Survival, cause-specific mortality, sex, and ages of American black bears in Washington state, USA

Gary M. Koehler[1], and D. John Pierce

Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501-1091, USA

Abstract: Wildlife managers often rely on data from hunter-harvested animals for monitoring structural and numerical changes of hunted animal populations, including American black bears (*Ursus americanus*). Some analyses of hunter-harvested animals assume that sex and age data from harvested animals accurately reflect the demographic structure of the population. We compared sex and age structure from black bears harvested by hunters to estimates of survival rates and causes of mortality for 136 radiomarked male and female black bears at 3 locations in Washington state. These areas reflect the vegetative and geographic variation within Washington and differ in amount of precipitation, vegetation conditions, behavioral ecology of bears, and hunter harvest. We estimated survival rates from marked bears for hunting and non-hunting seasons to determine whether these data may be represented in the hunter-harvest sample, and compared median age and survival rates for marked bears with life-table survival estimates for bears killed by hunters in each of the 3 regions during 1994–99. We compared survival rates from marked bears and from hunter-harvest data before and after a 1996 voter initiative that banned hunting bears with hounds and bait to determine whether changes in harvest regulations influenced survival of bears and was detectable in hunter-harvest data. Humans accounted for 98% of mortalities for study-marked bears, and legal hunter harvest and hunter-wounding loss accounted for 64% of documented mortalities. Survival rates calculated from marked males (0.73) and females (0.93) were similar to those from hunter-harvested males (0.76) and females (0.83). Median ages for bears from hunter-harvest data were greater than for study-marked bears. We lacked power to detect possible differences in survival rates between pre- and post-initiative periods among marked bears or hunter-harvest samples. We conclude that data from hunter-harvest reports may be adequate for management objectives; however, they do not represent all mortalities, with non-reported hunter harvest, wounding loss, and depredation control hunts likely accounting for additional mortalities.

Key words: American black bear, cause-specific mortality, survival, *Ursus americanus*, Washington

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Wildlife managers often rely on age and sex statistics from hunter-harvested animals to monitor the demographic structure and status of hunted populations (Caughley 1977). However, it is not known whether the age and sex of hunter-harvest samples accurately reflect age and sex of the population, and whether these data may serve as a barometer of population status. With hunting regulations coming under greater public scrutiny, knowledge of survival rates and cause of mortality is prerequisite for management of hunted wildlife populations (Bailey 1984, White and Garrott 1990).

In Washington state, age and sex ratios from hunter-harvested samples are used to monitor the status of black bear populations (Beecham and Rohlman 1994, Washington Department of Fish and Wildlife [WDFW] 2003). Black bears are an important game species, with an estimated 844–1,802 bears killed by hunters annually during the 1990s (Washington Department of Fish and Wildlife, 2000, 2000 Game Status and Trend Report, Olympia, Washington, USA). The extent that hunter-harvest data adequately reflects the age and sex of black bear populations is unknown, as is the ability of statewide hunter harvest data to track the status of bear populations in regions where habitat conditions and hunter access differ and may influence bear population structure and harvest vulnerability. Further, regional

[1]koehlgmk@dfw.wa.gov

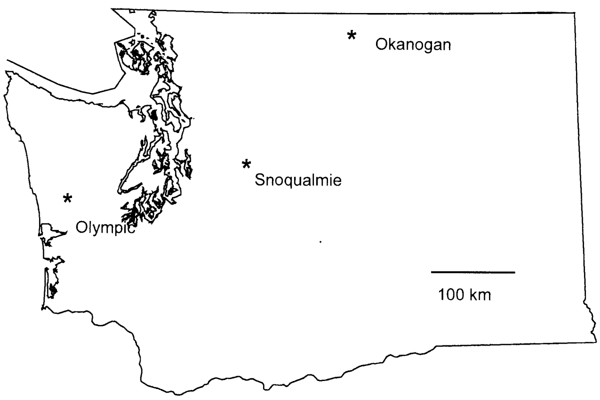

Fig. 1. Three study areas in Washington state used to compare population demographics from a radiomarked sample of black bears with demographics from hunter-harvest data, 1994–99.

differences in precipitation influence vegetative conditions, which influence black bear forage strategies and home range requirements (Koehler and Pierce 2003). Using harvest data to track population parameters could result in misguided population-monitoring efforts.

It is also not known what effect changes in hunting regulations may have on the structure of bear populations and whether harvest data will reflect those changes. In 1996, Initiative 655 prohibited the use of hounds and bait for hunting bears. Such hunter regulation changes may result in differences in age and sex of animals harvested.

In addition, harvest statistics may not document all sources of mortality or all sources of human-caused mortality. For example, black bears are considered a problem species on commercial forestlands in Washington. During spring and early summer when forage is limited, some bears peel bark off trees to feed on sapwood, resulting in death or damage to trees and an estimated $US 5 million during the 1990s in lost revenue in timber sales annually (Poelker and Hartwell 1973, Stewart et al. 1999, Ziegltrum and Nolte 2001, Collins et al. 2002). Non-lethal bear control methods to minimize damage on commercial forest lands include using supplemental feeders to dispense high-carbohydrate pellets as an alternative food source (Ziegltrum and Nolte 2001). In addition, landowners are permitted to protect their property by using snares or trained trail-hounds to capture and kill offending or suspect bears where damage is demonstrated. It is not known if all mortalities from such depredation control hunts are reported to WDFW or how such sources of mortality may influence the structure of regional populations of bears (Collins et al. 2002).

We tested whether (1) hunter-harvest data accurately represent the demographic structure of black bear populations in Washington, and (2) these data are sensitive to changes in hunting regulations, problem bear removal, and regional differences in black bear behavior. We compared hunter-harvest data to estimates of survival rates and documented cause-specific mortalities for radiomarked black bears at 3 study areas in Washington, 1994–99. Our objectives were to compare survival of radiomarked bears and survival as estimated from hunter-harvest data to assess whether (1) harvest data is sensitive to regional differences among bear populations, and (2) changes in hunting regulations influence harvest statistics.

Study areas

Three study sites, located approximately 150 km apart (Fig. 1), were selected to represent vegetative and geographic diversity, differences in vehicle access, and hunter harvests in the state (Koehler and Pierce 2003). The 3,100-km^2 Okanogan study area, east of the Cascade Mountains (48°N 120°W), was managed by the US Forest Service (USFS) and had limited or no road access. Less than 6% of this study area was privately owned ranches and residences. Elevations ranged from 535 to 2,763 m, and mean annual precipitation was 52 cm at 535 m elevation. Forests were dominated by Douglas-fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*).

The Snoqualmie study area, west of the Cascade Mountains (47°N 121°W), was 1,500 km^2. Elevations ranged from 134 to 1,826 m and annual precipitation was 200 cm at 134 m elevation. This study area was managed primarily (70%) as a private, commercial tree plantation; the remainder was managed for multiple-use or wilderness by the USFS. Douglas-fir, western hemlock (*Tsuga heterophylla*) and silver fir (*Abies amabalis*) were the dominant tree species, with trees occurring primarily in younger age classes (<40 years old) on intensively managed private forestlands. Private lands within the area had high road density (>1 km/km^2), but permits and gates limited public access.

The Olympic study area on the Pacific coast (47°N 123°W) encompassed 1,100 km^2 and included lands managed for multiple-use by the USFS (37%) and lands managed as commercial tree plantations (63%). Elevations ranged from 60 to 2,370 m, and mean annual precipitation was 380 cm at 60 m elevation. Douglas-fir, western hemlock, and silver fir were the dominant tree species. Road density and public access was similar to the Snoqualmie study area.

Methods

Captures and radiotelemetry

We captured bears in foot-hold snares in areas with road or trail access and darted bears from a helicopter in remote areas. Bears were anesthetized with tiletamine HCl and zolazepam HCl (Telazol™, Fort Dodge Laboratories, Inc. Fort Dodge, Iowa, USA) administered by jab-stick or dart gun in dosages of 6.4 mg Telazol™/kg of body mass (Koehler et al. 2001). We determined sex of the bears; the animals were then weighed, measured, ear tagged, and given lip tattoos. We extracted the first upper premolar for age estimation via cementum annuli (Stoneberg and Jonkel 1966). We marked bears with collar-transmitters fitted with canvas spacers (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA; Lotek Engineering Inc., Newmarket, Ontario, Canada) or surgically implanted intraperitoneal transmitters (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA; Koehler et al. 2001). Transmitters were equipped with mortality sensors that changed signals after 6–8 hours of inactivity.

We conducted aerial telemetry flights 1–2 times each week from 1 April (den emergence) to 15 November (den entrance) and monthly during hibernation. We plotted locations of radiomarked bears on 1:24,000 US Geological Survey topographic maps and recorded universal transverse Mercator (UTM) coordinates. We documented mortalities by investigating locations <1 week after transmitter signals indicated the bear was stationary or when we detected no changes in locations during 2–3 consecutive telemetry-flights during non-denning periods.

Survival, mortality, and analysis

We classified mortalities of radiomarked bears as natural (non-human related), legal hunter harvest, poaching (illegal kills), hunter-wounded loss, depredation control, accident, or unknown. Hunter-wounded mortalities occurred when a bullet or arrow wound was evident in the carcass or when carcasses were located near known hunter positions. We documented mortalities as depredation control for bears reported killed during April–June depredation-hunts on private forestlands. Mortalities identified as accidents were from known collisions with a vehicle. Three bears died as a result of study capture efforts and were not included in our survival estimates.

We compared survival rates among study areas because of differences in land management objectives, degree of road access, vegetation types, precipitation, geography, and behavior of bears (Koehler and Pierce 2003). Because we captured few bears >8 years old in all study areas, we compared survival rates among study areas only for male and female bears ≤ 8 years old. If statistical differences were not detected among these comparisons, we pooled data among study areas to calculate survival estimates for all males and females captured and marked during this study and compared these to estimates of survival rates from hunter-harvest data (see below).

We compared survival estimates for all study-marked bears between annual hunting and non-hunting seasons for periods when hunting with hounds and bait was permitted (pre-voter initiative, 1994–96) and when these hunting methods were illegal (post-voter initiative, 1997–99). In the Okanogan study area during the pre-initiative period, hunting seasons occurred from the first week in September until 31 October. Hunting seasons were increased post-initiative in the Okanogan by 4–5 weeks from 1 August through the first week in November. For the Snoqualmie and Olympic study areas, pre-initiative hunting season was from 1 August to the end of October; post-initiative hunting season extended through the second week of November. During both periods, hunters were required to report sex and submit a premolar within 10 days of killing a bear. However, hunters were not required to submit carcasses for inspection by Washington Department of Fish and Wildlife officials. Hunters were requested by WDFW not to kill female bears accompanied with cubs.

We used the Kaplan-Meier estimator to estimate survival rates for study-marked bears. Because bears were not radiomarked simultaneously, we treated the radiotracked sample with a staggered-entry design (Pollock et al. 1989). We treated bears that were recaptured as new entries on the day of recapture. We entered survival status of bears into the Kaplan-Meier model at weekly intervals (McLellan et al. 1999). We compared survival rates at weekly intervals because the length of hunting season increased ≥ 1 week during the post-initiative period and differed between study areas by ≥ 1 week. Within the Kaplan-Meier analysis, we censored bears the week that collars dropped or malfunctioned, or when bears dispersed beyond telemetry detection (Sorensen and Powell 1998). We pooled survival histories for all bears for each year within each study area and compared survival estimates between

Table 1. Mean annual survival rates *S* and standard errors for 136 black bears captured and marked with radiotransmitters for study areas in Washington, 1994–99. Survival rates were calculated by the Kaplan-Meier staggered-entry approach with status of individuals entered into the model at weekly intervals.

Study area (years)	Sex	*n*	*S*	SE
All study areas	Males	89	0.73	0.04
	Females	47	0.93	0.01
Okanogan (1994–98)	Males	31	0.77	0.01
	Females	11	0.95	0.03
Snoqualmie (1994–98)	Males	39	0.69	0.02
	Females	26	0.93	0.04
Olympic (1997–99)	Males	19	0.73	0.13
	Females	10	0.92	0.01

years and study areas. We tested for differences in survival functions and survival rates among study areas, years, hunting and non-hunting seasons, pre- and post-initiative, and sex via the log-rank test (Pollock et al. 1989, Kasworm and Thier 1994). We used 1-way ANOVA (analysis of variance) to examine differences for square roots of the arcsine-transformed weekly survival rates.

To examine whether censoring may have resulted from non-reporting of hunter harvests, we used a *t*-test of square root arcsine-transformed data (Zar 1984) to compare censoring rates among males and females between hunting and non-hunting periods. To assess whether some censored bears may have been killed and not reported, we compared weekly censoring rates for bears during hunting and non-hunting seasons.

Estimates of survival rates and sex ratios from hunter harvest data

We obtained information on sex and age of bears harvested by hunters during 1988–99 from teeth taken from bears killed by hunters (Washington Department of Fish and Wildlife 1996). We determined age class of these bears from tooth cementum analysis (Stoneberg and Jonkel 1966). Total number of bears killed was determined from mandatory report cards and hunter questionnaire. The normalized harvest (adjusted for hunter effort represented by bears killed per days hunted) did not show a significant change in the bear population estimates during this period (D.J. Pierce, unpublished data). Thus we assumed no population growth during the time represented by the harvest data and assumed that survival rates for each age class were constant among years.

We used age-class distribution from bears killed by hunters to estimate life table survival rates (Caughley 1977) according to sex and for areas west and east of the Cascade Mountains. Age distribution data from harvest records showed $\leq$1.5-year-old bears were underrepresented in the harvest (number of bears in the sample for these age classes were $<$2.5-year-old bears). Therefore, we assumed harvested bears were randomly collected only for animals $>$1.5 years old (Caughley and Sinclair 1994). As a result, we deleted data for bears $<$2.5-years old rather than estimate numbers in that age class in the survival analysis (Caughley 1977). We used a Cox proportional hazard model (S-Plus 2000 Release 2, Insightful Corp., Seattle Washington, USA) to examine covariate effects of sex and area on observed age distributions for bears killed by hunters.

We generated age-specific life table cumulative survival curves for bears reported killed by hunters. We estimated the sex ratio for the bear population from which the harvest sample came by using the ratio of the number of males to females in the sample by summing across all age classes using hypothetical male and female cohorts using these survival curves. We report annual survival rates as means with SE.

We derived an independent estimate for sex ratio of the marked population by using the sex bias for study-marked bears killed by hunters:

$$[1]\ \text{bias} = \text{males:female}_{\text{hunter harvest of study sample}} / \text{males:females}_{\text{study sample}},$$

$$[2]\ \text{male:females}_{\text{population}} = \text{males:females}_{\text{hunter harvest}} / \text{hunter bias}$$

Results

Median age and sex specific annual survival

We captured and monitored survival histories for 31 males and 11 females on the Okanogan, 39 males and 26 females on the Snoqualmie, and 19 males and 10 females on the Olympic study areas (Table 1). We collected pre-molars and estimated ages for 9 males and 5 females on the Okanogan, 24 males and 19 females the Snoqualmie, and 14 males and 6 females on the Olympic study areas. For study-marked bears, the median age was 4 years (range 1–18 years) for males and 7 years (3–13 years) for females on the Okanogan, 3 years (1–8 years) for males and 4 years (1–17 years) for females on the Snoqualmie, and 3 years (1–13 years) for males and 3 years (1–13 years) for females on the Olympic study area. For bears $\leq$8 years old, annual survival rates (F = 13.62; 1, 14 df; P < 0.01) and survival functions ($\chi^2 = 8.04$, 1 df, $P < 0.05$) differed for males and females as did survival rates ($F = 22.86$; 1 33 df; $P < 0.01$) and survival functions ($\chi^2 = 11.82$, 1 df, $P < 0.01$) for all 136 bears captured and marked during this study.

Hunting and non-hunting season and pre- and post-initiative survival

We calculated mean annual survival rates of 0.73 (SE = 0.04) for 89 males and 0.93 (SE = 0.01) for 47 females (Table 1). We tested for effects among study area, sex, hunting versus non-hunting season, and pre- and post-initiative on weekly survival rates for all study-marked bears (Table 2) and observed no difference among study areas ($F = 0.38$; 2, 1210 df; $P = 0.69$) or among pre- and post-initiative periods ($F = 2.28$; 1, 1210 df; $P = 0.13$). Male survival was lower than that for females ($F = 21.42$; 1, 1210 df; $P < 0.01$), and survival rates for all bears were lower during hunting than non-hunting periods ($F = 33.99$; 1, 1210 df; $P < 0.01$). We observed differences in survival functions for males ($\chi^2 = 16.22$, 1 df, $P < 0.05$) but not for females ($\chi^2 = 2.14$, 1 df, $P > 0.10$) between hunting seasons and non-hunting seasons in the 3 study areas.

Cause-specific mortality

We documented mortalities for 61 bears (Table 3). Of these, 34 bears were killed during hunting seasons, 5 died from hunter-wounding losses, one was poached, 15 were killed during spring depredation control hunts, 2 died from vehicle collisions, 3 adults died during capture procedures (1 in a foot-hold snare and 2 during helicopter captures), and 1 died of unknown causes. We were unable to determine the fate of 58 bears for which we lost transmitter signals due to assumed transmitter malfunction or the marked bear dispersing beyond the study area (Sorensen and Powell 1998) and these were coded as censored in the Kaplan-Meier analysis.

Of the 34 bears killed during hunting seasons, hunters reported killing 28. Six bears, known to have been killed by hunters, were not reported. The estimated reporting rate of 82% (28 reported of 34 bears killed) likely overestimates reporting rate for hunter-killed bears because some bears recorded as censored may have been hunter-killed and not reported. We detected differences ($t = -3.61$, 608 df, $P < 0.01$) for 19 males censored during hunting seasons (0.014, SE = 0.004/week) compared to 13 males censored (0.003, SE = 0.001/week) during non-hunting seasons. In contrast, censoring rates for females during hunting seasons (0.005, SE = 0.002/week, $n = 7$ bears) were similar ($t = 0.41$, 604 df, $P = 0.69$) to non-hunting periods (0.003, SE = 0.001/week, $n = 9$). This suggests that some of the 4.7-fold increase in censoring rates for males during hunting seasons may be additional hunter kills.

The 15 bears killed during April–July depredation control hunts on the Snoqualmie study area accounted for 50% of the documented human-caused mortality there. For all study areas, females composed 22.8% of bears killed ($n = 57$) by humans (excluding 3 capture-related mortalities).

Table 2. Mean weekly estimates of survival *S* (SE) for black bears in 3 study areas in Washington during pre- and post-initiative hunting and non-hunting seasons from 1994–99. Pre-initiative survival rates are calculated for radiomarked bears in the Okanogan and Snoqualmie study areas and during the post-initiative period in the Okanogan, Snoqualmie, and Olympic study areas. The initiative banned the use of trail hounds and bait to hunt bears after 1996.

Study area	Initiative and season	Males			Females		
		n	*S*	SE	*n*	*S*	SE
All bears		89	0.981	0.003	47	0.997	0.001
	non-hunting		0.997	0.001		0.999	0.001
	pre-initiative hunting	66	0.976	0.006	37	0.995	0.003
	non-hunting		0.998	0.001		0.999	0.001
	post-initiative hunting	22	0.986	0.003	26	0.999	0.001
	non-hunting		0.996	0.001		0.999	0.001
Okanogan	all years hunting	31	0.981	0.005	11	0.994	0.004
	non-hunting		0.999	0.001		1.0	0.0
	pre-initiative hunting	27	0.969	0.008	11	0.987	0.008
	non-hunting		0.999	0.001		1.0	0.0
	post-initiative hunting	12	0.988	0.007	8	1.0	0.0
	non-hunting		0.998	0.002		1.0	0.0
Snoqualmie	all years hunting	39	0.986	0.006	26	0.999	0.001
	non-hunting		0.994	0.002		0.998	0.001
	pre-initiative hunting	39	0.981	0.009	26	0.998	0.002
	non-hunting		0.996	0.002		0.997	0.002
	post-initiative hunting	10	0.996	0.004	18	1.0	0.0
	non-hunting		0.991	0.004		0.999	0.001
Olympic	post-initiative hunting	19	0.982	0.006	10	0.996	0.003
	non-hunting		0.999	0.001		0.998	0.002

Table 3. Cause of mortalities for 89 male and 47 female radiomarked black bears in 3 study areas in Washington, 1994–99.

	Okanogan		Snoqualmie		Olympic		
Cause of death	male	female	male	female	male	female	Total (%)
Unknown	0	0	1	0	0	0	1 (1.6)
Human-caused							
hunter kill	12	2	10	2	7	1	34 (54.8)
depredation	0	0	11	4	0	0	15 (24.2)
accident	2	0	0	0	0	0	2 (3.2)
poaching	0	0	0	0	0	1	1 (1.6)
wounding	0	0	3	0	2	0	5 (8.0)
study related	0	1	0	2	0	0	3 (4.8)
All deaths	14	3	25	8	9	2	61 (100)
Total bears	31	11	39	26	19	10	136

Relation of radiomarked bear mortalities to regional hunter harvest

We estimated annual survival of 0.76 for males and 0.83 for females from hunter-harvest data from life table age-structures (assumed to be stationary). Survival rates of males and females differed (Fig. 2; likelihood ratio test = 15.4, 1 df, $P = 0.001$, $n = 774$). Mean age was 6.4 years (SE = 0.2) for males and 7.8 (SE = 0.3) for females. We did not detect different survival rates among regions of the state (likelihood ratio test = 0.02, 1 df, $P = 0.89$, $n = 774$), nor could we state at $\alpha = 0.05$ that survival during pre-initiative and post-initiative periods differed (likelihood ratio test = 3.61, 1 df, $P = 0.06$, $n = 774$). Males outnumbered females in both our study and hunter-harvest data (Table 4). The average annual statewide sex ratios for 4,915 hunter-killed male black bears and 2,438 hunter killed female black bears during 1994–99 was 2.0 males:female. This ratio compared closely with the spring depredation hunt ($n = 856$) and captured study animals ($n = 136$ bears), which had a sex ratio of 1.9 males:females during the same period. The sex ratio for study-marked bears killed by hunters ($n = 34$) was 5.8 males:female; marked bears killed in depredation control hunts ($n = 15$) were 2.8 males:female.

The sex ratio of the population from which the harvest sample came derived from survival curve estimates of hunter harvest data (Fig. 2), was 0.73 males:females. The sex ratio for the population from which the study-marked population came was derived from the bias for the sexes of marked bears killed by hunters:

$$\text{bias} = 5.8 \text{ males:female}_{\text{hunter harvest study bears}} / 1.9 \text{ males:females}_{\text{study sample bears}} = 3.1 \text{ males/female.}$$

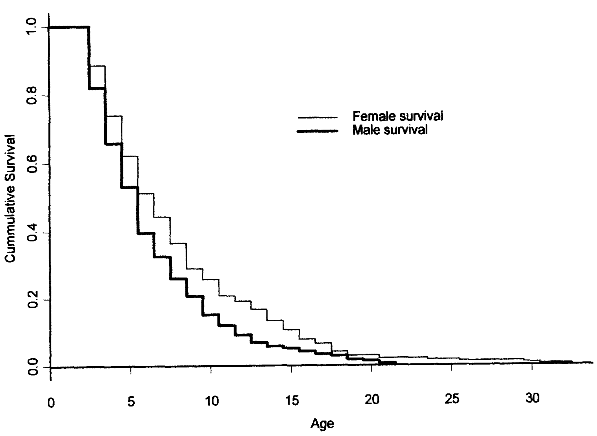

Fig. 2. Male and female black bear life-table cumulative survival curves, Washington State. Based on tooth-age data from hunter-killed bears ($n = 774$), 1988–99.

Table 4. Numbers and sex of black bears harvested statewide during general hunting season and spring depredation hunts (Washington Forest Protection Association, Olympia, Washington, USA, unpublished data) in Washington 1994–99. Data was obtained from bear transport tag sales, hunter questionnaires, and tag returns.

	General hunting season				Depredation hunts			
Year	Males	Females	M:F	Total[a]	Males	Females	M:F	Total[a]
1994	654	419	1.6:1	1,073	19	5	3.8:1	42
1995	850	368	2.3:1	1,218	17	11	1.6:1	56
1996	951	359	2.7:1	1,310	29	22	1.3:1	84
1997	546	298	1.8:1	844	68	36	1.9:1	109
1998	1,157	645	1.8:1	1,802	33	18	1.8:1	137
1999	757	349	2.2:1	1,106	97	46	2.1:1	165
Total	4,915	2,438	2.0:1	7,353	263	138	1.9:1	856

[a]Total includes bears for which sex was not reported.

This estimated the ratio of males to females in the population from which the study-marked sample came:

$$\text{male:female}_{\text{population}} = 2.0 \text{ males:female}_{\text{hunter harvest}} / 3.1 \text{ males:female bias} = 0.65 \text{ males:female}.$$

These independent estimates of sex ratios of the population from which the harvest and study sample came suggests the sex ratio from hunter harvest data is substantially skewed toward males and is likely significantly less than 1:1 in the population.

Discussion

Observations from research findings presume sex ratios of black bear populations to be equal (Pelton 1982, Beecham 1983, Kolenosky and Strathearn 1987, Garshelis 1990); these assumptions are frequently incorporated into management guidelines for black bears. On the other hand, Poelker and Hartwell (1973) speculated that bear populations might be biased toward males as evidenced from the preponderance of males in hunter-harvests.

In contrast to these assumptions, Bunnell and Tait (1980) argued that hunter harvests showing a bias toward males likely reflects an actual population where females predominate, an assertion consistent with our calculations of 0.65 males:female for Washington. For large contiguous habitats where juvenile males migrate between areas (Beecham 1983, Rogers 1987, Schwartz and Franzmann 1992), a more balanced sex ratio may be expected. Among heavily hunted small or isolated populations where males comprise the majority of the harvest, sex ratios may favor females (Beecham 1983) and may be representative of bear populations in Washington.

The increased vulnerability of male black bears to hunter-harvest mortality at large spatial scales is demonstrated in their significantly higher mortality rates throughout Washington. With the exceptions of findings from North Carolina where Sorensen and Powell (1998) did not detect differences in survival rates between males and females, research elsewhere has demonstrated significantly higher mortality rates for male black bears (Hellgren and Vaughan 1989, Beck 1991, Schwartz and Franzmann 1992, Kasworm and Thier 1994, Beringer et al. 1998).

The observed bias toward males from both study-marked and from hunter-harvest samples during 1994–99 in Washington and for other studies of black bears (Poelker and Hartwell 1973, LeCount 1982, Pelton 1982, Kolenosky 1986, Hellgren and Vaughan 1989, Kane and Litvaitis 1992) more likely reflects bear behavior and ecology than hunter preference for killing male bears. Although hunters were requested not to kill females accompanied with cubs, we believe this did not result in the sex ratios observed in the hunter-harvest because we documented similarly disparate sex ratios for study-marked bears. This bias toward males for study and hunter-harvested bears existed despite evidence that the population had a preponderance of females, as indicated by higher survival rates for females and estimated sex ratios of 0.65 male per female.

The bias for males in the harvest sample was likely not a result of hunters selecting for males because of their larger size and trophy value. Our data indicate that males were not selected based on their larger mass. The median age of 4.5 years for males killed by hunters and the smaller mass of 64.9 kg ($SE = 4.0$) for $\leq$4.5 year-old males and 119.8 kg ($SE = 4.2$) for males $>$ 4.5 years of age ($t = -8.9$, 83 df, $P < 0.01$) suggests bears were killed opportunistically and hunters did not seek large trophy males. A more plausible explanation for the bias is explained by male social behavior, which presents greater opportunities for males to be captured or harvested because of their larger home ranges, greater distances traveled, and more aggressive behavior (LeCount 1982, Pelton 1982, Hellgren and Vaughan 1989, Koehler and Pierce 2003).

Survival rates for study-marked males (0.73) and females (0.93) were similar to those for males (0.76) and females (0.83) harvested by hunters. Differences in male:female ratios between study-marked and hunter-harvest data may have resulted from unstable age distributions (contrary to our assumptions) or imprecise estimates of sex ratios and survival rates from harvest data. However, behavior differences for sexes and characteristics of study areas may also help explain why survival rates from study-marked and hunter-harvests samples differed. We captured most bears in areas where road access on private lands was limited or restricted by access permits and gates. The different survival rates for study marked bears suggests that access may affect survival. Differences in survival rates for males and females may have been due to females having smaller home ranges than males (Koehler and Pierce 2003) and therefore being less vulnerable to hunters than males (Bunnell and Tait 1980, Kolenosky 1986). As well, males may be more likely to disperse from protected areas (Kolenosky 1986, Hellgren and Vaughan 1989, Beck 1991, Beringer et al. 1998). Powell et al. (1996), on the other hand, found females to have lower survival rates than males because of poaching. They reasoned that small home ranges of females made them easier to locate and hence were more vulnerable to poaching.

Our observations of the increased probability for captures of males violates assumptions of equal capture probabilities for males and females and would bias population and survival estimates where data sets are pooled among sexes (Sorensen and Powell 1998). The imbalance in sex ratios among harvest samples may also misrepresent black bear population characteristics and demographics to management.

Kane and Litvaitis (1992) observed differences in age distributions and sex ratios for study and hunter-harvested bears in New Hampshire, and they cautioned against using a single method to assess bear population characteristics. In contrast, we observed similar sex ratios for hunter-harvested and study-marked bears and similar median ages of bears from hunter-harvest and study samples. These similarities for study and hunter harvest samples during our study may have resulted from larger samples and studies being conducted in different regions or similar biases among sampling methods. We assumed, from hunter-harvest data, that the status and structure of bear populations in Washington remained stable during the period of this investigation, which may be incorrect and may result in misguided management. However, estimates of status and structure of the population from study-marked bears and hunter-harvest data shows similar trends. Because telemetry studies are costly, managing bear populations based on hunter-harvest data may be adequate for monitoring the status of hunted populations.

Hunter-harvest statistics, however, do not accurately assess total mortality, nor do they accurately assess all hunter related mortality. Legal hunter-harvest and hunter-wounding loss accounted for 64%, poaching 1.6%, and depredation control 25% (Table 3) of documented non-study related mortalities. Hunter harvest has been shown to be a dominant mortality factor for bears (Bunnell and Tait 1980, LeCount 1982, Kolenosky 1986, Hellgren and Vaughan 1989, Kasworm and Thier 1994). Results from our study show that annual survival rates were lower for males and females during hunting seasons than during non-hunting periods. In addition, the 5 wounding losses accounting for 25% of hunter-caused mortalities in the Olympic and Snoqualmie study areas suggests that hunter-related mortalities may be greater than reported from hunter-harvest statistics. The dense understory vegetation in the Olympic and Snoqualmie study areas made locating dead or wounded bears difficult. Some hunters whom we interviewed indicated they spent >1 hour searching for a bear they shot.

Our estimates of reporting rates of 82% for hunter-harvested marked bears during this study likely overestimates reporting rates because some bears considered censored during hunting seasons were likely unreported hunter kills. Whereas censoring rates were similar for females during hunting and non-hunting periods, censoring rates for males were 4.7 times greater during hunting seasons than during non-hunting seasons. If we assume similar proportions of males and females were censored during hunting and non-hunting periods, then 9 of the 19 males censored during hunting seasons may have been killed and not reported, for a reporting rate of 65%. This is similar to the 62% hunter-reporting rate for telemetry-marked black bears in Montana (Kasworm and Thier 1994) and similar to the 66% survival rate for management problem bears in Alberta's Banff National Park (Hebblewhite et al. 2003). However, considering that hunter-harvest data suggest 2.0 males killed for each female, the number of censored males killed and not reported may have been higher, and the reporting rate therefore lower than 65%. This low reporting rate existed despite ear-tags on study-marked bears promising a reward for the return of the tag to WDFW. It also was mandatory that hunters report harvested bears $\leq$10 days after harvest. Reporting regulations are difficult to enforce.

Depredation control was a major mortality factor in the Snoqualmie study area where control activities were conducted on private forest plantations during April–July, when some bears feed on the sapwood of trees. The 15 bears killed in April–July depredation control hunts accounted for 50% of human-caused mortalities there. It is not known what effect depredation hunts have on black bear populations in Washington because not all bears killed during depredation hunts were reported.

We did not detect a change in weekly survival rates for study-marked bears between pre- and post-initiative periods. Although survival estimates were calculated from small numbers of bears, these observations agree with hunter-harvest data showing similar numbers of bears harvested during pre- and post-initiative periods. For the 3 years prior to passage of the initiative, approximately 1,200 bears were harvested annually; for the 3 years following, 1,250 bears were harvested annually. Although hunters were no longer permitted to hunt with hounds or bait, they were given additional hunting incentives, such as longer hunting seasons, reduced cost bear tags (from US$18.00 to US$10.00), an increased bag limit of 2 bears in western Washington, and options for hunters to purchase bear tags as part of a big game hunting license package with elk (*Cervus elaphus*), deer (*Odocoileus* spp.), and cougar (*Felis concolor*). As a result of these changes, bear tag sales increased from 11,530 to 12,868 during 1994 to 1996 to 20,891 in 1998 and 54,056 in 1999 (Washington Department of Fish and Wildlife, 2000, 2000 Game Status and Trend Report, Olympia, Washington). This increase in number of hunters who purchased bear tags likely did not represent a similar increase in hunting effort because many hunters may have intended to kill a bear only if an opportunity arose while hunting for other species.

During this study humans caused 98% of bear mortalities, of which hunting accounted for 56% of mortalities. The close agreement for bear population statistics obtained from study-marked bears and hunter-harvest suggests that hunter-harvest data would be less costly and may provide data adequate for statewide management goals. However, hunter-harvest data may not be adequate for monitoring population trends, particularly for local populations within game management units. This may be of concern where population segments may be in jeopardy, as in areas with a high density of roads because a bear there may be vulnerable to excessive hunter-harvest (Kasworm and Thier 1994) or in protected areas where a bear may be vulnerable to mortality due to management of problem bears (Hebblewhite et al. 2003). It is unknown, too, what effect depredation control has on local populations of black bears in Washington. Also, the low (<62%) reporting rate for bears killed by hunters may not provide harvest data adequate to manage local populations.

To improve harvest data, the Washington Department of Fish and Wildlife implemented mandatory hunter reporting in 2000 that required hunters to report their success or forfeit future opportunities to hunt bears. In addition to increased hunter reporting rates, there is a need for better reporting of bears killed during depredation and control activities.

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