American black bear nuisance complaints and hunter take

Adrian Treves^{1,3}, Kirsten J. Kapp^{1,4}, and David M. MacFarland^{2,5}

¹The Nelson Institute for Environmental Studies, University of Wisconsin-Madison, 30A Science Hall, 550 North Park Street, Madison, WI 53706-1491, USA

²University of Wisconsin-Madison, Department of Forest and Wildlife Ecology, 1630 Linden Drive, Madison, WI 53706, USA

Abstract: Regulated hunts of carnivores are believed to prevent property damage and other conflicts with people. Few studies have tested if public hunting reduces subsequent complaints about carnivores. We analyzed 10 years of data on nuisance complaints from a hunted American black bear (Ursus americanus) population in Wisconsin, USA. At the statewide scale, complaints about agricultural damage, other property damage, or human safety concerns did not correlate with each other or with number of bears taken by hunters in the preceding 1– 2 years. At the smaller scale of bear management zones, there were positive correlations between the number of bears taken by hunters in one year and all categories of nuisance complaints in subsequent years. Once corrected for the estimated bear population size, only property damage retained a significant positive correlation with hunter take in prior years. Age and sex profiles of bears taken by hunters differed significantly from those of bears live-trapped around sites of nuisance complaints. Hunters took significantly younger bears and a lower proportion of males. The most common method (shooting over bait) produced age-sex profiles most different from bears live-trapped after nuisance complaints. Although hunters removed 356 bears implicated in nuisance complaints, they took these bears in proportion to their availability. We conclude that the Wisconsin bear-hunting season did not show clear evidence of reducing nuisance complaints during 1995–2004, probably because hunting was not effectively designed for that goal. We call for additional research on hunter and bear behavior, including experimental tests of hunting individuals with different levels of involvement in property damage.

Key words: animal damage, bears, carnivores, depredation, harvest, human-wildlife conflict, hunting, Ursus americanus, Wisconsin

Ursus 21(1):30-42 (2010)

Large carnivores have recolonized parts of North America and Europe, benefiting ecosystem diversity and function (Berger et al. 2001, Gompper 2002, Smith et al. 2003, Ripple and Beschta 2004). But as they recolonize multi-use landscapes, carnivores sometimes prey on livestock, damage property, or threaten people (Woodroffe et al. 2005, Treves 2009). These threats—whether real or perceived can generate calls for control of wildlife populations as well as opposition to conservation policy and management actions. Balancing wildlife population viability with human needs can be challenging in the face of such conflicts. Such is the case with the American black bear (*Ursus americanus*), once considered a shy, sensitive species requiring large tracts of undisturbed habitat (Clark et al. 2002). In the last 30 years, our perspective on bears has changed as they have thrived in some rural and semiurban areas (Beckmann and Berger 2003).

Undesirable human-bear interactions sometimes result when bears move into human use areas or when development encroaches on bear habitat (Jorgensen et al. 1978, Garshelis 1989, Stowell and Willging 1992, Peine 2001). When bears become habituated to people or conditioned to human foods such as garbage or animal feed, they may regularly pose a nuisance to residents, farmers, and recreational visitors (Herrero and Higgins 1999, Rajpurohit and

³atreves@wisc.edu

⁴Present address: 525 E 8000 S Victor, ID 83455, USA, kjkapp@gmail.com

⁵Present affiliation: Wildlife and Forestry Research Section, Bureau of Science Services, Wisconsin Department of Natural Resources.

Krausman 2000). It is often assumed that any bear will take advantage of human food sources and become a nuisance, but many studies show individuals differ in propensity to develop problematic behavior or persist in it (Jope 1983, Jorgensen 1983, Linnell et al. 1999, Breck et al. 2008). Mattson (1990) reviewed a number of studies in the US that showed disproportionate numbers of female and sub-adult black bears engaged in nuisance behavior in Wyoming and Alaska. However, other studies showed that a higher percent of male black bears caused problems (Garshelis 1989). Beckmann and Berger (2003) found a high density of male black bears in developed areas of California and Nevada, suggesting that females avoid areas of human use to protect cubs.

Once begun, nuisance behaviors may persist, as observed in food-conditioned bears in Nevada and California that tended to remain in human-dominated areas rather than retreating from such habitat (Beckmann and Berger 2003). Attraction to areas of human use could have far-ranging ecological consequences. Beckmann and Berger (2003) proposed that the exploitation of human food sources caused a redistribution of black bear populations near Lake Tahoe, California. It also led black bears to change behavior, ecology, and life history, e.g., smaller home ranges, shorter denning periods, larger body size, and higher fecundity. However, problem behaviors may not persist. A recent study found transmission of problematic behaviors between individuals was not associated with genetic relatedness (Breck et al. 2008). Differences between individual carnivores involved in nuisances and those uninvolved could point the way to selective management methods (Odden et al. 2002, Wydeven et al. 2004, Breck et al. 2008).

Many countries use regulated public hunts of carnivores to manage conflicts with people (Sunde et al. 1998, Conover 2001, Sidorovich et al. 2003, Andren et al. 2006). Hunting carnivores is thought to prevent future threats to human safety or property, or increase tolerance among affected human populations (Linnell et al. 2001, Herfindal et al. 2005, Loveridge et al. 2007, Treves 2009). Hunting is expected to reduce carnivore populations, eliminate culprits selectively, or indirectly change the behavior of survivors. Yet, studies find equivocal evidence (Treves 2009). Some hunters pursue carnivores in areas where damage occurred and others prefer wilder areas (Sunde et al. 1998, Bunnefeld et al. 2006). Age–sex classes of carnivores taken by hunters sometimes resemble and sometimes differ from those of carnivores implicated in conflicts. As one might expect, therefore, property damages may not diminish after removal of carnivores (Allen and Sparkes 2001, Bartel and Brunson 2003, Treves 2009). Probably the most precise study found that hunting European lynx (*Lynx lynx*) around grazing areas in Norway produced a small but significant reduction in lamb losses (Herfindal et al. 2005).

These somewhat equivocal results for carnivores generally are mirrored for bears. American and Asiatic black (*U. thibetanus*) bear quotas have been set partly according to past damage levels (Jorgensen et al. 1978, Forbes et al. 1994, Huygens et al. 2004), or by allowing unlimited hunting in agricultural areas (Garshelis 1989). Working around Fundy National Park, Canada, Forbes et al. (1994) found hunting of black bears reduced conflicts with people. But more studies of bear hunting have not found such a link (Garshelis 1989, Obbard et al. 1997). For example, Huygens et al. (2004) found no association between depredation costs and the number of Asiatic black bears killed either in the same year or the year prior, despite >1,000 taken by hunters each year in Japan.

Here we assess if hunting American black bears reduced subsequent nuisance complaints in Wisconsin, USA (WI) and if the age-sex profiles of bears live-captured at sites of nuisance complaints resembled those of bears taken by hunters. We present these data to inform carnivore management and conservation policy broadly. Also, we present these data to catalyze a regional review of the assumptions that bears live-trapped around a site of nuisance complaint are indeed the cause of the nuisance, that nuisances are likely to recur unless the bears are manipulated, and that hunting bears reduces further nuisances.

Study area

Black bear population. The WI Department of Natural Resources (WDNR) estimated state black bear numbers at 13,000 in 2008 (WDNR 2009a, using a model modified from D.L. Garshelis and W. Snow, 1988, Minnesota Department of Natural Resources, Minneapolis, Minnesota, USA, unpublished). This modification to the model incorporates the sex and age composition of harvested bears and estimates of reproduction and natural mortality to adjust the population estimate from the prior year. The estimates generated from the model are fit to trends in the state's annual bait station survey. These estimates form the basis for bear management in the state, including the setting of harvest quotas. The accuracy of this method has recently been called into question because a mark–recapture study released in 2009 estimated more than twice as many individuals (MacFarland 2009) as were estimated by the model. Despite that study, we used official state bear population estimates from 1995–2004 for the 4 bear management units (BMUs: Table 1) because a retroactive correction factor has not yet been published (WDNR 2009a).

Black bear hunting. The WDNR managed bear hunting primarily for population and recreational management and in part because of the belief, "When hunters meet the established bear harvest quotas, problems associated with high bear populations such as nuisance bears and agriculture damage are reduced" (Koele 2006:1). Applications for bear permits increased from 1995–2004 (average = 48,033, range 30,090-61,726, average annual increase = 7.7%: WDNR 2009a). Each year, the WDNR issued an average of 5,029 (SD = 1,078) bear permits and hunters took 2,666 (SD = 475) bears (53% hunter success rate; WDNR 2009a). Hunting was designated in 4 bear management units (Fig. 1), across which average annual success of hunters varied: A and D summed = 54.4% (SD = 8.6%; B = 61.6% (SD = 8.5%); C = 37.0% (SD = 6.4%; WDNR 2009a). A and D (formerly A1) were summed because hunters with a permit for A or A1 could take a bear in A1 without it being noted on their permit, thereby inflating the apparent success of hunters in A1 and deflating it in A, prior to 2008.

From 1995–2004, bear hunters most often hunted with bait alone (61.6%), whereas the remainder used dogs (16.8% with bait and 20.6% without bait), guns only (<1%), or did not specify (WDNR 2009a). Hunters could use no more than 6 dogs at once to pursue bears. Different methods could be used in partly overlapping seasons that alternated every year. For example, in odd years, bear hunting could only be done with dogs during the first week of September, then for the remainder of the month all methods could be used until the first week of October, when dogs were no longer permitted (WDNR 2009a). Hunters were prohibited from killing any bear accompanied by a cub, which might depress take of reproductive females (WDNR 2009b).

Hunters were required to register bears taken and were asked to report the sex and turn in a premolar



Fig. 1. Management units for American black bear in Wisconsin, USA.

to a local collection site (such as a hardware store or tavern). The WDNR sexed and aged an average of 74.5% of bears taken by hunters annually (Rolley et al. 2004). The same laboratory estimated ages of all WI black bear premolars by counting annuli in the cementum of extracted premolars (Matson's Laboratory, Milltown, Montana, USA).

Nuisance complaints. Perceived threats to human safety accounted for most complaints about bears in WI during 1995–2004 (Table 1), followed by damage to property (such as bird feeders, structures), then agriculture (apiaries, crops, livestock) (Stowell and Willging 1992, Engstrom et al. 2006). The US Department of Agriculture Wildlife Services (USDA-WS) and WDNR co-managed nuisance bear complaints primarily through public education. If education alone could not resolve problems, or if bears damaged structures, attacked livestock, or destroyed crops, agents live-trapped and relocated bears from complaint sites to wilder areas averaging 78 km away, where bear hunting was likely (Kapp 2006; R. Willging, USDA–WS, Rhinelander, Wisconsin, USA, personal communication, 2005). Agents killed <1% of captured bears from 1995-2004 (D. Ruid, USDA-WS, Rhinelander, Wisconsin, USA, personal communication, 2005).

		Bear numbers		Nuisance complaints			Bear numbers		Nuisance complaints			
Year	Unit	Population	Take	Agriculture	Property	Safety	Unit	Population	Take	Agriculture	Property	Safety
1993	А	4217	475	-	-	-	В	2192	275	-	-	-
1994		4546	355	-	-	-		2344	278	-	-	-
1995		5085	395	154	47	346		2530	399	18	27	156
1996		5722	801	107	59	310		2592	396	18	16	107
1997		5975	719	150	42	325		2671	382	21	17	170
1998		6361	1257	46	27	105		2800	470	9	13	126
1999		6157	1167	66	22	131		2859	400	15	17	204
2000		6038	1257	57	27	148		3008	457	6	10	296
2001		5818	1014	39	18	58		3120	489	9	15	287
2002		5425	961	35	41	157		3257	424	32	34	370
2003		5433	1013	39	30	204		3421	461	21	37	389
2004		5295	987	61	21	190		3578	658	21	19	348
1993	С	1048	153	-	-	-	D	4157	351	-	-	-
1994		1103	97	-	-	-		4728	578	-	-	-
1995		1237	193	32	9	52		5182	750	87	92	419
1996		1285	184	28	1	26		5470	944	60	66	326
1997		1363	173	39	2	49		5558	904	94	42	246
1998		1476	235	22	6	64		5709	1222	56	60	217
1999		1548	225	32	9	72		5471	1089	65	60	364
2000		1653	228	29	8	128		5276	1129	61	35	357
2001		1791	276	24	11	119		4867	1207	47	17	207
2002		1869	217	60	19	175		4673	835	38	50	285
2003		2084	365	44	26	198		4425	959	37	30	315
2004		2156	494	90	10	146		4023	924	61	24	305

Table 1. Annual bear population estimate, hunter take, and nuisance complaints by bear management unit in Wisconsin, USA.

In 1995, USDA-WS agents began collecting age and sex data on most live-trapped bears after immobilization. Bears implicated in agricultural damages in August (e.g., sweet corn in late summer and early fall; Stowell and Willging 1992) were not immobilized because the chemical agent was deemed dangerous to people who might ingest bear meat containing the chemical metabolites (D. Ruid, personal communication, 2005). However 84% of complaints were about human safety and property, which often prompted live-trapping and immobilization, which yielded age and sex data. Agents used culvert traps to capture and relocate bears from sites of complaints. They immobilized bears with ketamine:xylazine at a ratio of 5:1, tagged them with 1-2red ear tags with the USDA-WS telephone number, sexed most, and extracted a premolar for aging as above.

No data were available to confirm whether live-trapped bears were indeed the causes of nuisances, so we cannot evaluate non-target error (Treves and Naughton-Treves 2005). Therefore, we assumed that live-trapped bears in all our analyses were the individuals that caused the nuisance complaint.

Methods

Our analysis had 3 parts. First, we analyzed nuisance complaints in relation to prior hunter take at the state and BMU scales over a 10-year period. Second, we examined age and sex classes of black bears live-trapped in response to nuisance complaints in comparison with classes of bears taken by hunters. We examined data from hunters using 3 different methods to take bears as a way to further refine that test. Finally, we tested whether hunters selectively took the individual, ear-tagged bears that had been live-trapped at sites of nuisance complaints and relocated by USDA-WS.

Bears taken by hunters. We present WDNR data on hunter take 1993–2004 by BMU (Table 1) and statewide (Table 2) to test for a 2-year lag in nuisance complaints. We collated WDNR data on sex (n = 21,156) and age (n = 17,337) of bears taken by hunters separately for each hunting method (1995–2003). The aging method met the demands of our analysis for precision and accuracy, particularly for bears <6 years old (Costello et al. 2004). Accordingly, we analyzed age in 6 classes of 1, 2, 3, 4, 5, and >5.

	Nuisance	complaint	Bears			
Year	Agriculture	Property	Safety	Hunter take	Live- trapped	
1993	-	-	-	1254	-	
1994	-	-	-	1308	-	
1995	291	175	973	1737	206	
1996	213	142	769	2325	242	
1997	304	103	790	2178	191	
1998	133	106	512	3184	102	
1999	178	108	779	2881	113	
2000	153	80	929	3075	73	
2001	119	61	671	2986	28	
2002	165	144	987	2437	86	
2003	141	123	1106	2798	80	
2004	233	74	989	3063	-	
Sum	1930	1116	8505	26664	1121	

 Table 2. Nuisance complaints and black bears livetrapped or taken by hunters statewide.

To assess if hunting reduced subsequent nuisance complaints, we had to contend with the possibility that a larger bear population might generate more nuisance complaints as well as higher hunter take without any meaningful relationship between the two. However we could not use multiple regression because hunter take was highly collinear with the population estimate 1993–2004 (n = 48 BMU yrs, r_s = 0.89, P < 0.0001). This was not surprising because the bear population estimate partially reflected hunter take and was used to set the quota. Hunters took an average of 7% more than the quota 1995– 2004 (SD = 16%, range = -22-41%; WDNR 2009a).Similarly, the annual bear population estimate was positively correlated with each component of complaints in the same year (n = 40 BMU yrs, $r_s = 0.42$, 0.57, and 0.74, respectively, P < 0.0005 in all tests; Table 1). With multivariate linear regression inappropriate, we therefore sought to eliminate the confounding effect of the bear population estimate statistically by using boot-strapping. In doing so, we replaced the null hypothesis of no correlation (zero slope) with the observed positive correlation relating nuisance complaints to the bear population estimate and searched for deviations from that positive slope that might reflect the actions of hunters.

We calculated the expected positive slope (H_{exp}) using simulated nuisance complaints, which were proportional to the bear population estimate. We generated 200 sets of simulated nuisance complaints by multiplying each annual bear population estimate by a random number bounded by 0 and 1 with normal distribution centered around the observed annual mean and standard deviation of complaints divided by the annual bear population estimate (Table 1; mean = 0.075, SD = 0.017, range = 0.046–0.103). This produced our null model of expected positive correlations with a random, normal distribution mimicking the real one.

We compared the expected positive correlations against the set of observed correlations (H_{obs}) of hunter take and nuisance complaints in subsequent years. H_{obs} took on 6 different values because nuisance complaints were of 3 types (agriculture, property, safety; Table 1) over 2 time lags: years t +1, and t + 2. If any H_{obs} lay outside the distribution of H_{exp} , we rejected the null hypothesis in favor of the hypothesis that hunter take and nuisance complaints were related to each other independently of the bear population size (Treves 2001). Half of the proportion of H_{exp} values exceeding H_{obs} provided exact probabilities P for our 2-tailed tests of significance.

Age and sex of live-trapped bears. We collated statewide records of complaints reported to the USDA–WS by bear management unit (Table 1). We related nuisance complaints by county to the BMU that county overlapped most (WDNR 2009a). During 1995-2004, USDA-WS live-trapped 950 bears 1,120 times in response to 9.7% of all nuisance complaints. USDA-WS recaptured 146 (15.4%) of these bears; 75% twice and 25% 3-5 times. Forty of the 146 recaptures were in the same year, whereas 106 were recaptured in subsequent years. USDA-WS provided data on sex (n = 943) and estimated age (n = 943)= 944) of live-trapped bears from the same lab used by the WDNR for bears taken by hunters. Of the 944 bears live-trapped after nuisance complaints and aged, 85 (9%) were cubs at initial capture (36 female, 48 male, 1 unknown) and 57 were females with cubs (6%). We discarded the cubs from subsequent analyses except 5 recaptured when older, because cubs are protected from hunting. For analysis of the fate of ear-tagged bears, we had data on 1,034 releases from 1995-2004, including recaptured and re-released individuals.

The age and sex data derive from a subset of nuisance complaints that resulted in capture of ≥ 1 bear. Hence our sample of live-trapped bears may contain bias that deserves consideration. USDA–WS may have trapped more intensively at sites of repeated complaints or those with costly property damage. In addition, trapping effort varied with season, weather, and idiosyncrasies of trappers (D.

Ruid, personal communication, 2005). Also bears caught after causing agricultural damage in August did not contribute data because they were not immobilized. Similarly, the propensity of residents to complain about bears may have reflected the complainant's location, familiarity with wildlife, nature values, or other reasons (Naughton-Treves and Treves 2005). Some sources of trapping bias might reflect bear characteristics. For example, larger bears may cause more damage or fear, hence more frequent or strident complaints (Garshelis 1989). Another bias might have arisen if data were not collected systematically from all live-trapped bears. Indeed, trappers did not always pull teeth for aging but might instead classify a live-trapped bear as yearling or adult by size. Clearly, bears aged imprecisely by size could not be included uncritically in our sample aged by premolars (tooth-aged, hereafter). Nor could they be discarded summarily, lest small bears be undercounted. Therefore, we quantified this potential source of bias by examining a subset of bears aged both by size and by teeth. Other sources of bias could not be assessed rigorously so we treated the live-trapped bear data with caution.

To determine if hunters took ear-tagged bears out of proportion to their availability, we calculated their proportion available in the standing population annually and tested if annual hunter take of eartagged bears exceeded chance levels. Only 2 models were considered. One estimated all parameters for each year, whereas the other was time independent. We estimated survival probabilities for ear-tagged bears using the Burnham joint live and dead encounters model in Program MARK (Burnham 1993, White and Burnham 1999). Survival was modeled independently of sex and age differences, but 'captures' reflected both USDA live recaptures and recoveries of dead bears from any cause. The annual survival rate calculated from this procedure was 0.50 (SE = 0.02). Animals known to be alive from subsequent capture were entered as a complete animal. Individuals with an unknown fate were entered as a partial animal based on a survival decay function. For example, a bear with a 5-year encounter history of 1, 0, 1, 0, 0, where 1 = captureand 0 = no capture would enter our survival analysis for each year as follows: 1, 1, 1, 0.5, 0.25. If instead the second capture in year 3 was a known mortality, the bear would enter the survival analysis as follows: 1, 1, 1, 0, 0. This approach accounted for the known number of tags based upon capture history and uses survival to estimate the number of tags available after the last known capture. We calculated 2 proportions: the proportion of ear-tagged bears taken by hunters divided by the number of nontagged bears taken by hunters in 1995–2004, and the number of ear-tagged bears estimated in the standing population divided by the number of non-tagged bears estimated in the population for those same years. The first proportion (hunter selectivity) was tested against the second proportion (availability) to detect non-zero deviations.

We used χ^2 tests and Cramer's ϕ for strength of association to compare sex ratios and age ratios. We used Walloon's signed-rank test statistic W to compare proportions across years. We calculated Spearman rank correlation coefficients r_s between annual hunter take in year t and nuisance complaints in years t + 1 and t + 2 statewide (n = 10 yrs) and at bear management unit scale (n = 7 yrs). We used Spearman tests again for regressions over time. We ran statistics in JMP 8 (SAS Institute, Inc. 2009) with significance at P < 0.025 to correct for the number of tests.

Results

Nuisance complaints in relation to hunter take. Of 11,543 WI nuisance bear complaints recorded from 1995-2004 (Table 2), 73.6% were recorded as threats to human safety, 9.7% related to property damage, and 16.7% related to agricultural damage. Statewide, we found no correlations between the number of agriculture and property complaints (n = 10 years, $r_s = 0.25$, P = 0.49), agriculture and safety complaints ($r_s = 0.30$, P =0.40), or property and safety complaints ($r_s = 0.31$, P = 0.38) in the same year. Statewide, the number of bears taken by hunters increased over time (n = 12 years, $r_s = 0.71$, P = 0.01) and the number of nuisance complaints increased slightly $(n = 10 \text{ years}, r_s = 0.53, P = 0.12)$, but the number of bears live-trapped decreased (n = 9 years, $r_s =$ -0.88, P = 0.0053). From 1995–2004, hunters took 26,664 bears (Table 2). Statewide, bears taken by hunters in year t did not correlate with any of the components of nuisance complaints in year t + 1 or t+ 2 ($|r_{s}| < 0.41$, P > 0.05 in all 6 tests). However, these tests lacked power (n = 10) and spatial resolution.

At the finer resolution of bear management unit, we noted differences among BMUs (Table 1). BMU B (Fig. 1) had the highest proportion of complaints relating to safety (88.7%); BMU A had the lowest (65.2%). BMU B had the lowest proportion of the estimated population taken by hunters (15.2%); BMU D had the highest (21.4%). Across BMUs, neither the number of complaints in each category (Table 1: n = 40 BMU yrs, agriculture $r_s = -0.06$, P = 0.72; property $r_s = -0.06$, P = 0.71; or safety $r_s =$ 0.18, P = 0.26) nor the bear population size estimate changed significantly over time (n = 48 BMU yrs, r_s = 0.15, P = 0.33). In contrast, hunter take increased $(n = 48 \text{ BMU yrs}, r_s = 0.41, P = 0.0041)$. However, 2 BMUs showed changes in nuisance complaints and the bear population size estimate over time (BMU A: agriculture complaints decreased, $r_s = -0.74$, P =0.015; BMU C: take increased $r_s = 0.87$, P = 0.0002, property damage complaints increased $r_s = 0.76$, P = 0.011, and safety complaints increased $r_s = 0.92$, P = 0.0002).

At the scale of BMUs, the number of bears taken by hunters in year t was positively correlated with the number of complaints in year t + 1. Those correlations were significantly positive for agriculture, safety, and property complaints (n = 36 BMU yrs, $r_s = 0.38$, 0.39, 0.58, respectively, P < 0.016 for all tests). The correlations remained significant for safety and property in year t + 2 (n = 32 BMU yrs, r_s = 0.42 and 0.58 respectively, P < 0.007 in both cases) but not agriculture ($r_s = 0.27$, P = 0.09). We used those r_s values as H_{obs} in the boot-strap analyses.

Boot-strap. With 200 iterations, H_{exp} averaged 0.24, SD = 0.15 (range = -0.22–0.56). The minimum $H_{obs} = 0.27$ for agriculture in year t + 2 was higher than 74 values of H_{exp} (hence P = 0.37), but the maximum $H_{obs} = 0.58$ for property in year t + 2 (above) was not exceeded by any H_{exp} (hence P < 0.005). The other H_{obs} , ranging from 0.38–0.42, were not significant (P > 0.10 in every case). These results contradicted the prediction that hunter take would diminish nuisance complaints in subsequent years.

Sex and age of bears. Bears live-trapped after nuisance complaints were predominantly male (63.9%, n = 943, $\chi^2 = 72$, 1 df, P < 0.001, Cramer $\phi = 0.28$). Similarly, the majority of bears taken by hunters were males (54.7%, $\chi^2 = 200$, P < 0.001, Cramer $\phi = 0.10$), but a lower proportion than in the nuisance sample ($\chi^2 = 31$, P < 0.001, Cramer ϕ = 0.18). The WDNR recorded sex and hunting

Table	3.	Male	black	bears	(%)	taken	by	hunting
metho	d i	n Wise	consin,	USA (n = 2	3512).	-	_

	Hunting method						
Year	Dogs only	Bait only	Bait and dogs	Other			
1995	62.0%	54.4%	57.2%	50.0%			
1996	60.8%	56.5%	56.8%	65.0%			
1997	57.3%	55.6%	50.0%	52.6%			
1998	60.4%	54.3%	57.3%	50.0%			
1999	56.6%	50.6%	55.0%	70.0%			
2000	62.8%	49.8%	57.1%	68.2%			
2001	58.5%	52.7%	57.8%	60.9%			
2002	58.5%	51.5%	55.7%	40.0%			
2003	57.1%	53.5%	60.7%	64.3%			
Average	59.3%	53.2%	56.4%	57.9%			
SD	2.2%	2.3%	2.9%	10.2%			
n	4319	15046	3922	225			

method for 23,512 bears taken by hunters from 1995-2003 (Table 3). For the specified methods (excluding Other), proportions of male bears differed significantly in all pair-wise comparisons across years (Table 3: n = 9 yrs, dogs only versus bait only W = 22.5, P = 0.002; dogs only versus both bait and dogs W = 15.5, P = 0.02; and nearly so for bait only versus both bait and dogs W = 15.5, P = 0.037). This justified splitting the data by hunting method to test the prediction that hunters took bears of a similar age and sex as observed among bears livetrapped after nuisance complaints. Even the most male-biased sample of bears taken by hunters (using dogs only) had a significantly lower proportion of males (59.3%) than among bears live-trapped after nuisance complaints (63.9%; $\chi^2 = 14$, P < 0.001, Cramer $\phi = 0.20$, Table 3).

Of 864 non-cubs live-trapped after nuisance complaints, 554 (64.1%) were aged using cementum annuli (range 1–21 yrs, Table 4), and another 307 were aged imprecisely by size in the field (size-aged). The proportion in each tooth-age class did not differ

Table 4. Age (yr) of American black bears taken by hunters compared with bears live-trapped in Wisconsin, USA, 1995–2004.

	Live-trapped a	fter nuisances	Taken by hunters			
Age	Females, %	Males, %	Females, %	Males, %		
1 ^a	12.6	14.6	23.0	36.2		
2	15.7	32.3	24.8	27.7		
3	13.6	22.8	14.1	14.5		
4	14.1	9.8	8.2	7.4		
5	8.6	7.0	6.9	4.0		
>5	35.4	13.5	23.1	10.3		

^aExcluding cubs <1 yr old.

among years (W < 6, P > 0.30 for all pair-wise tests), so we pooled the data from 1995–2004. A higher proportion of yearlings occurred in the size-aged sample than the tooth-aged samples of both sexes ($\chi^2 > 103$, P < 0.0001 in both cases).

To assess trapper bias or error (such as smaller, older bears misclassified by size), we examined 263 bears aged by both methods (in which trappers were unaware of the age as estimated from cementum annuli). Among 17 size-aged 'yearlings', 2 females and 5 males were tooth-aged 1 year old (41% accuracy), whereas 6 females and 4 males were misclassified in the field (tooth-aged 2–6 yrs and 2 yrs, respectively). Hence size-aging produced an estimated 59% error rate for 'yearlings.' Among 246 size-aged 'adults,' 91 females and 147 males were >1 year by tooth-aging (96.7% accuracy), whereas 8 were yearlings by tooth-aging (1 female, 7 males). Hence, size-aging produced an estimated 3.3% error rate for 'adults.'

We used these error estimates to correct the yearling-to-adult ratio for the 307 size-aged bears. After correction, the ratios of yearlings-to-adults converged among tooth-aged and size-aged females $(\chi^2 = 0, P = 0.99)$, but not among males $(\chi^2 = 24, P)$ < 0.01, Cramer $\phi = 0.35$). Hence, we found still more male yearlings among the size-aged sample than expected from the tooth-aged sample. We concluded the tooth-aged bears were a biased sample of bears live-trapped after nuisance complaints. To correct our final age distribution, we added the bears aged by size as follows: we reclassified yearlings and adults using the error rates from above and randomly assigned ages to the remaining adults from 2 to >5 following the observed tooth-aged distribution.

Males live-trapped after nuisance complaints differed in age structure from females (Table 4: χ^2 = 162, 5 df, *P* < 0.0001, Cramer ϕ = 0.33). Using our corrected estimate for age, 71% of live-trapped males were 1–3 years old compared with 43% of nuisance females. Similarly, nuisance females >3 years old were twice as frequent as nuisance males of those age classes (Table 4).

Among 13,359 aged and sexed bears taken by hunters, age distributions did not differ among years (P > 0.20 for all pair-wise comparisons). Females differed in age structure from males (Table 4: $\chi^2 =$ 1,404, P < 0.0001, Cramer $\phi = 0.32$), with a greater proportion of older females than older males (30.9% of females >4 yr and 15.9% of males >4 yr), and a greater proportion of 1–2 year-old males (64.4%) than 1–2 year-old females (47.8%). Bears taken by hunters differed in age distribution from bears live-trapped after nuisance complaints (Table 4: females $\chi^2 = 1,256$, P < 0.001, Cramer $\phi = 0.31$; males, $\chi^2 = 2,819$, P < 0.001, Cramer $\phi = 0.46$).

Annually, 103.4 (SD = 68.0) ear-tagged bears were released into the population after being livetrapped after nuisance complaints. During 1995– 2004, hunters took an average of 35.6 (SD = 16.9) ear-tagged bears, which comprised 1.33% (SD = 0.7) of the total hunter take of 2666.4 (SD = 474.8) bears annually. The estimated annual number of eartagged bears was 192.3 (SD = 87.2), which constituted an estimated 1.26% (SD = 0.5) of the estimated 15,233.5 (SD = 581.4) bears in the population (Table 1). Hunters took slightly more ear-tagged bears than expected in 7 of 10 years, although this difference was not significant (W =-15.5, P = 0.065 comparing the relative rankings of positive and negative deviations each year).

Discussion

To assess the effectiveness of black bear hunting as a conflict-reduction strategy, we analyzed hunter take relative to 10 years of complaints about agricultural damages, property damages, and threats to human safety, as well as the ensuing management response. Bears were legally hunted in virtually all counties in Wisconsin, and live-trapped bears were often relocated to areas used by hunters during the annual 5-week bear-hunting season (Stowell and Willging 1992). Examined statewide and by bear management units, the annual number of complaints did not diminish 1-2 years after higher levels of hunter take. Indeed, property complaints (which did not include agricultural complaints) may have increased after years of higher hunter take, taking into account the corresponding changes in the estimated bear population size ($r_s = 0.58$ in the boot-strap analysis). This could mean in years of heavier hunting pressure, bears moved closer to residences to avoid hunters and thereby caused more damage to bird feeders, structures, or other property. However, property damage complaints were rare, and we found no evidence of variation among the more common categories of agricultural damage and nuisance complaints. Moreover, the increase in property damage complaints following years with higher hunter take might be due to Bear Management Unit C, which showed strong increases in both over time.

Interpreting the effectiveness of hunting and management on Wisconsin's black bears and their associated nuisance complaints is challenging in light of the recent evidence that the bear population size may have been underestimated by more than half for several years (MacFarland 2009). Indeed, there are a series of assumptions that underlie Wisconsin black bear management that deserve scientific scrutiny. First, it has been long assumed that bears livetrapped after nuisance complaints have some relationship to the nuisance. Moreover, approximately 10% of all nuisance complaints resulted in livetrapping, so many potential, 'nuisance' bears remained at large. Relocating live-trapped bears into public lands that are used for hunting assumes the bears will stay and be selected by hunters. Finally, it is widely assumed that hunters will reduce the bear population size or the number of likely nuisance bears. This may not hold if hunters simply take too few bears or bears rarely repeat their nuisance behavior in our study area. In the face of so many unverified assumptions, we urge a cautious interpretation of our preliminary results that hunting does not reduce future nuisance complaints.

Hunter selection for bears released after livetrapping around nuisance sites. Data on the age and sex of hunted bears indicated a different age-sex distribution than those implicated in threats to property or safety. Hunters took a lower proportion of males and younger bears than those live-trapped after nuisance complaints. Even the hunting method that took the highest proportion of male bears (dogs only) took a significantly lower proportion than found in our samples of bears live-trapped after nuisance complaints. Moreover, the most common method (bait) took the lowest proportion of males and the youngest bears of the methods examined. Although most bears implicated in agricultural damage could not be included in our age-sex analysis, the latter represented only one-sixth of all complaints.

The discrepancy between age and sex distributions of bears taken by hunters and bears live-trapped at nuisance sites could arise in several ways. First, it might be an artifact of measurement error or bias. The observed age–sex distribution of nuisance bears might be inaccurate if the adult male bears aged imprecisely and inaccurately by size were actually 1or 2-year old males. Our analyses suggest such errors were few (3.3%), especially compared to the countervailing errors we observed in classification of adult bears as yearlings based on size (59%). Moreover we found a pattern very similar to that reported for black bears in neighboring Minnesota (Garshelis 1989). There, males aged 1–3 years and females >3 years predominated in 'nuisance' samples. Weaver et al. (2004) also found that 'nuisance' black bears in Virginia tended to be older than 'nonnuisance' ones. Had hunters or the WDNR underreported older or larger females, we might have seen the observed discrepancy. Neither bias seems plausible; therefore, we conclude hunters took a different subset of the bear population than that live-trapped after nuisance complaints.

Hunters tended to take ear-tagged bears slightly out of proportion to their availability. Any underestimate of the bear population referenced above would increase this trend toward hunter selection of nuisance bears. The agency practice of releasing livetrapped bears into public lands within bear hunting units might increase their exposure to hunters, but we would also expect the homing ability of bears to reduce bears' exposure to hunters (Linnell et al. 1997). Finer spatial and temporal resolution of the fates of ear-tagged bears in the subsequent hunting season will be needed to illuminate hunter selection for ear-tagged bears.

Hunting to prevent conflicts. We also examined whether years with fewer nuisance complaints followed years of higher hunter take. We found no evidence of such a relationship. Rather, we found the expected, strong, positive relationship to the estimated bear population size, suggesting that hunter take and nuisance complaints both rise when the bear population increases. Related to this, bear food abundance might underlie all 3 variables. Several studies show that in years of poor wild food availability, bears were more vulnerable to hunters (Gilbert et al. 1978, Noyce and Garshelis 1997) and were more likely to engage in nuisance behavior (Jorgensen et al. 1978, Peine 2001). However, correlations to food availability can be equivocal (Garshelis 1989). Therefore, we recommend examining wild and anthropogenic food availability and quality at the scale of bear home ranges in relation to bear and hunter behavior.

We are left with a set of other plausible explanations that years with higher hunter take were not followed by years with lower nuisance complaints. First, hunters might have killed too few to detect an effect in the face of a steady increase in bear numbers and spatial extent, especially given that the number of bears appears to have been systematically underestimated for years (MacFarland 2009). Second, new bears or homing bears might have rapidly filled vacancies, and then triggered new nuisance complaints. This probably played some role but seems unlikely to explain the fact that older females were live-trapped after nuisance complaints, because older females have lower dispersal distances than males. However, the apparently greater involvement of males in nuisances suggests bear behavior is an important variable, as reported for other problem species (Sukumar 1995, Linnell et al. 1999). Male involvement may reflect risk-taking behavior, larger home ranges, and longer dispersal distances, all of which bring male black bears into more frequent contact with humans (Rogers 1987, McLean and Pelton 1990, Garshelis 1994, Clark et al. 2002). Third, perhaps too many potential 'nuisance' bears remained in place. For example. Horstman and Gunson (1982) estimated a maximum error rate of 70% in similar bear control operations in Alberta, Canada; their necropsy data suggest many captured bears were not the intended targets, with errors mounting as traps were left in place for longer periods (Horstman and Gunson 1982). In Wisconsin, fewer than 10% of nuisance complaints led to live-trapping. Furthermore, females with cubs may have been spared by hunters and then repeated their nuisance behavior, producing both male-biased distributions in the hunter take and a bias among females toward older individuals in the live-trapped sample, both patterns observed here. Fourth, trappers may have missed the bear that caused the nuisance. Perhaps male bears congregated to associate with a 'nuisance' female during the mating season and were live-trapped in her stead. Overlapping home ranges of bears could place many around trapping sites at different times. Bear biologists in WI report nuisance complaints can lead to the capture of multiple bears (B. Woodbury, WDNR, Madison, Wisconsin, USA, personal communication, 2006)-such overlap in individual ranges near agricultural property has been noted for Tremarctos ornatus also (Goldstein 1991, Zug 2009). Finally, the bears responsible for nuisance complaints might escape hunters, either by shifting range use during the hunting season or by leaving hunted areas after relocation (Linnell et al. 1997). Many animals-including bears-seem to be aware of hunter locations, seasons, or behavior (Bechet et al. 2003, Ruth et al. 2003, Diefenbach et al. 2005). Range shifts could result in the age-sex profiles we saw and have broader social consequences. For example young bears—especially young males—might be excluded from safer, unhunted habitat by dominant ones. Dominant bears might choose areas free of hunting, inadvertently exposing them to higher risk of live-trapping and relocation.

We urge continued study of the role of hunting on wildlife damage reduction. Different methods and locations for hunting and trapping remove wildlife of different ages and sexes. We found such differences for Wisconsin black bears. Hunters who used dogs without bait took bears of more similar ages to bears live-trapped after nuisance complaints than those using other methods. This echoes an earlier finding that hunting with dogs took older bears than hunting over bait (Kohlmann et al. 1999). Careful design of hunting regulations to maximize the elimination of probable problem animals might require focus on problem areas or on individual animal behavior. Yet this may conflict with the goal of broad public involvement in public hunts, a balancing act that calls for research into human dimensions.

Acknowledgments

We thank biologists from USDA–WS in Rhinelander, Wisconsin, and the WDNR who shared valuable data and expertise. We are grateful for the advice given by J. Cary, B. Koele, R. Rolley, D. Ruid, T. van Deelen, K. Warnke, R. Willging, and 2 anonymous reviewers. The Berryman Institute and the Zoological Society of Milwaukee provided funding.

Literature cited

- ALLEN, L.R., AND E.C. SPARKES. 2001. The effect of dingo control on sheep and beef cattle in Queensland. Journal of Applied Ecology 38:76–87.
- ANDREN, H., J.D.C. LINNELL, O. LIBERG, R. ANDERSEN, A. DANELL, J. KARLSSON, J. ODDEN, P.F. MOA, P. AHLQVIST, T. KVAM, R. FRANZEN, AND P. SEGERSTROM. 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation 131:23–32.
- BARTEL, R.A., AND M.W. BRUNSON. 2003. Effects of Utah's coyote bounty program on harvester behavior. Wildlie Society Bulletin 31:738–743.

- BECHET, A., J. GIROUX, G. GAUTHIER, J.D. NICHOLS, AND J.E. HINES. 2003. Spring hunting changes the regional movements of migrating greater snow geese. Journal of Applied Ecology 40:533–564.
- BECKMANN, J.P., AND J. BERGER. 2003. Using black bears to test ideal-free distribution models experimentally. Journal of Mammalogy 84:594–606.
- BERGER, J., B. STACEY-PETER, L. BELLIS, AND M.P. JOHNSON. 2001. A mammalian predator-prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11: 947–960.
- BRECK, S.W., C.L. WILLIAMS, J.P. BECKMANN, S.M. MATTHEWS, C.W. LACKEY, AND J.J. BEECHAM. 2008. Using genetic relatedness to investigate the development of conflict behavior in black bears. Journal of Mammalogy 89:428–434.
- BUNNEFELD, N., J.D.C. LINNELL, J. ODDEN, M.A.J. VAN DUIJN, AND R. ANDERSEN. 2006. Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: Effects of sex and reproductive status. Journal of Zoology 270:31–39.
- BURNHAM, K.P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–213 in J.D. Lebreton and P.M. North, editors. Marked individuals in the study of bird populations. Birkhauser Verlag, Basel, Switzerland.
- CLARK, J.E., F.T. VAN MANEN, AND M.R. PELTON. 2002. Correlates of success for on-site releases of nuisance black bears in Great Smokey Mountains National Park. Wildlife Society Bulletin 30:104–111.
- CONOVER, M.R. 2001. Effect of hunting and trapping on wildlife damage. Wildlife Society Bulletin 29:521–532.
- COSTELLO, C.M., K.H. INMAN, D.E. JONES, R.M. INMAN, B.C. THOMPSON, AND H.B. QUIGLEY. 2004. Reliability of the cementum annuli technique for estimating age of black bears in New Mexico. Wildlife Society Bulletin 32:169–176.
- DIEFENBACH, D.R., J.C. FINLEY, A.E. LULOFF, R. STED-MAN, C.B. SWOPE, H.C. ZINN, AND G.J. SAN JULIAN. 2005. Bear and deer hunter density and distribution on public land in Pennsylvania. Human Dimensions of Wildlife 10:201–212.
- ENGSTROM, P., R. WILLGING, AND D. RUID. 2006. Black bear damage and nuisance complaints 2006. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.
- FORBES, G., P. CHAMBERLAND, E. DAIGLE, AND W. BALLARD. 1994. The lack of problem bear issues in Fundy National Park. Pages 89–94 in G. Forbes and E. Daigle, editors. Black bear ecology and management issues for Atlantic Canadian National Parks. Parks Canada Ecosystem Science, New Brunswick, Canada.
- GARSHELIS, D. 1989. Nuisance bear activity and management in Minnesota. Pages 169–180 in M. Bromley,

editor. Bear-people conflicts. Proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

- GARSHELIS, D.L. 1994. Density-dependent population regulation of black bears. Pages 3–14 in M. Taylor, editor. International Conference on Bear Research and Management Monograph Series 3.
- GILBERT, J.R., W.S. KORDEK, J. COLLINS, AND R. CONLEY. 1978. Interpreting sex and age data from legal kills of bears. Proceedings Eastern Workshop on Black Bear Research and Management 4:253–263.
- GOLDSTEIN, I. 1991. Spectacled bear predation and feeding behavior on livestock in Venezuela. Studies on Neotropical Fauna and Environment 26:231–235.
- GOMPPER, M.E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of north-eastern North America by coyotes. Bioscience 52:185–190.
- HERFINDAL, I., J.D.C. LINNELL, P.F. MOA, J. ODDEN, L.B. AUSTMO, AND R. ANDERSEN. 2005. Does recreational hunting of lynx reduce depredation losses of domestic sheep? Journal of Wildlife Management 69:1034–1042.
- HERRERO, S., AND A. HIGGINS. 1999. Human injuries inflicted by bears in British Columbia: 1960–97. Ursus 11:209–218.
- HORSTMAN, L.P., AND J.R. GUNSON. 1982. Black bear predation on livestock in Alberta. Wildlife Society Bulletin 10:34–39.
- HUYGENS, O.C., F.T. VAN MANEN, D.A. MARTORELLO, H. HAYASHI, AND J. ISHIDA. 2004. Relationships between Asiatic black bear kills and depredation costs in Nagano Prefecture, Japan. Ursus 15:197–202.
- JOPE, K.M. 1983. Habituation of grizzly bears to people: A hypothesis. International Conference on Bear Research and Management 5:322–327.
- JORGENSEN, C.J., R.H. CONLEY, R.J. HAMILTON, AND O.T. SANDERS. 1978. Management of black bear depredation problems. Proceedings of the Eastern Workshop on Black Bear Management and Research 4:297–321.
- ———. 1983. Bear–sheep interactions, Targhee National Forest. International Conference on Bear Research and Management 5:191–200.
- KAPP, K. 2006. Socioecological correlates of human–black bear conflict in northern Wisconsin. Thesis, University of Wisconsin, Madison, Wisconsin, USA.
- KOELE, B. 2006. 2006 Wisconsin bear hunting regulations. Department of Natural Resources, Madison, Wisconsin, USA.
- KOHLMANN, S.G., R.L. GREEN, AND C.E. TRAINER. 1999. Effects of collection method on sex and age composition of black bear (*Ursus americanus*). Northwest Science 73:34–38.

- LINNELL, J.D.C., R. AANES, J.E. SWENSON, J. ODDEN, AND M.E. SMITH. 1997. Translocation of carnivores as a method for managing problem animals: A review. Biodiversity and Conservation 6:1245–1257.
 - —, J. ODDEN, M.E. SMITH, R. AANES, AND J.E. SWENSON. 1999. Large carnivores that kill livestock: Do problem individuals really exist? Wildlife Society Bulletin 27:698–705.
- , J.E. SWENSON, AND R. ANDERSEN. 2001. Predators and people: Conservation of large carnivores is possible at high human densities if management policy is favorable. Animal Conservation 4:345–349.
- LOVERIDGE, A.J., J.C. REYNOLDS, AND E.J. MILNER-GUL-LAND. 2007. Does sport hunting benefit conservation? Pages 224–241 in D.W. Macdonald and K. Service, editors. Key topics in conservation biology. Oxford University Press, Oxford, UK.
- MACFARLAND, D. 2009. Population estimation, habitat associations and range expansion of black bears in the upper Midwest. Dissertation, University of Wisconsin, Madison, Wisconsin, USA.
- MATTSON, D.J. 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management 8:33–56.
- McLEAN, P.K., AND M.R. PELTON. 1990. Some demographic comparisons of wild and panhandler bears in Smokey Mountains. International Conference on Bear Research and Management 8:105–112.
- NAUGHTON-TREVES, L., AND A. TREVES. 2005. Socioecological factors shaping local support for wildlife in Africa. Pages 253–277 in R. Woodroffe, S. Thirgood, and A. Rabinowitz, editors. People and wildlife, conflict or coexistence? Cambridge University Press, Cambridge, UK.
- NOYCE, K.V., AND D.L. GARSHELIS. 1997. Influence of natural food abundance on black bear harvests in Minnesota. Journal of Wildlife Management 61: 1067–1074.
- OBBARD, M.E., B.A. POND, AND E.J. HOWE. 1997. Appendix 10: Analysis of relationships among black bear nuisance activity, food availability, and harvest in Ontario. Wildlife Research and Development Section, Ministry of Natural Resources, Peterborough, Ontario, Canada, http://www.mnr.gov. on.ca/mnr/ebr/nbrc/appendix_10.pdf.
- Odden, J., J.D.C. LINNELL, P.F. MOA, I. HERFINDAL, T. KVAM, AND R. ANDERSEN. 2002. Lynx depredation on sheep in Norway. Journal of Wildlife Management 66:98–105.
- PEINE, J.D. 2001. Nuisance bears in communities: Strategies to reduce conflict. Human Dimensions of Wildlife 6:223–237.
- RAJPUROHIT, R.S., AND P.R. KRAUSMAN. 2000. Humansloth bear conflicts in Madhya Pradesh, India. Wildlife Society Bulletin 28:393–399.

- RIPPLE, W.J., AND R.L. BESCHTA. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? Bioscience 54:755–766.
- ROGERS, L. 1987. Effects of food supply and kinship on social behaviour, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 97.
- ROLLEY, R.E., A.M. ROTH, AND P.S. ENGSTROM. 2004. Black bear population analyses 2004. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.
- RUTH, T.K., D.W. SMITH, M.A. HAROLDSON, P.C. BUOTTE, C.C. SCHWARTZ, H.B. QUIGLEY, S. CHERRY, K.M. MURPHY, D. TYERS, AND K. FREY. 2003. Largecarnivore response to recreational big-game hunting along the Yellowstone National Park and Absaroka-Beartooth Wilderness. Wildlife Society Bulletin 31: 1150–1161.
- SAS INSTITUTE, INC. 2009. JMP 8. Cary, North Carolina, USA.
- SIDOROVICH, V., L. TIKHOMIROVA, AND B. JEDRZEJEWSKA. 2003. Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000. Wildlife Biology 9:103–111.
- SMITH, D.W., R.O. PETERSON, AND D.B. HOUSTON. 2003. Yellowstone after wolves. Bioscience 53:330–340.
- STOWELL, L.R., AND R.C. WILLGING. 1992. Bear damage to agriculture in Wisconsin. Proceedings of the Eastern Wildlife Damage Control Conference 5:96–104.
- SUKUMAR, R. 1995. Elephant raiders and rogues. Natural History 104:53-61.
- SUNDE, P., K. OVERSKAUG, AND T. KVAM. 1998. Culling of lynxes *Lynx lynx* related to livestock predation in a heterogeneous landscape. Wildlife Biology 4: 169–175.
- TREVES, A. 2001. Reproductive consequences of variation in the composition of howler monkey social groups. Behavioral Ecology and Sociobiology 50:61–71.
- ——, AND L. NAUGHTON-TREVES. 2005. Evaluating lethal control in the management of human–wildlife conflict. Pages 86–106 in R. Woodroffe, S. Thirgood, and A. Rabinowitz, editors. People and wildlife, conflict or coexistence? Cambridge University Press, Cambridge, UK.
- Journal of Applied Ecology 46:1350–1356.
- WEAVER, H.W., J.T. ANDERSON, J.W. EDWARDS, AND T.L. DOTSON. 2004. Physical and behavioral characteristics of nuisance and non-nuisance black bears in southern West Virginia. Thesis, West Virginia University, Morgantown, West Virginia, USA.
- WHITE, G.C., AND K.P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:120–138.

WISCONSIN DEPARTMENT OF NATURAL RESOURCES. 2009a. Black bear population and distribution. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

— 2009b. 2009 Wisconsin bear hunting regulations. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

- Woodroffe, R., S. Thirgood, and A. Rabinowitz, editors. 2005. People and wildlife, conflict or coexistence? Cambridge University Press, Cambridge, UK.
- Wydeven, A.P., A. Treves, B. Brost, and J.E. Wieden-HOEFT. 2004. Characteristics of wolf packs in Wiscon-

sin: Identification of traits influencing depredation. Pages 28–50 in N. Fascione, A. Delach, and M.E. Smith, editors. People and predators: From conflict to coexistence. Island Press, Washington, DC, USA.

Zug, R. 2009. Individual identification and habitat use of Andean bears on private lands in the Ecuadorian Andes. Thesis, University of Wisconsin, Madison, Wisconsin, USA.

Received: 1 April 2009 Accepted: 22 January 2010 Associate Editor: C. McLaughlin