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Demographic trends of a harvested American black bear population in northwestern South Carolina

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Abstract: As American black bears (*Ursus americanus*) reoccupy portions of the eastern United States, it is important to implement sustainable management practices based in a strong understanding of the dynamics of these recovering populations as they expand into areas with increasing anthropogenic pressures. We used the Downing population reconstruction technique on harvest records to establish baseline abundance and population growth-rate trends over 15 years for a population of black bear in northwestern South Carolina, USA. The total population in 2013 was estimated to be a minimum of 412 black bears, increasing from approximately 97 bears in 1998. We established age structure and sex structure in harvest, which were consistent with sustainably harvested bear populations. We recommend using these data as a baseline to determine the maximum sustainable harvest rate for this population. We also recommend future investigation into the development of research priorities and harvest management decisions for the population to maintain desired levels of black bear recovery.

Key words: abundance, American black bear, Downing, harvest, population reconstruction, *Ursus americanus*

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Attitudes toward carnivores and large mammals in North America have changed substantially over time, from persecution in the times of European immigrant settlements (Taber and Payne 2003) to a gradual shift toward protection beginning with the era of wildlife management in the early 20th century (Miller et al. 2013). More recently, since the 1980s, factors such as habitat expansion through abandonment of small farm holdings, removal of bounties, listing of threatened species, and harvest age–sex–bag regulations have led to persistence as well as, in some cases, expansion of large-mammal populations (Maehr et al. 2001, Hristienko and McDonald 2007, Miller et al. 2013). A leading example has been the recovery of American black bear (*Ursus americanus;* hereafter, black bear) in the eastern United States, with overall populations reportedly growing by 13% from 1970 to late 1980s, 24.4% from 1988 to 2001, 6.5% from 2001 to 2008, and approximately 8% from 2009 to 2011 (Cowan 1972, Garshelis and Hristienko 2006, Hristienko et al. 2009, Noyce 2011a). Recently the black bear was estimated to occupy 65–75% of its historical range in North America (Scheick and McCown 2014), and 36 of 41 U.S. states with a resident black bear population report either stable or increasing trends (Hristienko et al. 2009, Noyce 2011b).

In South Carolina, USA, according to historical accounts, black bears once roamed throughout the state, and were so numerous at this period [1750] in the upper country that, "a common hunter could kill in the autumnal season as many bears as would make from two to three thousand weight of bear bacon" (Ramsay 1809:305). By 1859, Logan (1859) declared from pelt records and local lore that the black bear was probably extinct in the region as a result of a combination of human inhabitation and cultivation of land, and hunting for meat and sport by the English. More than a century later, Cely and Hamilton (1981) reported a "guestimate" of the South Carolina mountainous population at several dozen, warning that rapid urban development was fragmenting bear habitat. As of 2016, South Carolina possesses 2 recognized distinct resident black bear populations—in the northwestern mountainous region (legally hunted since 1981) and in the eastern upper coastal plain (legally hunted since 2011). Annual status reports estimated a stable northwestern population at approximately 90–100 bears from 1989 to 1992, and overall population of approximately 175–200 bears in 1994 (Fendley 1991; Stokes 1992, 1994). In 2003, based on results from a multistate study (Settlage 2005), the northwestern population was estimated at 300–450

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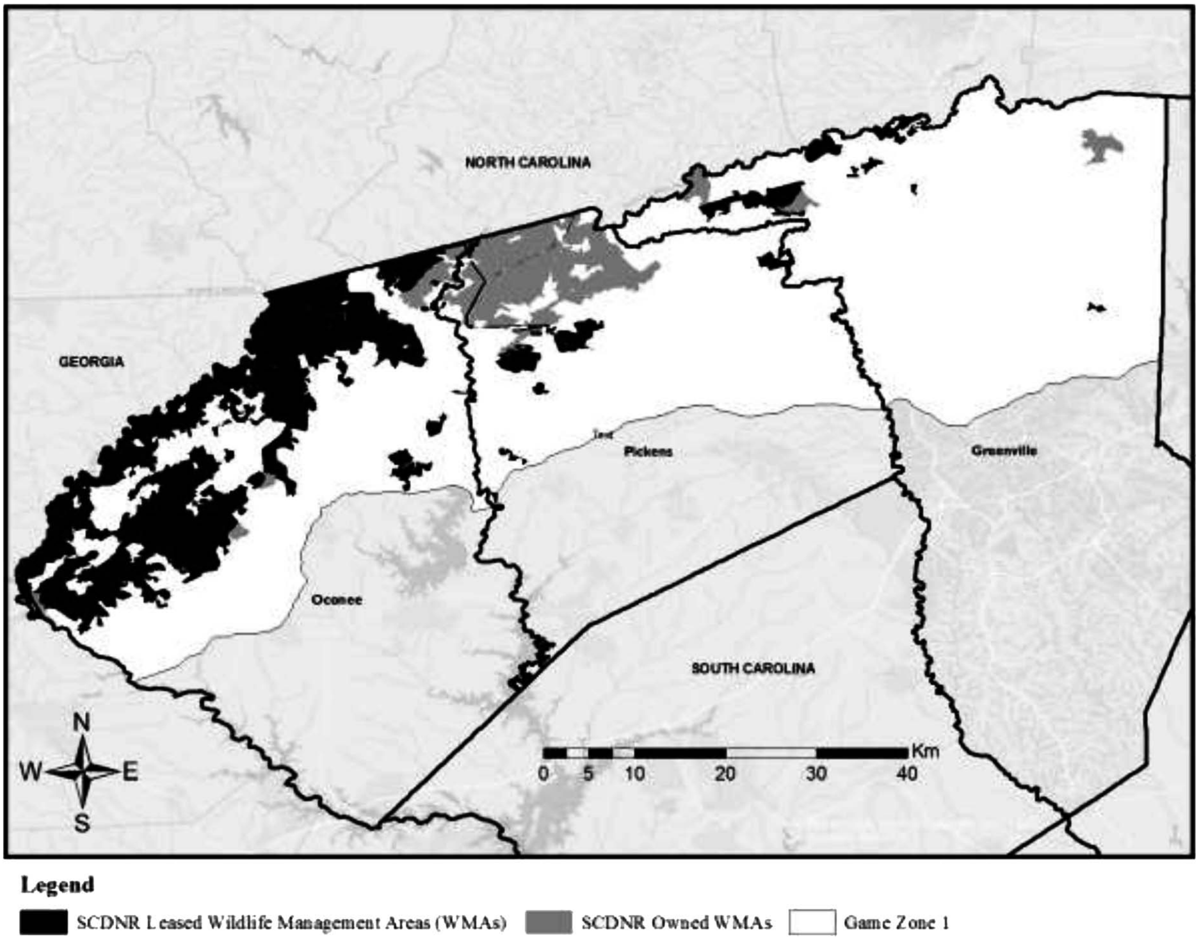

Fig. 1. Location of the South Carolina Department of Natural Resources (SCDNR) -defined Game Zone 1 for American black bear (*Ursus americanus*) harvest in the northwestern region of South Carolina, USA, and Wildlife Management Area lands in the Zone.

bears (S. Still, South Carolina Department of Natural Resources, personal communication). Annual status reports in 2007 and 2011 reported a statewide population estimate of approximately 1,150 and approximately 1,800 bears, respectively (Still 2007, Morton 2011) derived from personal observations by state wildlife personnel of increasing harvest numbers, bear sightings, and bear–human conflict. However, no specific population research had verified these estimates, leading to uncertainty about appropriate regulations for recreational hunting to maintain desired population levels or trends. Thus, there was a need to estimate abundance and population dynamics of South Carolina black bears and determine possible effects of harvest on the population.

Our objective was to estimate the long-term population trends and current status of black bears in the northwestern region of South Carolina. We selected a longstanding harvest data set to perform population reconstruction using deterministic models that estimated a minimum abundance from age- and sex-specific harvest data by carrying out a backward addition of cohorts (Downing 1980).

Study area

We defined the study area as the region where regulated bear hunting was permitted in northwestern South Carolina composed of Oconee, Pickens, and Greenville counties. The South Carolina Department of Natural Resources (SCDNR) characterized this region as 'Game Zone 1' (Fig. 1). Harvest was permitted on private lands as well as public state-owned or -leased Wildlife Management Area (WMA) lands (Fig. 1). The region was typically composed of forested habitat containing shortleaf pine (*Pinus echinata*), chestnut oak (*Quercus prinus*), and scarlet oak (*Q. coccinea*) mixes on the southern Appalachian mountain slopes (Willey 1995, Butfiloski 1996). The cooler northern slopes consisted of yellow poplar (*Liriodendron tulipifera*), white pine (*P. strobus*), eastern hemlock (*Tsuga canadensis*), and mixed mesophytic hardwood overstories (Willey 1995, Butfiloski 1996). Slopes and coves often had dense understories of mountain laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron maximum*), and intermediate stands were generally oak–pine mixtures (Myers et al. 1986). The study area was generally characterized by a mean annual temperature of 15.5°C and mean annual precipitation of 160 cm over the study period considered (1998–2015; NOAA–National Climatic Data Center 2015).

Methods

Data collection

We used 24 years of annual harvest records (1992–2015) maintained by the SCDNR to reconstruct black bear populations in northwestern South Carolina, and identify mortality trends and age structures and sex structures in harvest. In South Carolina, bear hunts were undertaken annually in 2 forms: still hunts (bears taken by single hunters without the use of dogs) and party dog hunts (bears bayed or treed by a pack of dogs belonging to hunters [party of 1–25 hunters]). The season for still hunts consistently ran between 17 and 23 October during the study period (S.C. Code Ann. § 50-11-430; T. Wactor, personal communication). The limits on each hunter (consistent through the data set period) were 1 bear/hunting season; adult females with cubs and bears ≤45 kg were not legal to take. The season for party dog hunts ran between 24 and 30 October. The limit on each party (of up to 25 hunters) was 5 bears/hunting season, or 1 bear/person for parties of <5 people; the same prohibition on take of adult females with cubs and bears ≤45 kg applied (S.C. Code Ann. § 50-11-430). South Carolina DNR personnel recorded the sex and location (WMA or private lands) of kill for each harvest reported, and collected a tooth for age analysis using the cementum annuli technique (Wiley 1974). However, tooth analysis was carried out beginning in 1992, so age estimates were only available for 1992 onward. The number of unaged bears (i.e., harvested bears from which teeth were not collected) was also recorded for every year. Harvest numbers varied considerably each year but we noted that, prior to the mid-1990s, bear harvest was generally ≤10 bears/year. Thereafter, harvest levels increased to a high of 120 in 2013 (Table 1).

Statistical model

We used a Downing (1980) adaptation of the Virtual Population Analysis developed by Fry (1949) to reconstruct the northwestern South Carolina black bear population through backward summation of cohorts. This technique is suitable for analysis of age- and sex-specific harvest data that are typically collected by managers (Warburton 1996, Bender 1997, Jones 2005, Noyce 2011b). Evaluation and limitations of the Downing method had been documented in the literature and could serve as a guide in reporting population estimates (Tilton 2005, Davis et al. 2007, Klopfer 2011).

The Downing method does have some assumptions regarding the data collection and structure that we considered. First, similar to other hunted bear populations; we assumed that the primary source of mortality for the population was harvest (Wooding and Hardisky 1994, Klenzendorf 2002). However, to help account for other known sources of mortality, we augmented our data by including roadkills, illegal kills, euthanized bears, trapped bears, and other unknown mortalities in the harvest. Second, we assumed harvest of black bear was non-differential toward age or sex for all age classes ≥1 (cubs <1 yr of age were not allowed to be harvested). Third, we assumed that because of non-differential harvest, the 2 oldest age classes of the population had equal mortality rates, with the ratio of harvest to non-harvest mortality constant over time. Because a varying number of bears each year were reported as unaged, we improved robustness by inflating harvest records by a factor equal to the proportion of unaged bears in the data set for that year (Davis et al. 2007).

Reconstruction technique

We applied the Downing technique to a subset of the harvest database, from 1998 to 2015. Tooth-aging data, and thus age-specific harvest, were unavailable prior to 1992. In both 1993 and 1997, no harvest occurred, and we could not apply the Downing equations to those years. We used the Python packages *xlrt* and *xlwd* to develop models to analyze the harvest data sets (version 2.7; van Rossum and Drake 1995). We first collapsed harvest records for older age classes into a single age class. We calculated an "average harvest" (H) and "average mortality rate" (M) for the 2 oldest age classes over the past 3 years, and divided H by M to derive a "starting abundance" (A; Davis et al. 2007). We used A along with the ratio of actual harvest to H to derive abundances for the 2 oldest

Table 1. Distribution of mortality data used in population reconstruction for the northwestern South Carolina, USA, American black bear (*Ursus americanus*) population, in 1992–2015, including mean percentage of total mortality and standard error (SE) over the study period.

		Harvest			
Year	Total	Wildlife Management Areas	Private lands	Roadkills or Illegal kills	Unknown or Unrecorded
1992	17	8	—	0	9
1993	—	—	—	—	—
1994	11	7	—	3	1
1995	12	11	1	0	0
1996	15	13	—	0	2
1997	22	19	2	1	0
1998	15	11	3	1	0
1999	21	17	2	2	0
2000	61	27	21	11	2
2001	24	16	6	2	0
2002	29	24	2	1	2
2003	65	46	12	5	2
2004	31	28	1	2	0
2005	23	—	—	—	23
2006	52	45	6	1	0
2007	62	51	8	1	2
2008	48	41	5	2	0
2009	107	79	14	12	2
2010	54	33	10	11	0
2011	99	69	10	13	7
2012	83	68	13	2	0
2013	135	62	55	18	0
2014	81	49	12	20	0
2015	92	54	36	2	0
Mean %		72.29	14.63	8.50	4.58[a]
SE		14.71	11.59	8.02	11.41[a]

[a] Values from 2005 were excluded as an outlier in this estimate.

age classes (Davis et al. 2007). We estimated abundance over all other age classes by backward summation.

We ran reconstruction models on 7 data sets derived by collapsing age classes to 3+, 4+, 5+, 6+, 7+, 8+, and 9+ years. However, we only reported abundance from models for 3+, 4+, and 5+ collapses because we observed that harvest counts were sparser for older age classes, leading to incomplete cohort construction and computational biases in the models when we collapsed age classes ≥6 years. Reconstruction is complete when a cohort passes through the harvested population; therefore, collapsing to $n+$ age classes allowed a complete reconstruction up to the $(n - 1)$th year prior to present. Accordingly, collapsing to 3+–5+ age classes is a standard protocol in the estimation of black bear abundance by wildlife managers using the Downing technique (Tilton 2005, Klopfer 2011, Noyce 2011a). It should be noted that the Downing technique provides a yearly point estimate of abundance with no method for calculating variance within a year. Therefore, we reported mean of abundance estimates from the 3 collapsed models but no estimate of variance around the mean.

We estimated abundance using all harvest records (on both WMA as well as private lands). We also established population growth rate and age-specific survival. Note that because we collapsed higher age classes, oldest age classes were not the true oldest age classes. Thus, survival estimates for later years increased to >1.0 and were removed from the results.

Results

We estimated that abundance had been generally increasing in the entire northwestern region over the study period, jumping from a mean (average of the values of the 3+, 4+, and 5+ age collapsed models) of 96.7 bears in 1998 to 412.0 bears in 2013 (Fig. 2). Mean population growth rate was 1.111/year (SE = 0.128). With the exception of 2000, 2003, and 2012, population growth rate averaged over models was >1.0 for every year since

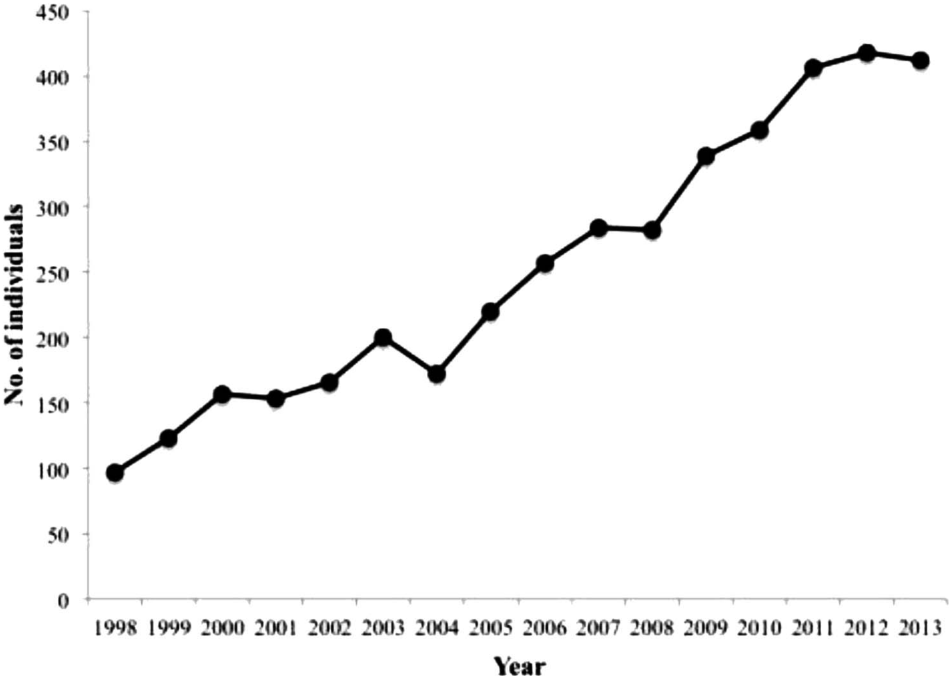

Fig. 2. Model-averaged abundance (no. of individuals) trends of the American black bear (*Ursus americanus*) population of northwestern South Carolina, USA, estimated over Game Zone 1, in 1998–2013.

1998. There was no significant difference ($P > 0.878$) between Downing abundance estimates for WMA and private lands collectively and Downing abundance estimates for only WMA lands inflated by the ratio of WMA harvests to collective harvest.

We found that WMA land harvest accounted for 100% of all harvest in 1970 to 1991; and annual harvest was ≤10 bears in that period. In 1992 to 2015, WMA land harvest accounted for an annual mean of 72.29% of all recorded mortality (SE = 14.71) and private lands harvest accounted for an annual mean of 14.63% of all recorded mortality (SE = 11.59; Table 1). Harvest from dog hunts accounted for more of the annual mortality on WMA lands (annual $\bar{x} = 72.7\%$, SE = 16.3) than did still hunts (annual $\bar{x} = 24.2\%$, SE = 17.5) in 1992–2015 (Table 2). The opposite was true for harvest on private lands, with still hunting accounting for 58.4% of all mortality (SE = 32.0) as compared with 20.5% for dog hunting (SE = 26.0; Table 2). We attributed larger standard error in private land harvest to smaller sample sizes (Table 2). Overall, between 1992 and 2015, dog hunts contributed to the majority of harvest across WMA and private lands (annual $\bar{x} = 67.8\%$, SE = 14.5).

We estimated average age of male bears harvested in the region as 3.36 years (SE = 1.72; Table 3) and average age of harvested females as 4.20 years (SE = 1.58; Table 3). Harvest sex ratios were biased toward males ($\bar{x}$ F:M ratio = 0.83, SE = 0.26; Table 3) with the exceptions of 1995, 2007, and 2014, when females comprised 58.33, 51.67, and 59.26% of the harvest, respectively.

There was no difference in survival, considering both males and females combined in each age class, across models of different collapses ($P > 0.24$ for all age classes; Table 4). This suggested that the Downing method was robust to survival estimates within an age class. Mean annual survival ranged from 0.684 to 0.843 depending on the age class (Table 4). Excluding the oldest age class (7, biased because of collapse of older age classes), we found no significant evidence of consistently low or high survivorship of any particular age class relative to the others, reinforcing our assumption that harvest was non-differential toward age.

Discussion

Populations of black bear in South Carolina appear to be increasing over the past 2 decades, although at a slower rate than was previously estimated (Still 2007, Morton 2011). Our data suggest that even assuming a 15% underestimation by Downing reconstruction

Table 2. Distribution of harvest in 1992–2015, by method of take, on Wildlife Management Areas (WMA) and private lands, and mean and standard error (SE) over the entire period, for the American black bear (*Ursus americanus*) population in northwestern South Carolina, USA.

	WMA lands				Private lands			
Year	Sample size	% Still harvest	% Party dog harvest	% Non-harvest mortality	Sample size	% Still harvest	% Party dog harvest	% Non-harvest mortality
1992	8	37.50	62.50	—	—	—	—	—
1993	—	—	—	—	—	—	—	—
1994	7	—	71.43	28.57	—	—	—	—
1995	11	36.36	63.64	—	1	—	100.00	—
1996	13	15.38	76.92	7.69	—	—	—	—
1997	19	21.05	78.95	—	2	—	50.00	50.00
1998	11	90.91	9.09	—	3	—	66.67	33.33
1999	17	11.76	88.24	—	2	50.00	—	50.00
2000	27	29.63	70.37	—	21	47.62	—	52.38
2001	16	31.25	62.50	6.25	6	83.33	16.67	—
2002	24	12.50	79.17	8.33	2	50.00	—	50.00
2003	46	21.74	73.91	4.35	12	58.33	16.67	25.00
2004	28	21.43	75.00	3.57	1	100.00	—	—
2005[a]	—	—	—	—	—	—	—	—
2006	45	26.67	71.11	2.22	6	83.33	16.67	—
2007	51	27.45	72.55	—	8	62.50	25.00	12.50
2008	41	17.07	82.93	—	5	80.00	20.00	—
2009	79	21.52	78.48	—	14	64.29	14.29	21.42
2010	33	24.24	75.76	—	10	20.00	—	80.00
2011	69	20.29	69.57	10.14	10	80.00	—	20.00
2012	68	22.06	77.94	—	13	76.92	23.08	—
2013	62	32.26	67.74	—	55	78.18	14.55	7.27
2014	49	22.45	77.55	—	12	91.67	8.33	—
2015	54	12.96	87.04	—	36	83.33	16.67	—
Mean		24.19	72.71	3.09		58.39	20.45	21.15
SE		17.46	16.34	6.41		31.96	25.98	24.66

[a] Although mortality was recorded for 2005 (Table 1), the usual categories of WMA or private lands or method of harvest were not recorded for individuals.

(Tilton 2005), the 2011 report of the northwestern South Carolina bear population (Morton 2011) overestimated abundance by a factor of approximately 3. We attribute this to the original estimates being inaccurately derived from changes in sightings and harvest rather than empirical population estimates. To validate our predicted abundance, we compared our results with non-spatial and spatially explicit models used to analyze capture–recapture data from a hair-snare study in South Carolina in 2013–2014 (Azad 2016). Point abundance estimates of the Downing method in 2013 (412.0 bears) agreed with both non-spatial (model-averaged $\bar{x} = 402.73$, SE = 109.67) and spatial models (model-averaged $\bar{x} = 360.70$, SE = 51.53). This indicates that our Downing reconstruction technique was likely robust enough to predict long-term trends, and it is likely that fewer black bears exist in northwestern South Carolina than previously reported.

Our study also documented a shift in trends of method and location of take in this bear population over time. Overall, across our 18-year study period, the majority of harvest continued to be on WMA lands. We attributed this to the method of harvest because dog hunting contributed to more than two-thirds of all harvest and the majority of dog hunts ($\bar{x} = 91.61\%$, SE = 18.64) were carried out on WMA lands that tended to have larger parcel sizes compared with private lands. However, over time there was a general trend toward increasing still-hunting harvest on private lands, suggesting that bears are increasing in abundance as well as increasing use of private lands in the state. Moreover, deer-baiting with corn (which also attracts bears) has been permitted for South Carolina Game Zone 1 hunters since 2013 on private, but not public, lands (T. Wactor, personal communication). Our hypothesis of dispersion is further supported by this recent opportunity to attract bears to private lands using deer bait and the generally increasing trend in bear–human interactions over the past decade (Azad 2016).

Table 3. Average age (yr) of males (M) and females (F) in harvest, and sex ratio (F:M) in harvest in 1992–2015, and mean and standard error (SE) over the entire period, for the American black bear (*Ursus americanus*) population in northwestern South Carolina, USA.

Year	Sample size	Average age (M)	Average age (F)	Sex ratio (F:M)
1992	17	8.50	5.00	0.89
1993	—	—	—	—
1994	9	4.40	7.00	0.50
1995	12	6.25	5.00	1.40
1996	14	4.71	6.43	1.00
1997	21	—	2.00	0.62
1998	15	2.13	1.50	0.67
1999	20	3.29	3.38	1.00
2000	48	2.93	2.75	0.37
2001	23	3.67	4.45	0.92
2002	27	2.78	4.50	0.80
2003	60	2.78	4.53	0.71
2004	30	3.36	2.67	1.00
2005	26	2.14	5.22	0.63
2006	52	3.10	4.74	1.00
2007	60	3.96	4.10	1.07
2008	46	2.75	3.80	0.53
2009	103	3.26	3.44	0.75
2010	42	3.00	5.75	0.75
2011	89	2.80	5.00	0.68
2012	85	3.15	4.38	0.93
2013	133	3.21	5.45	0.90
2014	81	4.93	5.50	1.45
2015	94	3.54	4.26	0.62
Mean		3.36	4.20	0.83
SE		1.72	1.58	0.26

Harvest is a major source of mortality for hunted bear populations, so examining the age and sex structures in harvest can provide insight into local flux in population dynamics (Beecham 1983, Wooding and Hardisky 1994). A number of studies report greater male vulnerability to harvest for the American black bear (McIlroy 1972, Fraser et al. 1982, Kohlmann et al. 1999, Malcolm and Van Deelen 2010), and studies postulate that a consistent male bias and relatively higher female average age of harvest indicates a lightly harvested population (Johnson and Pelton 1980; Fraser et al. 1982; Garshelis 1990, 1994). For the population studied, harvest was consistently biased toward males, with average age of males gradually declining and females gradually increasing over the study period. Therefore, our results suggested an expanding population and did not suggest overharvest. However, we recommend these trends be monitored for the population for any sharp and consistent deviations in trend that cannot be explained by other monitored environmental factors or changes in hunting regulations.

The Downing method has been proven robust to population trajectories over a long-term data set (Downing 1980, Tilton 2005, Davis et al. 2007); however, we recommend that it be considered a baseline estimate of abundance each year. We suggest the future incorporation of hunting effort and/or harvest reporting rates to improve the robustness of the method (Gove et al. 2002, Skalski et al. 2007, Fieberg et al. 2010, Etter 2011, McDonald et al. 2011, Clawson 2015). Simulation runs of the method have reported a tendency to underestimate point abundances typically by 11–15%, but sometimes by as much as 30% (Tilton 2005, Davis et al. 2007). We recommend that these estimates be calibrated against future mark–recapture (or similar) surveys to better determine extent of underestimation. In addition, although the Downing method assumed non-differential harvest for all individuals, South Carolina regulations did not permit

Table 4. Age-specific survival of American black bear (*Ursus americanus*), reported as mean and standard error (SE) for each model[a] in 1998–2013, and *P*-value for analysis of variance between models, for the northwestern population in South Carolina, USA.

	Age class													
	1		2		3		4		5		6		7	
Model	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Collapse to 9+	0.786	0.125	0.712	0.170	0.771	0.142	0.717	0.296	0.715	0.107	0.696	0.174	0.843	0.99
Collapse to 8+	0.797	0.117	0.723	0.178	0.781	0.135	0.734	0.213	0.738	0.146	0.684	0.208		
Collapse to 7+	0.785	0.127	0.692	0.180	0.743	0.179	0.696	0.267	0.795	0.077				
Collapse to 6+	0.807	0.129	0.744	0.173	0.805	0.132	0.781	0.163						
Collapse to 5+	0.801	0.103	0.703	0.218	0.716	0.296								
Collapse to 4+	0.806	0.124	0.739	0.184										
P-value	0.99		0.96		0.71		0.78		0.24		0.90		—	

[a]'Collapse to $X+$' represents a harvest reconstruction model where equations were applied to a data set in which older age classes in harvest were collapsed to a single age class of age X years.

harvest for females with cubs and bears <45 kg. However, we assumed that the following year, cubs would be weaned from their mothers and grow to >45 kg. Thus, 1 year later, individuals excluded from the harvest data set in the previous year would be considered equal opportunity in harvest. To account for this transition, we recommended that reconstruction estimates be considered incomplete for recent years to allow these individuals to progress to the harvestable population. We also recommend that the SCDNR carry out future surveys of hunter effort and bias (if any) toward harvest of bears in any particular age, sex, or weight class.

Although increasing human densities have historically strongly corresponded with declining large mammal populations, implementation of effective legislation and management strategies can allow wild populations to expand even in regions of high human densities (Kellert et al. 1996, Treves and Karanth 2003, Linnell et al. 2009). For the American black bear, the picture emerging over the past 2 decades in the eastern United States is of bears repopulating former ranges, nearing the cultural carrying capacity of the bear–human landscape, and state programs moving toward more scientifically informed management (Kellert 1994, Noyce 2011b). In South Carolina, a black bear population was once declared probably extinct (Logan 1859), but was reestablished to a few dozen individuals a century later amidst great public distrust, illegal kills, and increasing urban development (Cely and Hamilton 1981). A decade later, the population increased to approximately 100 individuals (Fendley 1991), and is currently steadily expanding over its former range while sustaining an annual recreational harvest. Moreover, the South Carolina population is considered a subset of the larger southern Appalachian population, and the effects of harvest could potentially be mitigated by its connectivity to the larger, more robust North Carolina and Georgia, USA, populations (Hammond 2011, Olfenbuttel 2011). Our findings indicate, however, that this recovery has been much slower than previously reported (with population numbers as low as one-third below previous estimates). Therefore, we suggest that there may be a need to define desired population levels and revaluate research priorities for the population, including a possible assessment of immigration and emigration from the southern Appalachian metapopulation. We also suggest further investigation using projection models to understand how ecological factors and harvest management decisions can maintain black bear populations in the state for desired levels of annual recreational harvest as well as minimization of bear–human conflict.

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