site Effect	Annual Survival	
								ONF	Lynne
Lognormal	Yes	3	0	0.479	4.824	1.614	1.364	0.252 (0.092)	0.571 (0.108)
Log-logistic	Yes	3	2.108	0.167	4.835	0.964	1.196	0.249 (0.091)	0.534 (0.111)
Exponential	No	1	3.761	0.073	5.775	–	–	0.322 (0.080)	–
Exponential	Yes	2	3.809	0.071	5.493	–	0.617	0.223 (0.093)	0.445 (0.127)
Lognormal	No	2	4.025	0.064	5.535	1.814	–	0.420 (0.083)	–
Log-logistic	No	2	4.871	0.042	5.503	1.029	–	0.405 (0.083)	–
Weibull	Yes	3	4.992	0.039	5.556	1.184	0.751	0.263 (0.107)	0.492 (0.133)
Weibull	No	2	5.051	0.038	5.894	1.175	–	0.366 (0.095)	–
Gamma	No	3	5.842	0.026	5.137	2.059	–	0.448 (0.208)	–
Average								0.282 (0.109)	0.507 (0.135)

of 6763 radio-days. We documented 13 mortalities of cubs in ONF and 8 in Lynne, from causes including intraspecific aggression (a leading cause), malnutrition, trauma, and vehicular accidents (Supplementary Table 1; also see Garrison et al., 2007).

We estimated annual cub survival using five parametric survival distributions, each with and without the effect of the study site. The generalized gamma distribution with study site included did not converge and we rejected it. Of those that remained, the lognormal distribution with study site included had the lowest AIC score (Table 3). The projected model-averaged annual estimates of survival rates for cubs were 0.282 (SE 0.109) for ONF, 0.507 (SE 0.135) for Lynne, and 0.382 (SE 0.107) for the combined population (Table 3).

3.3. Population growth rates and sensitivity analysis

The asymptotic population growth rate (λ) ranged from 1.014 to 1.100 for the ONF study site, between 0.917 and 0.969 for the Lynne study site, and between 0.985 and 1.037 for the combined population, depending on the value of yearling survival used (Fig. 3). In the combined population, λ reached 1.0 with a yearling survival of ~ 0.48 . The 95% confidence intervals for both study sites, as well as for the combined population, overlapped 1.0 for most or all values of yearling survival (Fig. 3). Elasticity analyses revealed that λ was proportionately most sensitive to changes in survival of ≥ 2 year-old females (Supplementary material).

3.4. Evaluating the effects of removal

For the ONF study site, the proportion of adults and yearlings that could be removed annually and maintain a population growth rate of 1 ranged between 0.014 and 0.100, depending on the value of yearling survival used (Fig. 4a). The sustainable removal rate for the combined population ranged between less than 0 (additions of bears required to reach $\lambda = 1$) and 0.040, depending on the value of yearling survival used (Fig. 4b). The population growth rates ranged between 0.868 and 1.100 for ONF and 0.846 and 1.037 for the combined population, depending on values of yearling survival and removal rate (Fig. 4). Results of elasticity analyses of lower-level parameters indicated that elasticity of λ to the removal rate increased as the removal rate itself increased (see Supplementary material for details).

4. Discussion

Low population densities, large home ranges, and potential conflicts with humans render large mammalian carnivores particularly

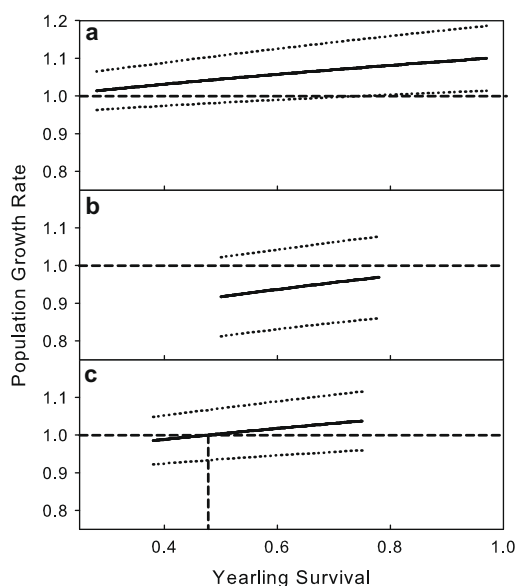


Fig. 3. Asymptotic population growth rates for (a) Ocala National Forest (ONF), (b) Lynne, and (c) the combined population. The estimates of growth rates depend on the values used for annual yearling survival rate, which were allowed to range from the estimated annual cub survival rate for each population (0.282, 0.507, and 0.382, for ONF, Lynne, and combined population, respectively) and the estimated survival rate of 2-year olds for each population (0.966, 0.776, and 0.744, for ONF, Lynne, and combined population, respectively). The dashed horizontal lines represent a growth rate of one (stable population), and the dotted lines represent approximate 95% confidence intervals.

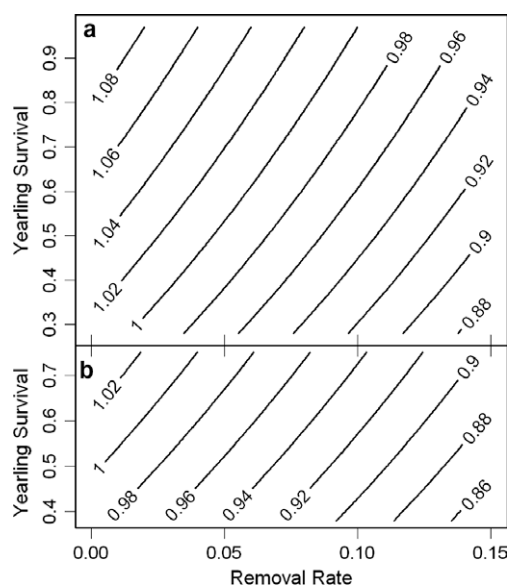


Fig. 4. Evaluating the effects of removal rate on asymptotic population growth rates for (a) Ocala National Forest (ONF) and (b) the combined population. The estimates of growth rates depend on the values used for annual yearling survival rate and removal rate. Yearling survival rates were allowed to vary from the estimated annual cub survival rate for each population (0.282 and 0.382, for ONF and the combined population, respectively) and the estimated survival rate of 2-year olds for each population (0.966 and 0.744, for ONF and the combined population, respectively). Removal rates were allowed to range between 0 and 0.15.

vulnerable to the effects of habitat fragmentation and other anthropogenic influences (Noss et al., 1996; Woodroffe and Ginsberg, 1998; Crooks, 2002). Large carnivores have also been shown to be sensitive to the effects of roads (Kerley et al., 2002; Ruediger, 2004; Waller and Servheen, 2005). Given that remaining wildlife habitats will continue to be fragmented to accommodate

needs of an expanding human population, an understanding of how habitat fragmentation, roads, and other anthropogenic activities influence dynamics of wildlife populations would help guide future conservation efforts. To that end, our goal was to elucidate effects of anthropogenic influences on demography and population dynamics of Florida black bears in a human-dominated landscape in the rapidly urbanizing state of Florida.

We found that habitat in Lynne was more fragmented as it consisted of smaller patches and was more dispersed (i.e., less aggregated) than in ONF. Furthermore, Lynne experienced a greater degree of anthropogenic activities including a higher density of paved roads, higher traffic volume and presence of a resident human population. We believe that these differences, particularly density of paved roads and traffic volume, were the main cause of the demographic disparities between the two sites, because of the high road mortality seen in our study sites, reported here and elsewhere (Simek et al., 2005; McCown et al., 2009). The proximity of the two study sites and the similar proportion of available suitable habitat suggest that other differences between them were probably minor.

In the contiguous habitat of ONF, survival of adult females was higher than that in the fragmented habitat in Lynne. All recorded deaths of radio-collared females in Lynne were from anthropogenic causes, while no radio-collared females died of anthropogenic causes in ONF. The annual adult female survival rates and age-specific fecundities observed in our study fall within the range reported from other populations in the southeast US, although the survival rate in Lynne was low for an un hunted population (McLean and Pelton, 1994; Sorensen and Powell, 1998; Freedman et al., 2003; Dobey et al., 2005). Lower survival of adult females in Lynne than in ONF and other un hunted black bear populations was most likely because of high density of roads, higher traffic volume, and increased negative interactions with humans.

Contrary to our expectation, survival of cubs in ONF was lower than that in Lynne. This result was unexpected because survival of adult females in Lynne was lower, and death of mothers typically leads to a complete litter failure. We note, however, that there was little evidence of a site effect for some survival distributions considered in our study (Table 3). Although the model averaged estimates incorporate this uncertainty to some extent, it is possible that the site effect we observed was spurious. A greater proportion of cubs in ONF died due to intraspecific aggression than in Lynne, perhaps a result of a higher bear density in ONF; this may have contributed to the observed differences in survival of cubs between the two sites (Garrison et al., 2007). Cub survival rates, especially in ONF, were substantially lower than those reported from most other studies of black bears (Garrison et al., 2007). There was no evidence that reproduction of bears in Lynne differed from that in ONF.

The combined population reached an asymptotic population growth rate (λ) of 1.0 with a yearling survival of 0.48. A review of published survival rates for yearling bears (Supplementary Table 2) suggests that the yearling survival rate at our study site may be similar to or higher than that, implying that the population may be stable or slowly growing. We note that our population models are deterministic, and do not consider factors such as demographic and environmental stochasticity and catastrophic events, due to data limitations. It is well known that the aforementioned factors will reduce population growth rates (Tuljapurkar, 1990; Caswell, 2001). Thus, long-term growth rates of our study population is likely to be lower than that reported here. Increases in mortality due to increased human impacts over time may further reduce population growth rate.

The asymptotic population growth rates (λ) estimated from the demographic rates for Lynne were lower than those for ONF, despite mixed patterns of anthropogenic influences on the demographic rates. The population growth rate of <1.0 in Lynne

suggests that this population may be a “sink” that would not persist without immigrants from the ONF. We recognize that our study was based on one group of bears inhabiting highly fragmented and human-dominated habitat and another group occupying contiguous and less disturbed habitat. This situation is not ideal for rigorous statistical inference, but replicated field studies of large carnivores that permit rigorous statistical inferences are rarely possible. Nevertheless, two important results emerge from our study that have broad implications. First, the population as a whole could probably not sustain itself if it faced the level of adult mortality seen in Lynne. Second, in the fragmented habitat in Lynne, all deaths of adult, radio-collared females were from anthropogenic causes (collision with vehicles and poaching). There is little doubt about the negative effects of anthropogenic influences for many species, but the mechanisms by which this can occur can vary among species (Fahrig, 2003; Letcher et al., 2007; Stuchbury, 2007). Our study provides an example of demographic mechanisms by which anthropogenic activities can influence population dynamics.

To examine the possible effects of increased mortality, which can arise due to an increase in traffic volume as the human population increases or due to other anthropogenic influences, we simulated a range of removal rates for the ONF study site and the combined population. Depending on the value used for yearling survival, the combined population might need addition of bears to reach a stable population, or it might be able to sustain a removal rate as high as 0.040 per year. These results suggest that the population may sustain a low level of additional mortality (e.g., increased road-related mortality or nuisance bear removal). However, these should be interpreted cautiously because stochastic events such as prolonged drought, mast failure and disease can reduce survival and reproductive rates (and thus, population growth rate) below replacement level.

Elasticity analyses revealed that λ was proportionately more sensitive to changes in survival (particularly of reproductive age classes) than to reproductive parameters (Supplementary material). These results are similar to those reported by Freedman et al. (2003) for black bear populations of the Southeastern Coastal Plain, and also are consistent with broader elasticity patterns for long-lived mammals with relatively low reproductive rates (Heppell et al., 2000; Oli and Dobson, 2003). Elasticity analysis of the model that included the removal term showed that the absolute value of the lower-level elasticity of λ to the removal rate was generally lower than that to changes in survival or fecundity rates, but it increased as the removal rate increased. However, these results were based on asymptotic analysis of matrix model and should be interpreted with caution. Asymptotic population growth rates and elasticities, although informative and generally robust (Caswell 2001), may not always reflect short-term growth rates or elasticities (Caswell 2007; Ozgul et al., 2009). Analysis of transient dynamics requires estimates of abundance for each age class, which are not available for our study population; consequently, we could not evaluate how results of transient analyses might compare to those of asymptotic analyses reported here.

Florida is experiencing a rapid population growth, and this trend will likely continue in foreseeable future (US Census Bureau, 2005). Thus, wildlife habitat will continue to be lost to commercial and residential developments, and construction or expansion of roads will further fragment remaining habitat. In our study site, the Florida 2060 model (Zwick and Carr, 2006) predicts that the future increase in urban area by the year 2060 would result in a loss of suitable habitat within Lynne of 13.0 km² and in ONF of 3.3 km², as compared to the 2003 land cover layer. Thus, fragmentation will increase as preferred habitat decreases in Lynne at a much faster rate than may occur in ONF. In addition, the widening of SR40 from

2 to 4 lanes through the Lynne study area has been approved. These changes would likely lead to an increase in traffic volume. A series of eight large-species wildlife crossing structures is planned for the approximately 22.8 km section of the road to mitigate the effects of this highway on bears and other species of concern. We believe this is a prudent step to mitigate the potential effects upon bear mortality and dispersal and to help ensure demographic and genetic connectivity of the population.

The future challenge for wildlife conservation in Florida and other rapidly urbanizing states or countries is one of managing wildlife populations in a fragmented, human-dominated landscape. This requires an adequate understanding of how demographic rates and population dynamics are affected by habitat fragmentation and other anthropogenic influences. In this study, we demonstrated an apparent population level effect of anthropogenic influences, mediated through reduction in survival due primarily to road-related fatalities. An increase in yearling and adult mortality due to anthropogenic causes may lead this population from stable or increasing to declining, especially with increasing habitat fragmentation. We recommend efforts to maintain or increase survival of adult Florida black bears, such as highway underpasses, careful management of residential and commercial developments, and vehicular traffic, reduced speed limits during periods of low visibility, and increased efforts to reduce illegal killing of bears.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.05.029.

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