

Demographics of American black bear populations following changes in harvest policy

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Abstract: Harvest can affect the size and composition of wildlife populations. American black bear (*Ursus americanus*) populations in the Central Interior Highlands, Arkansas, USA, were nearly extirpated as a result of harvest and habitat change, but have expanded geographically and demographically since reintroduction in the late 1950s and early 1960s. Harvest levels have increased since baiting was permitted on private land in 2001; therefore, we initiated demographic analyses of 2 black bear populations to evaluate the effect of this policy change. We evaluated composition of harvest in response to baiting and used noninvasive genetic sampling in conjunction with capture–recapture methods to estimate density, survival, and population growth rate (λ) of black bear populations at locations within the Ouachita (2006–2008) and Ozark (2009–2011) national forests, Arkansas. More males were harvested than females with the use of bait. Capture probability varied annually; thus, multi-year data were valuable for capturing accurate population parameters. Density was approximately 14 bears/100 km² in the Ouachita and approximately 26/100 km² for the Ozarks, which was greater than estimates from historical data (1989–1990). Thus, these populations maintained or exceeded previous density estimates while the use of bait was allowed on private land. However, as with any harvested population, it will be important to continue to monitor the population to be able make decisions about appropriate harvest policies going forward.

Key words: American black bear, Arkansas, bait, density, policy change, reintroduction, spatially explicit capture–recapture, *Ursus americanus*

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Wildlife populations exhibit demographic responses to harvest, with shifts in population size, population growth, and reproductive rates (Festa-Bianchet 2003, Milner et al. 2007). When a particular segment of the population is targeted (i.e., trophy males, juveniles, etc.), populations are especially vulnerable to harvest pressures (Festa-Bianchet 2003, Milner et al. 2007). Changes in age structure and sex ratio have been observed, with resultant delays in development, shifts in timing of births, and variation in sex ratio and weight of offspring (Ginsberg and Milner-Gulland 1994, Holand et al. 2006, Milner et al. 2007). As a consequence, alteration in social organization may ensue as well, including changes in dominance hier-

archy and social structure, which may influence stress, reproduction, and rates of infanticide (Berger 1983, Swenson et al. 1997, Wielgus and Bunnell 2000, Milner et al. 2007, Wielgus et al. 2013).

Both American black bears (*Ursus americanus*; hereafter, ‘black bears’) and brown bears (*U. arctos*) have experienced demographic changes in response to harvest pressure. Adult survival, especially for females, is a key determining factor in population growth of black and brown bears (Eberhardt et al. 1994, Mace and Waller 1998, McLellan et al. 1999, Freedman et al. 2003, Hebblewhite et al. 2003). Harvest is often the principal cause of adult mortality in hunted populations and influences population growth and persistence (Hellgren and Vaughan 1989, Koehler and Pierce 2005, Beston 2011). However, harvest mortality varies across sex and age classes (Bunnell and Tait 1980, Fraser et al. 1982, Boulay et al. 1999, Kohlmann et al. 1999). Males, particularly

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young males, are harvested more often than females, in part because of prohibition of harvest of females with young in some jurisdictions and in part because males range over larger areas than females and therefore have a greater likelihood of encountering hunters (Bunnell and Tait 1980, Fraser et al. 1982, Boulay et al. 1999, Kohlmann et al. 1999, Krofel et al. 2012). Thus, in addition to altering population size, harvest may influence age and sex structure of the population (Ginsberg and Milner-Gulland 1994, Milner et al. 2007).

States and provinces set their policy related to the methods by which bears may be harvested, including firearm and/or bow hunting, harvest over bait, use of dogs, harvest limits, number of licenses or permits, and spring harvest (Hristienko and McDonald 2007). The method of harvest may influence the composition of harvested bears and have implications for population demography (Litvaitis and Kane 1994, Kohlmann et al. 1999, Hristienko and McDonald 2007). Baiting and hunting with dogs may allow the hunter greater selectivity in size and/or sex of the bear (Litvaitis and Kane 1994). In some localities, a larger proportion of males and of younger individuals were harvested over bait (Litvaitis and Kane 1994, Boulay et al. 1999, Kohlmann et al. 1999); however, this effect was not observed consistently (Boulay et al. 1999, Heward and Black 2004, Bischof et al. 2008). Additionally, natural food availability governs movement, activity, and space use; therefore, it also influences susceptibility to harvest and responsiveness to bait (Noyce and Garshelis 1997, Baruch-Mordo et al. 2014).

Harvest has affected black bear population size in the state of Arkansas, USA. By 1910, black bears were virtually extinct in northern and western Arkansas as a result of overharvest and habitat reduction, and the eastern population of black bears was reduced to 25–50 individuals by the 1940s (Dellinger 1942, Holder 1951, Smith et al. 1991). Hunting was banned statewide in 1927 because of population declines. To restore the state's bear population, 254 bears from Minnesota, USA, and Manitoba, Canada, were released into the Ozark and Ouachita mountains in the Central Interior Highlands of Arkansas from 1958 to 1968 (Rogers 1973, Smith and Clark 1994). This reintroduction has been cited as one of the most successful reintroductions of black bears, with the population size in the state thought to be roughly 2,500 by the early 1990s (Smith et al. 1991, Smith and Clark 1994). As a result of the success of the reintroduction, autumn harvest was resumed in 1980. Harvest numbers increased over time, particularly since baiting was permitted in 2001 (Fig. 1).

Maintaining sustainable harvest levels requires rigorous data on current population status (Noyce and

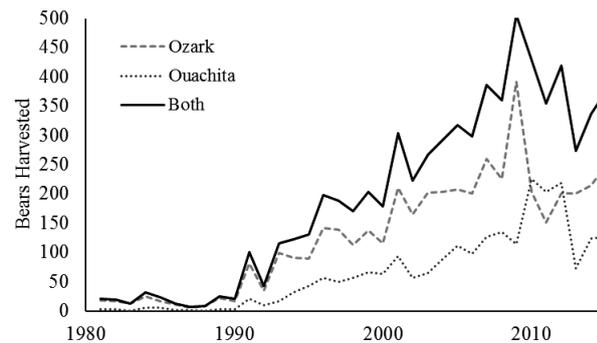


Fig. 1. Number of American black bears (*Ursus americanus*) harvested in the Central Interior Highlands of Arkansas, USA, since 1980. Numbers are by area: Ozark National Forest (Harvest Zone 1), Ouachita National Forest (Harvest Zone 2), and both.

Garshelis 1997). Our goals for this study were to investigate harvest composition due to policy changes and evaluate demographic characteristics of the 2 black bear populations in the Central Interior Highlands of Arkansas. Specific objectives were to (1) quantify the effect of baiting on the sex and age composition of harvested bears; (2) explore how increases in harvest influenced population density, growth, and sex ratios; and (3) estimate historical and more recent bear density. Prior to the policy change instituting baiting on private lands (in the late 1980s to early 1990s), Clark and Smith (1994) completed the most recent estimate of black bear densities using live captures, with estimates of 9.0 and 7.5 bears/100 km² in sites in the Ouachita and Ozark national forests, respectively. The information gathered in this study updates these estimates, allowing managers to make more informed decisions about harvest limits and methods.

Study area

We sampled 2 areas in the Central Interior Highlands of Arkansas, USA, with one site each in the Ouachita and Ozark national forests. The section of the Ouachita National Forest that constituted one study area is roughly bound by Highways 71 and 270 along the north and Highway 88 along the south, and comprises 827 km², with elevations ranging from 190 m to 800 m; it corresponds to the Muddy Creek Wildlife Management Area (Fig. 2). The Ouachita site primarily consists of shortleaf pine (*Pinus echinata*) and mixed pine–hardwood (Clark 1991). In contrast to the primarily forested Ouachita area, the White Rock Wildlife Management Area that we sampled in the Ozark National Forest has many inholdings,

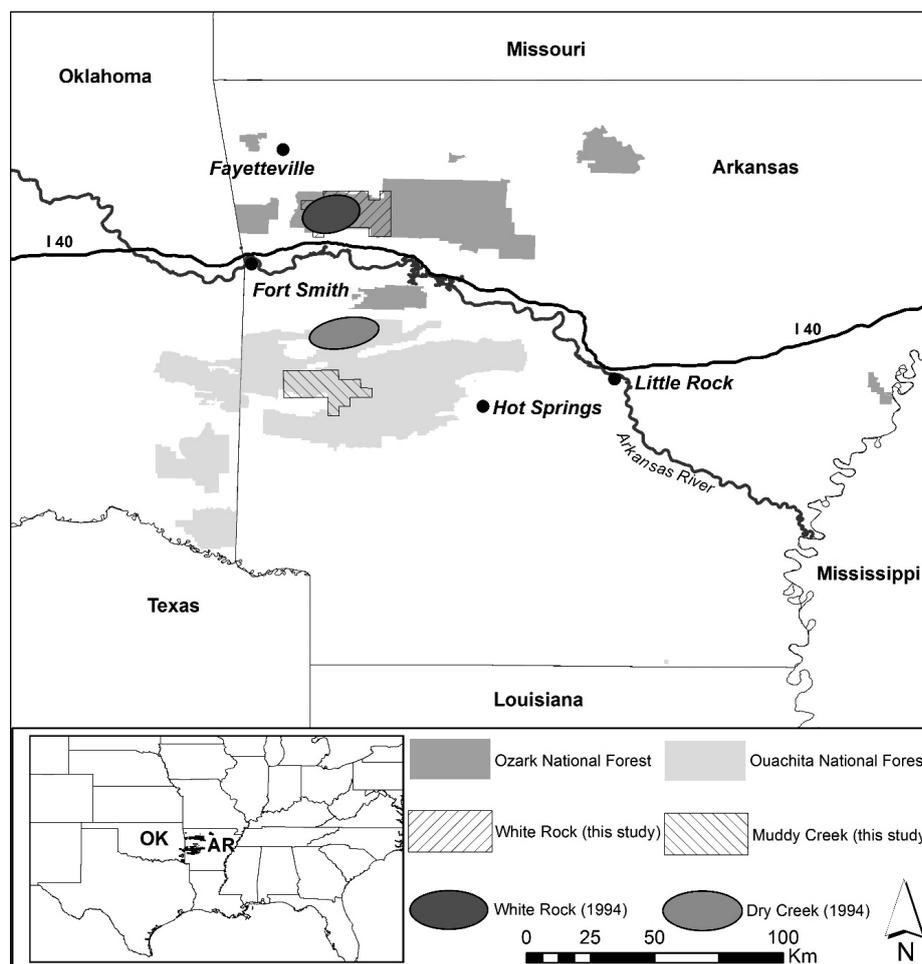


Fig. 2. Locations of study sites for bear hair snares deployed from 2006 to 2011 in Arkansas, USA. The northern site is in the Ozark National Forest and the southern site is in the Ouachita National Forest. Historical sampling sites are indicated by ovals in each region (Clark and Smith 1994). Gray areas denote public lands, including forests and national parks.

many of which contain private dwellings (Fig. 2). The area sampled is 1,080 km² in size, with elevations ranging from 125 m to 754 m. Mountains and ridges are separated by narrow valleys throughout the Ozark site, which predominantly consists of oak–hickory (*Quercus* sp.–*Carya* sp.) forest (Clark 1991).

Methods

Harvest data

In Arkansas, harvest is governed by zone and use of quotas started in 2002 (Tables S1, S2). Hunting with dogs is not permitted and hunters are asked not to take females with cubs. It is illegal to take radiocollared bears. Bag

limit per license is one bear and hunters are required to report the harvest within 24 hours. Black bear harvest data, including sex of bear, method of harvest, and use of bait, have been collected by Arkansas Game and Fish Commission wardens since a regulated hunting season was reinstated in Arkansas in 1981. When possible, age of bears was estimated using cementum alluli (Stoneburg and Jonkel 1966). We display data through 2015 (Fig. 1), but age data were only available through 2009, so we limited our analyses to data through 2009. Data on sex were available for 99.6% of harvested bears; age data were available for 60% of bears. Baiting was permitted starting in 2001. We used χ^2 tests of independence to determine if there was a difference across groups from

2001 to 2009 for each of the following: sex composition ($N = 3,242$) when bait was present versus absent and age composition when bait was present versus absent ($N = 776$). We defined juveniles as bears age ≤ 3 years and adults as >3 years of age.

Hair sampling

We imposed a systematic grid across each study area, with each cell being 6 km \times 6 km to approximate female home-range size (Clark 1991). We used 11 (2006), 13 (2007), and 23 (2008) grid cells for the Ouachita site and 30 grid cells for the Ozark site. We selected ≥ 2 snare sites within each cell, keeping each snare >1.6 km away from any other snare within the study area. We specifically selected sites on public land that were accessible by, but not visible from, forest roads. Presence of roads can influence movements and increase mortality of bears (Benn and Herrero 2002, McCown et al. 2009, Evans et al. 2018); however, the roads we were using to access our snare sites were infrequently used, unpaved forest roads. Though we acknowledge it is possible that roads may have impeded access to snares, roads with low traffic that are surrounded by vegetation (as these were) are more frequently crossed by bears than are primary roads (Chruszcz et al. 2003, Graham et al. 2010). Based on accessibility, we used 32, 50, and 60 snare sites in the Ouachita site in 2006, 2007, and 2008, respectively; accessibility varied by year because of road work and fallen debris on forest roads. In Ozark site, in 2009, the mean number of bears detected for cells with 2 snares (7.34, SE = 0.20) was smaller than the mean detected in cells with 4 snares (18.13, SE = 0.89; $t = -3.22$, $P = 0.022$). Thus, we increased the number of snares per cell to 4/cell where possible in 2010 and 2011. We used 65 snares in 2009, 98 in 2010, and 94 in 2011.

Hair snares (Woods et al. 1999, Mowat and Strobeck 2000, Poole et al. 2001) consisted of a single strand of 4-pronged barbed-wire positioned 50 cm above the ground, with a diameter of 4–5 m. At the center of each hair snare, we hung a nylon mesh bag containing rancid fish entrails and a secondary scent, suspended ≥ 3 m off the ground to minimize accessibility of contents. We used carp and catfish as the primary scent and rotated secondary scents each year to prevent a waning response. Secondary scents included sardines, beef fat, dog food, pastries, molasses, peanut butter, and fish fertilizer.

We examined every barb on each hair-snare for black bear hair every 7 days, which we defined as a trapping session for this study, for 5 weeks during June and July 2006–2008 (Ouachita National Forest) and 2009–2011 (Ozark National Forest). Restricting trapping to a short

time frame helps reduce changes in population number due to deaths, and we avoid additions from births by conducting the study in the summer. We flamed each barb that contained hair after collecting the sample to ensure that all hair was removed. We stored hair samples in coin envelopes in cool, dry conditions. The Ouachita samples were analyzed by Wildlife Genetics International, Nelson, British Columbia, Canada; and the Ozark samples were transferred weekly to the University of Arkansas in Fayetteville, Arkansas, for DNA extraction and later were genotyped at the University of Missouri, Columbia, Missouri, USA.

We estimated black bear population density using historical live-trapping data from a prior study, which took place in close proximity to our study areas (Clark and Smith 1994). Clark and his team collected physical mark–recapture data May–July 1988–1990 in White Rock Wildlife Management Area, Ozark National Forest and Dry Creek, Ouachita National Forest (Clark and Smith 1994). The area sampled on White Rock overlapped the area we sampled, though we sampled farther east (Fig. 2). Dry Creek and Muddy Creek are both parts of the Ouachita National Forest, with 22 km separating the 2 sites (Fig. 2).

Microsatellite analysis

We identified individual black bears using microsatellite genotyping. Wildlife Genetics International in Nelson, British Columbia, used sex-specific polymorphisms in the amelogenin gene to determine sex and the following 7 loci to identify individuals from the Ouachita site: CXX20, G10C, G10H, G10J, G10M, G10P, and G1D (Ostrander et al. 1993; Paetkau et al. 1995, 1998; Paetkau and Strobeck 1995; Taberlet et al. 1997).

For Ozark samples, we followed previously published protocols for DNA extraction and multiplex microsatellite genotyping (Kristensen et al. 2011). The microsatellite loci we used were G1A, G1D, G10B, G10C, G10J, G10L, G10M, and G10P (Paetkau et al. 1995, 1998; Paetkau and Strobeck 1995). We used variation in the amelogenin gene to determine the sex of black bears (Kristensen et al. 2011). We used Micro-Checker (van Oosterhout et al. 2004) to identify loci that showed evidence of null alleles. We used the Microsatellite Toolkit for Excel (Park 2001) to identify matching samples and identify pairs of samples that differed at 1–4 alleles and re-checked these samples for genotyping or data entry errors. We used Program DROPOUT (McKelvey and Schwartz 2005) to detect and remove any individuals that may have been misidentified as a result of problems with allelic dropout.

For all samples, we used Program Identity (Wagner and Sefc 1999) to determine the probability that full siblings would have the same genotype (P_{SIBS}) and the probability that 2 randomly selected individuals would share the same genotype (P_{ID}). We conducted chi-square goodness-of-fit tests to determine if the individuals detected deviated from a 1:1 sex ratio. We used the Microsatellite Toolkit to calculate average expected and observed heterozygosity and Genepop 4.0.10 (Raymond and Rousset 1995, Rousset 2008) to detect deviations from expected heterozygosity values under Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium. G10P was found to be in linkage disequilibrium with G10L in the Ozark population, so we removed G10P from further analyses.

Population survival

We used the Robust design (Pollock 1982, Kendall et al. 1995) with the Huggins estimator (Huggins 1991) in Program MARK to estimate survival (White and Burnham 1999). We assumed demographic closure was met because births do not occur during the trapping period, survival is high, and yearly study sessions were short in duration, but that geographic closure may have been violated because movement was not restricted to the study areas. We considered the influence of trapping session by year, time, behavior, sex, and combinations thereof on capture probability (p). A behavioral response indicates a change in capture probability, based on whether the organism was captured previously or not. We investigated whether survival differed over time in the following ways: a time-independent model (i.e., all sampling intervals have their own estimate; t), a linear model through time (T), and a quadratic model over time (TT). To estimate survival, models must consider both a forward transition (or whether an organism is present at the next step—i.e., is still alive and in the study area); and a reverse transition (or whether it was indeed present at the previous time step—i.e., immigrated or was born into the population; Cooch and White 2010). The reverse transition is represented in the model as γ_i . γ_i is defined as the probability of being present at time $i - 1$, given that the individual organism was present and alive at time i (Cooch and White 2010). Gamma was not the primary parameter of interest, so we used a null model (one with no specified predictor variables) for this parameter. Models containing a year effect on survival did not converge, and thus were not used. We evaluated models based on the Akaike Information Criterion for small sample sizes (AIC_c), ΔAIC_c , and model weight (Burnham and Anderson 2002). We determined population estimates and capture probability (p) through use of model averages

based on AIC_c weight; we included only models with a $\Delta AIC_c < 2$ (Burnham and Anderson 2002).

Population growth

We used the Pradel Robust Model with Survival and Lambda, with the Huggins closed capture estimator, in Program MARK to estimate λ for the Ozark population (Pollock 1982, Huggins 1991, Kendall et al. 1995, Pradel 1996, White and Burnham 1999). Data from the Ouachitas were too sparse to accommodate this model. In this model, λ is the realized growth, estimated by dividing ϕ_i by $(\gamma_i + 1)$. The parameter ϕ_i is the probability of surviving and remaining present in the population from time i to time $i + 1$ (Cooch and White 2010). We used the top models from the Robust model with Huggins estimator from above, to set up predictors for capture probability (p) for the Ozark population. The model containing behavior as a predictor of p would not converge, and hence, we did not include it in our analysis. As above, we evaluated models using AIC_c , ΔAIC_c , and model weight (Burnham and Anderson 2002). We estimated population growth (λ) through use of model averages based on AIC_c weight and included only models with a $\Delta AIC_c < 2$ (Burnham and Anderson 2002).

Density estimation

To have a more direct comparison with our contemporary estimates, we used spatially explicit capture–recapture (SECR) models (Efford and Fewster 2013) on historical data (Clark and Smith 1994). We also sought to update demographic information on black bears in the Central Interior Highlands of Arkansas by using the data collected from the hair snares to estimate density for 2 black bear populations: the Ouachita National Forest from 2006 to 2008, and Ozark National Forest from 2009 to 2011. We further estimated regional density with habitat covariates with SECR (Efford et al. 2009, Drewry et al. 2013) to afford a broader picture of population size in the region.

Study areas. We used the SECR package in Program R (Efford and Fewster 2013) to calculate contemporary multi-year density estimates for each study area for each sex, using both data collected for this study and historical data (Clark 1991, Clark and Smith 1994). We separated sexes because there were differences in capture probability for males and females obtained from the Robust model with Huggins estimator in Program MARK. We used the suggest.buffer function to determine the appropriate buffer size. We set the buffer at 7.5 km for females and 10 km for males for the recent data (2006–2011), and 7.5 km for females and 12.9 km for males for

the historical data (1989–1990). We then used all 3 years of data to calculate density for each sex at each location during the recent and historical time frames. The base model for all data sets was the null model for detection probability ($g_0 \sim 1$), spatial extent ($\sigma \sim 1$), and density ($D \sim 1$). Spatial extent refers to the area in which an organism may be detected. We also ran models with time (T), behavior (b), and a trap-specific behavior (bk) as predictors of g_0 ; a session-specific model ($g_0 \sim \text{session}$, $\sigma \sim \text{session}$); and a model with session as a predictor of density. T refers to a linear trend in time, b refers to a response to previous capture, and bk refers to a response to previous capture at a specific trap location. Session refers to the trapping session in the SECR package; and for this study, it is the equivalent to the year of sampling. We had more data for recent years and expected a year effect, so we also ran models with the year-specific model ($g_0 \sim \text{session}$, $\sigma \sim \text{session}$) as a base and added time (T), behavior (b), and a trap-specific behavior (bk) as predictors of g_0 , and session as a predictor of density for these data. We ranked models using AIC. Because $\Delta\text{AIC} > 2$ did not encompass a considerable proportion of the weight for some populations or time periods, we chose a cutoff of 10 ΔAIC for models included in the model average for the density estimate. Typically, using models within 3 ΔAIC included the majority of the weight; the additional model was very similar to the model preceding it in rank, which is likely what caused the higher ΔAIC values (Tables 1, 2, S3). For some models, data were too sparse to produce estimates; we included only models without maximization errors in AIC comparisons. For contemporary data, we estimated the population size using the top-ranked model with the region.N option in SECR.

Regional. We were interested in modelling density over the national forest land in Arkansas and regional density models allowed us to use predictor variables to help extrapolate from our study area to the full region. We modeled regional density for recent data for each sex by including data from both locations and incorporating habitat covariates. We constructed a mask from a spatial grid covering each study area, with locations spaced at 250 m and a buffer of 10 km beyond the perimeter of each detection array. As per Drewry et al. (2013), we used 2 search radii, one based on hourly movement rates (Clark 1991) and the other on the shortest mean recapture distance (\bar{d}) calculated in SECR; these were 0.36 km and 1.1 km, respectively.

Food availability and canopy cover are important determinants of bear distribution (Pelton 2003), so we used percent forest cover as a spatial covariate in

Table 1. Top spatially explicit capture–recapture models for density estimation of American black bears (*Ursus americanus*), from 2006 to 2008 (Ouachita) and 2009 to 2011 (Ozark), in the Central Interior Highlands of Arkansas, USA. Model selection based on Akaike’s Information Criterion (AIC_c). \hat{D} was modeled as a constant (.) or as a function of year (yr). Probability of detection (g_0) was modeled as a function of behavior (b), trap-specific behavior (bk), year (yr), linear time (T), a combination of year and trap-specific behavior (y+bk), or a constant (.). Spatial scale (σ) was modelled as a function of (yr) or constant (.).

Model and parameters	K^a	AIC_c^b	ΔAIC_c^c	w_i^d
Ouachita—Males				
$\hat{D}(\cdot), g_0(\text{bk}), \sigma(\cdot)$	4	709.4	0.0	1
Ouachita—Females				
$\hat{D}(\cdot), g_0(\text{yr}+\text{bk}), \sigma(\text{yr})$	8	778.5	0.0	0.94
$\hat{D}(\cdot), g_0(\text{bk}), \sigma(\cdot)$	4	785.6	5.5	0.06
Ozark—Males				
$\hat{D}(\text{yr}), g_0(\text{yr}+\text{bk}), \sigma(\text{yr})$	10	3,250.0	0.0	0.77
$\hat{D}(\cdot), g_0(\text{yr}+\text{bk}), \sigma(\text{yr})$	8	3,251.8	2.5	0.23
$\hat{D}(\cdot), g_0(\text{bk}), \sigma(\text{yr})$	4	3,258.9	9.1	0.01
Ozark—Females				
$\hat{D}(\cdot), g_0(\text{yr}+\text{bk}), \sigma(\text{yr})$	8	2,724.2	0.0	0.76
$\hat{D}(\text{yr}), g_0(\text{yr}+\text{bk}), \sigma(\text{yr})$	10	2,726.7	2.5	0.22
$\hat{D}(\cdot), g_0(\text{bk}), \sigma(\cdot)$	4	2,731.8	7.7	0.02

^aNo. of parameters.

^bAkaike Information Criterion adjusted for small sample sizes.

^cDifference in AIC_c compared with the AIC_c smallest model.

^d AIC_c model wt.

^eModel deviance.

Table 2. Model selection results for regional density estimation of American black bear (*Ursus americanus*) abundance from 2006 to 2011 in the Central Interior Highlands of Arkansas, USA, based on Akaike’s Information Criterion (AIC_c). The base model contained trap-specific behavior (bk) as a predictor of probability of detection (g_0). Models within ΔAIC of ≤ 2 are shown.

Model and parameters	K^a	AIC_c^b	ΔAIC_c^c	w_i^d
Males				
\hat{D} (forest 1.1 km)	5	4,993.4	0.00	0.620
\hat{D} (forest 1.1 km, road 5 km)	6	4,994.5	1.13	0.351
Females				
\hat{D} (forest 1.1 km)	5	3,528.1	0.00	0.738
\hat{D} (forest 1.1 km, road 5 km)	6	3,530.2	2.07	0.262

^aNo. of parameters.

^bAkaike Information Criterion adjusted for small sample sizes.

^cDifference in AIC_c compared with the AIC_c smallest model.

^d AIC_c model weight.

^eModel deviance.

regional density estimates. Using the 2006 National Land Cover Database land-cover layer, we combined deciduous, coniferous, and mixed forest into one forest class through using the reclassify tool in ArcMap™ v. 10.1 (ESRI 2011; Environmental Systems Research Institute, Redlands, California, USA). We then extracted percent of land cover coded as forest for each mask location at 2 search radii, 0.36 km and 1.1 km, using focal neighborhood functions in ArcMap™ v. 10.1 (ESRI 2011). We also used roads as a spatial covariate. We extracted road density in km/km², for each mask location from 15 August 2012 Arkansas Highway and Transportation Department roads vector data at 2 search radii, 1.1 km and 5 km, using line density functions in ArcMap™ v. 10.1 (ESRI 2011). We used 2 search radii because bears may respond to landscape features at different scales (Drewry et al. 2013), 1.1 km represents the mean recapture distance (as above), and 5 km provides the opportunity to detect response at a broader scale. Road density at the 5-km scale was a predictor for black bear density in South Carolina, USA (Drewry et al. 2013). Many of our 3-year models highly ranked the model with session as a predictor for g_0 and σ and behavior as a predictor of g_0 . Therefore, we used models with these specifications ($g_0 \sim \text{session} + \text{behavior}$ and $\sigma \sim \text{session}$) as a base model onto which we added the habitat covariates as a predictor for density. However, these models would not converge, so we removed session-specificity, and just used $g_0 \sim \text{bk}$ as the base model onto which we added habitat covariates. We included models with forest at the 0.36-km and 1.1-km scales as a predictor of density. Roads may also influence black bear distribution (Beringer et al. 1990), but potentially at a broader scale, so we also used models with density of roads at the 1.1-km and 5-km scales as a predictor of bear density.

Results

Harvest data

Mean annual harvest was 65.5 (SE = 16.1) for the Ouachita National Forest, 127.8 (SE = 10.8) for the Ozark National Forest, and 193.3 (SE = 25.3) overall from 1981 to 2015. The number of black bears harvested increased after the policy change to permit baiting in 2001 (Fig. 1). From 2001 to 2009, 3,242 bears were harvested in Arkansas, with 39% harvested over bait. When bait was present, females were harvested less often than males ($\chi^2 = 5.88$, $P = 0.015$; Fig. S1), though there was no difference in age class harvested in the presence of bait ($\chi^2 = 0.70$, $P = 0.40$).

Ursus 29(2):147–162 (2019)

Hair sampling

We collected 658 hair samples at the Ouachita site and 2,890 at the Ozark site (Tables S4, S5). Across the 3 years of sampling, the individuals detected in the Ouachita population had a greater proportion of females detected ($\chi^2 = 4.10$, $P = 0.043$; Table S5); however, the Ozark site did not differ from a 1:1 sex ratio ($\chi^2 = 0.66$, $P = 0.42$; Table S5). There was little chance that individuals shared genotypes and failed to be detected as unique in either study area. P_{ID} was 1.02×10^{-9} and 3.49×10^{-10} for the Ouachita and Ozark sites, respectively; P_{SIBS} was 9.83×10^{-4} and 6.91×10^{-4} for the Ouachita and Ozark sites, respectively. There was considerable variation in trap success (no. of traps visited/no. of traps available) among years, with the middle year having the lowest success for each location (Table S4). The Ouachita site had lower trap success than the Ozark site ($F = 8.09$, $P = 0.047$). Correspondingly, the number of black bears detected varied by year (Table S5).

Population growth and survival

Survival rate varied with sex at the Ozark site (Table S6). Ozark survival (S) was estimated at 0.58 (CI = 0.45–0.71) for males and 0.82 (CI = 0.60–0.93) for females over the course of the study. For realized λ (population growth), sex and year were important predictors in top models (Table S7). Realized λ was 1.11 (CI = 0.87–1.35) between 2009 and 2010 and 1.03 (CI = 0.88–1.18) between 2010 and 2011 for males. For females, realized λ was 1.16 (CI = 0.96–1.35) and 1.08 (CI = 0.89–1.26), respectively. For the Ozark population, the top models included sex as a predictor of ϕ (how likely it is that an individual will be present in the study area during the next year or time step). For males, ϕ was 0.47 (CI = 0.40–0.55) and for females, ϕ was 0.66 (CI = 0.57–0.75).

Density estimation

Study areas. For historical and recent data, where sufficient data were available, trap-specific behavior response and session (year) were important predictors of g_0 (probably of detection at home range center). Session (year) also was a predictor of σ (spatial extent) for some models (Tables 1, S3). Recent Ouachita male density was 3.1/100 km² (SE = 0.7), which was comparable to estimates made with historical data (Fig. 3). For Ouachita females, the recent estimate was 11.0/100 km² (SE = 1.6; Fig. 3). Thus, overall density is approximately 14 black bears/100 km² (Fig. 3). Over the course of the study, an average of 140 females and 50 males were estimated to be in the study area (Table S8). There were not enough data to calculate a historical estimate for Ouachita

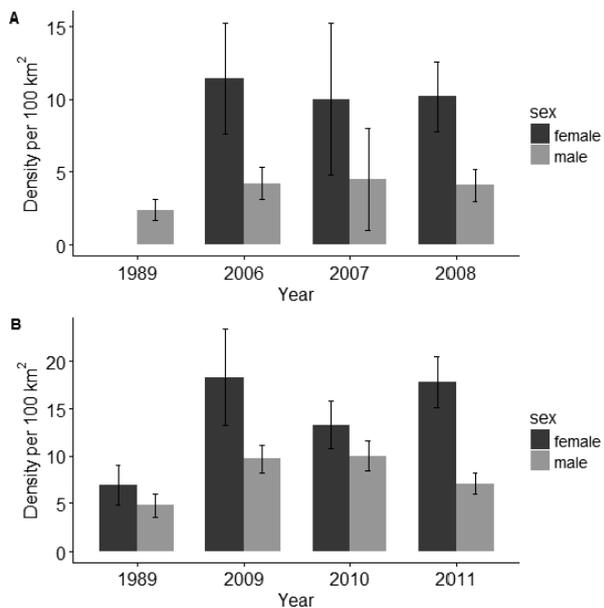


Fig. 3. Comparative densities of American black bears (*Ursus americanus*) in the Ouachita (A) and Ozark (B) National Forest sites, respectively, Arkansas, USA. Includes historical (Clark and Smith 1994) and recent (2006–2011) estimates. Density estimates were made using spatially explicit capture–recapture methods on historical data and recent data, and presented as density of bears per 100 km² with standard error bars. There were insufficient historical data to estimate Ouachita density for females.

females with SECR, but the recent Ouachita female estimate was nearly twice Clark and Smith’s (1994) estimate of 5.9/100 km² (SE = 1.0; Fig. 3, Table S3).

Yearly density for the recent Ozark site was estimated between 7.2 (SE = 1.1) and 10.0 (SE = 1.6)/100 km² for males and between 16.4 (SE = 2.5) and 17.9 (SE = 3.1)/100 km² for females (Fig. 3). Overall density is approximately 26 black bears/100 km² (Fig. 3). An average of 317 females and 212 males were estimated to be in the study area (Table S8). Both male and female density were higher than historical estimates using SECR for the Ozark National Forest (M = 4.8/100 km², F = 6.9/100 km²; Fig. 3, Table S3).

Variation in capture probability and sigma

Capture probability (p) varied across years for each study area, with the middle year having the lowest capture probability in Robust models with the Huggins estimator (Fig. 4). Males tended to have equal or greater capture probability than females (Fig. 4). There was similar variation in g_0 or probability of capture at the home

range center in SECR models (Fig. S2). However, males did not consistently have higher estimates of g_0 than females across all years. The most marked difference was for 2010 in the Ozark site, where female g_0 exceeded that of males.

Sigma represents the spatial scale of the detection function and can contribute to the ability to detect organisms in the sampling area. Sigma also varied across years of study and by sex (Fig. S3). In general, lower sigma corresponded to higher capture probability (g_0 ; Figs. S2, S3).

Regional. For both males and females, models that included forest cover at the 1.1-km scale had much greater weight than both the null and other habitat covariate models (Table 2). There was a positive association with forest cover (males: $\beta = 4.4$, CI = 1.7–7.1, females $\beta = 6.0$, CI = 2.3–9.8). The second-highest-ranked model also contained road density at the 5.0-km scale as a predictor of black bear density. Although the confidence interval crosses zero, there was a slight negative association with road density (males: $\beta = -0.5$, CI = -1.4–0.5, females: $\beta = -0.05$, CI = -0.9–0.8).

Discussion

We compared black bear densities of contemporary populations with reanalyzed data collected in 1989 and observed an increase in density over time. Interestingly, this time period spanned the implementation of baiting in 2001 and a renewed concern that an increase in hunter success due presence of bait would result in unsustainable harvest. Our results show an increase in bear density since the last survey from 1989 despite increased harvest; however, we observed changes in the sex ratio of harvested bears in the presence of bait and disparities in density estimates across sex.

Harvest

Harvest policies influenced the quantity and composition of black bears harvested over time. The number of bears harvested steadily increased from the time harvest was reinstated in 1981 through 2009 when number of harvested bears began to decline again. Extending the length of harvest season may have contributed to the increasing number of bears harvested, as has been seen with other non-sedentary species with extended harvest seasons (Sunde and Asferg 2014). Threshold restrictions, including quotas, on harvest can prevent overharvest (Lande et al. 1995). Implementation of quotas kept harvest numbers from continuing to increase past 2009. As observed elsewhere (Litvaitis and Kane 1994, Boulay et al. 1999, Kohlmann et al. 1999), male black

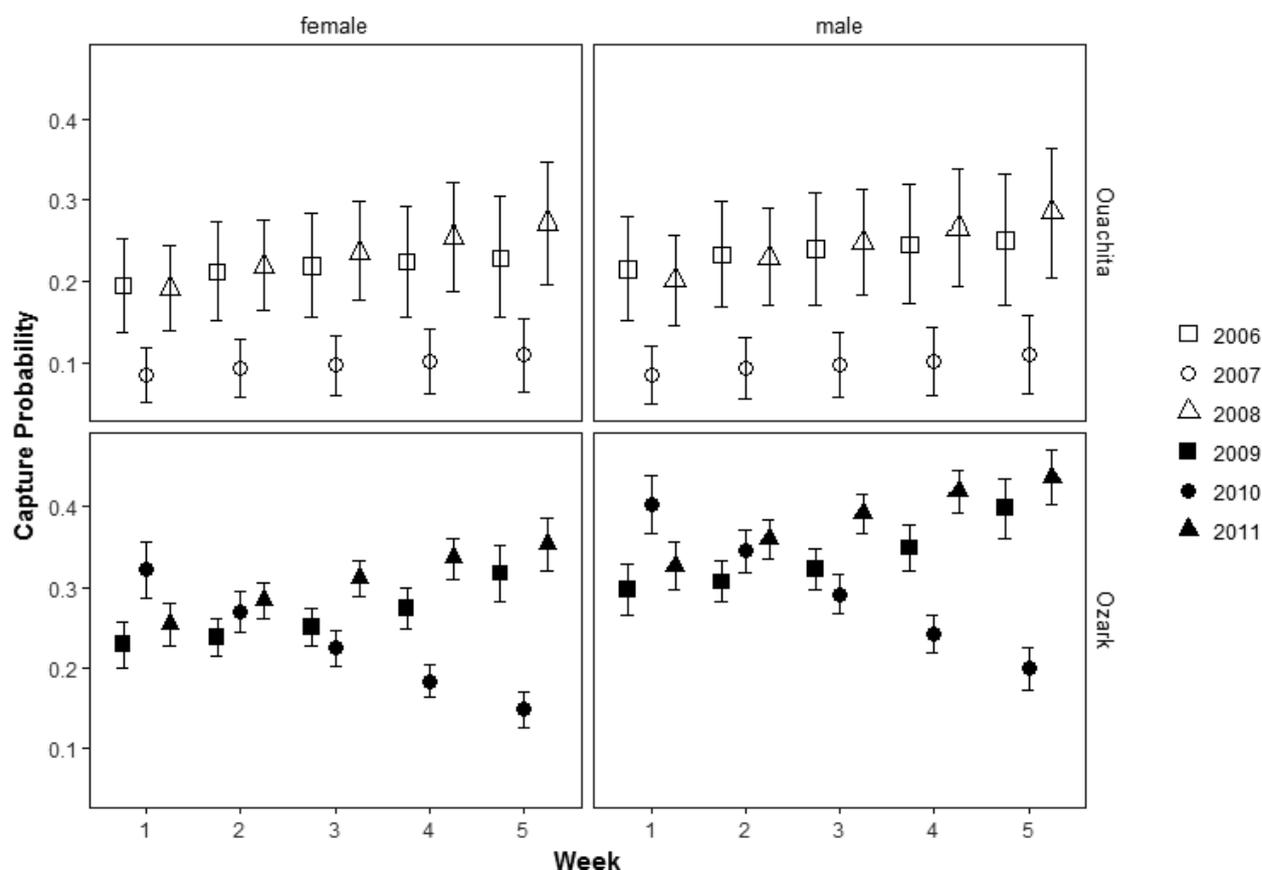


Fig. 4. Capture probabilities of American black bears (*Ursus americanus*) in the Ouachita and Ozark national forests, respectively, from 2006 to 2011 in Arkansas, USA, estimated via the Robust Model in Program MARK. Error bars represent standard error. Males were separated from females for estimates.

bears were harvested more often over bait than were females, though there was not a difference in age class harvested in response to presence of bait. Hunter guidelines include a request to avoid harvesting females with cubs. This could contribute to the male-biased harvest, and also might contribute to young male bears not being harvested over bait if these bears are perceived as cubs. Age data were not available for all bears, so it is also possible that we were not able to detect a difference in age of bears harvested because sample size was smaller for age comparisons than sex comparisons.

Population demography

The density of male black bears in the Ouachitas was comparable to estimates using historical data, whereas the recent female density estimate exceeds that of Clark and Smith (1994). Overall density of approximately 14/100 km² was larger than the Clark and Smith (1994) estimate of 9.0/100 km². For the Ozark National Forest, the den-

sity of approximately 26 bears/100 km² exceeded Clark and Smith's estimate of 7.5/100 km², with estimates for each sex also exceeding estimates from historical data (Clark and Smith 1994). Realized λ was >1 in the Ozarks, suggesting that this population may be continuing to increase; however, the confidence interval included values <1 , so definitive conclusions about population trajectory cannot be made.

Thus, population density is following different patterns by region and by sex. Both regions have a higher density of female black bears than males; but, while other groups increased in density over time, the Ouachita males did not increase. Males generally have lower survival than females (McLellan et al. 1999, Koehler and Pierce 2005), and males are being harvested more than females, which may contribute to the differences in density of males versus females. Additionally, the Ouachita population is expanding into Oklahoma, USA, and males tend to be the dispersing sex (Rogers 1987, Costello 2010, Roy

et al. 2012), so it is possible that male bears are leaving Arkansas to establish home ranges in the neighboring state (Bales et al. 2005). Oklahoma harvest policies prohibit harvest of cubs and females with cubs (ODWC 2018); thus, males exploring the area may be harvested. Density is also higher in the Ozarks than in the Ouachitas. There are more inholdings in the Ozarks; though the inholdings are typically homes rather than farms, garbage and kitchen gardens can contribute to higher density (Evans et al. 2017). The land cover in the Ozarks tends more toward deciduous than coniferous forests, so this could contribute to the differences in density in the 2 areas as well.

We also modelled density regionally to provide a clearer picture of density in the Central Interior Highlands of Arkansas, which also afforded the opportunity to explore habitat covariates associated with black bear density. The top regional density model included percent forest cover as a predictor. Black bears are associated with forested regions (Pelton 1982), so it is not surprising that percent forest cover was positively associated with bear density. Roads also can influence black bear distribution (Beringer et al. 1990) and top regional models for bear density in South Carolina included road density (Drewry et al. 2013). Our models support this finding, with the model containing a positive effect of percent forest having the greatest weight and the model with a combination of a positive effect of percent forest and negative effect of road density having the second-greatest weight.

Spatially explicit capture–recapture (SECR) models provide a means of estimating density without concerns about lack of closure, and are increasingly used in estimates of black bear density across the range (Efford and Fewster 2013, Royle et al. 2013). Recent density estimates, using SECR, show that density is highly variable across populations within the range of black bears in North America (Gardner et al. 2010, Obbard et al. 2010, Wilton et al. 2014). Estimates from the Ozark National Forest of Arkansas were similar to earlier estimates of the isolated White River population in eastern Arkansas (25/100 km², Clark et al. 2010) and the population in central Georgia, USA (23–24/100 km²; Hooker et al. 2015). We obtained lower estimates in the Ouachitas than these areas. Generally, black bear density obtained from SECR models ranges from 1.7 to 46/km² (Gardner et al. 2010, Obbard et al. 2010, Wilton et al. 2014). Some of this variation may be explained by isolation of populations or variation in habitat, including dominant vegetation, resource availability, road density, and patterns of human development (Obbard et al. 2010, Drewry et al. 2013,

Wilton et al. 2014, Evans et al. 2018); however, it would be valuable as we move forward to further explore variables that can help to predict black bear density over large areas, particularly because of the wide-ranging nature of the species.

Capture probabilities

Often, it is difficult to obtain sufficient data to incorporate heterogeneity into models, select the top candidate models, and precisely estimate density for large mammalian carnivores (Royle et al. 2009, Sollmann et al. 2011, Howe et al. 2013). Our regional estimates incorporated habitat variables, which can allow a more accurate picture of density over large areas (Drewry et al. 2013, Howe et al. 2013). Additionally, multi-year studies can contribute to obtaining requisite data for accurate population modelling of large carnivores (Howe et al. 2013). Our data provide strong evidence that gathering data over multiple years for mark–recapture estimates of black bears is advantageous. Year (session) was an important predictor in both the Robust and SECR models. Both 2007 and 2009 had poor capture probabilities and a reduction in number of samples collected. We suspect this was due to limited food availability in these years, which altered bear movements, especially by expanding their home ranges (Garshelis and Pelton 1981, Rogers 1987, Hellgren et al. 1991). In 2007, in particular, there was a frost after plants started budding (Fig. S4), which reduced available forage and increased nuisance complaints, suggesting that bears were moving out of the study area to find food (M. Means, Arkansas Game and Fish Commission, personal communication). The reduction in samples and capture probability affects the ability to model population size and density (Sun et al. 2014). In 2007, there were not enough data for an individual year model of male density in the Ouachitas. Additionally, confidence intervals were much larger for population and density estimates for both sexes in 2007, even within the 3-year models. Yearly variation in estimates of density and population abundance and in vital rates such as survival and λ is difficult to estimate without sufficient data. Our findings support previous studies, which found that data acquired across multiple years were needed to accurately estimate vital rates and are more likely to provide sufficient data to pick appropriate models to estimate those rates (Brongo et al. 2005, Harris et al. 2011).

Sex differences

We detected differences in the composition of harvest and demographic characteristics by sex. As mentioned above and similar to other studies, males were harvested

more often over bait than were females, though there was not a difference by age class (Litvaitis and Kane 1994, Boulay et al. 1999, Kohlmann et al. 1999). There was a female-biased sex ratio for individuals identified in the Ouachitas for this study (2006–2008). Survival of females was higher than that of males at the Ozark site. Further, sex had an impact on all model types and influenced estimates of capture probability (p), detection probability (g_0), spatial extent (σ), density, realized growth (λ), presence at the following time step (φ), and survival (S). This disparity was particularly apparent in the estimates of density from the SECR models. Female density was higher than male density both historically (Clark et al. 1994) and in this study for the Ouachita population ($M = 3/100 \text{ km}^2$ and $F = 11/100 \text{ km}^2$). With contemporary data, we also found that female density was higher than male density at the Ozark site, though neither Clark and Smith (1994) nor SECR models for the same data showed a difference historically.

Hair-snare sampling does not allow for differentiation by age, so some of the disparity in survival of black bears by sex may be due to age, because dispersing juvenile males in particular have lower survival rates than both juvenile females and adult bears (Schwartz and Franzmann 1992, Beringer et al. 1998, Obbard and Howe 2010). Adult females typically have higher survival rates than males, which also could contribute to the differences observed (Hellgren and Vaughan 1989, Schwartz and Franzmann 1992, Beringer et al. 1998, Koehler and Pierce 2005). The mating system is polygynous (Rogers 1987, Schenk and Kovas 1995); therefore, population growth in black bears is limited by the number of females and their ability to produce cubs successfully, so the discrepancies in sex ratio we found may not be cause for concern.

Conversely, a discrepancy in sex ratio can result in changes in dispersal patterns, competition, reproductive rates, and cub survival (Swenson et al. 1997, Wielgus and Bunnell 2000, Milner et al. 2007). In particular, when dominant male bears are removed from an area, some populations experience an influx of younger male bears (Wielgus and Bunnell 1995, Sargeant and Ruff 2001). Subsequently, either these incoming bears or resident adult males increase rates of sexually selected infanticide (LeCount 1987; Wielgus and Bunnell 1995, 2000; Swenson et al. 1997; Gosselin et al. 2015). This has cascading effects from reducing recruitment and population growth, to destabilizing the male social structure (Swenson et al. 1997). However, removal of adult males does not universally result in an influx of younger males nor increases in infanticide for black bears (McLellan 2005,

Czertwytynski et al. 2007). Despite this inconsistency, additional problems may result from discrepancies in sex ratio. Removing large males may decrease genetic variation and alter phenotypic characteristics, such as body weight or size, of a population (Coltman et al. 2003, Allendorf et al. 2008). The resiliency of polygynous species to changes in sex ratio also may be limited; and if the sex ratio becomes too skewed, fecundity may decline (Ginsberg and Milner-Gulland 1994). Distribution of bears can also change when adult males are removed, potentially altering female access to food resources (Wielgus and Bunnell 2000). Thus, continued monitoring of demography will be important for these Central Interior Highlands black bear populations.

Management implications

Both black bear populations in the Central Interior Highlands of Arkansas have densities above estimates from the late 1980s. We detected a harvest bias for males in the presence of bait. Sampling efforts for our 2006–2011 studies, described here, were conducted during a period of high harvest levels, which were subsequently reduced by instituting a quota system. To assess the impact of variable harvest levels and their potential influence on sex ratio, population size should be reassessed periodically to determine whether maintaining harvest at the level of the new quotas is affecting the population. This study provides a strong basis for comparison for such future estimates. If possible, a multiple-year study should be undertaken to obtain a reliable estimate of the density of bears present, given the likelihood of natural variation in estimate parameters by year.

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Supplemental material

Table S1. American black bear (*Ursus americanus*) harvest dates by year (1980–2015) and zone in Arkansas, USA. Data are from Arkansas Game and Fish Commission Hunting Regulation Guides. Zones correspond to those currently in use: <https://www.agfc.com/en/hunting/big-game/bear/>. Harvest was not permitted in zones 5 and 5A until 2001.

Table S2. American black bear (*Ursus americanus*) harvest quotas by year and zone in Arkansas, USA. Harvest started in 1981, but quotas were not used until 2002. Data are from Arkansas Game and Fish Commission Hunting Regulation Guides.

Table S3. Model selection results for historical density estimation (bears/100 km²) of American black bears (*Ursus americanus*) in the Central Interior Highlands of Arkansas, USA. Data were gathered from 1988 to 1990. was modeled as a constant (.). Probability of detection (g_0) was modeled as a function of behavior (b), trap-specific behavior (bk), year (yr), or a constant (.). Spatial scale (σ) was modelled as a function of (yr) or constant (.).

Table S4. Success of hair-snare traps and sample identification for American black bear (*Ursus americanus*) trapping in Ouachita and Ozark National Forest study

sites in the Central Interior Highlands of Arkansas, USA, from 2006 to 2011. Hair was collected each week for 5 weeks during each year of study.

Table S5. Number of American black bears (*Ursus americanus*) detected at each site per year and overall in the Ouachita and Ozark national forests of the Central Interior Highlands of Arkansas, USA, from 2006 to 2011. Hair was collected each week for 5 weeks during each year of study.

Table S6. Top-ranking models for estimating population parameters of American black bears (*Ursus americanus*) in the Ozark National Forest (2009–2011) in Arkansas, USA, using the Robust model with Huggins estimator in Program MARK.

Table S7. Top-ranking models for estimating the population of American black bears (*Ursus americanus*) in the Ozark National Forest (2009–2011) in Arkansas, USA, using the Pradel model with Huggins estimator in Program MARK.

Table S8. Population estimates^a of American black bears (*Ursus americanus*) in 2 sampling locations in the Central Interior Highlands of Arkansas, USA, using spatially explicit capture–recapture models. Data were gathered from 2006 to 2011. Population estimate and standard error (in parentheses) are reported.

Fig. S1. Comparison of composition of harvested American black bears (*Ursus americanus*) by sex (A) and age (B) in the presence or absence of bait in

Arkansas, USA. Following policy change in 2001, baiting has been permitted in Arkansas on private lands.

Fig. S2. Capture probabilities at home range center (g_0) over the 3 years of study of American black bears (*Ursus americanus*) in the Ouachita (A) and Ozark (B) sites in the Central Interior Highlands of Arkansas, USA, estimated using spatially explicit capture–recapture models with error bars representing standard error. Data were gathered from 2006 to 2011. Males were separate from females for estimates. For Ouachita females, there were not enough data to calculate a separate estimate by year, so the estimate across years is included.

Fig. S3. Sigma (spatial scale parameter of detection function) over the 3 years of study of American black bears (*Ursus americanus*) in the Ouachita (A) and Ozark (B) sites in the Central Interior Highlands of Arkansas, USA, estimated using spatially explicit capture–recapture models with error bars representing standard error. Data were gathered from 2006 to 2011. Males were separate from females for estimates. For Ouachita females, there were not enough data to calculate a separate estimate by year, so the estimate across years is included.

Fig. S4. Temperature (A) and precipitation (B) from 2007 compared with the 30-year mean for the Ouachita National Forest, Arkansas, USA. Temperature dropped below freezing (red line in A) very late in the season with correspondingly high rainfall (B). Data from NOAA Climate Data (NOAA 2018).