DIFFERENTIAL VULNERABILITY OF BLACK BEARS TO TRAP AND CAMERA SAMPLING AND RESULTING BIASES IN MARK–RECAPTURE ESTIMATES

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Abstract: The accuracy of population estimates derived from mark–recapture sampling will be compromised when marked animals are more or less likely to be recaptured than unmarked animals. We used a "test" population of radiocollared black bears (*Ursus americanus*) to identify the sources and extent of sampling biases in trapping, camera-trapping, and hunter harvest. We investigated whether and how sex, age, family status, and percent of time on the study area affected the likelihood of bears (in this test population) being sampled by each of these methods and calculated biases in resulting population estimates. Vulnerability to trapping and camera sampling varied by sex and age; trapping was biased toward adult females without cubs and subadult males (3–5 years old) and against juvenile females (1–2 years old) and adult males. Bears present in the study area >50% of the time were trapped and camera-trapped more often than those that spent less time there. All sampling methods showed bias toward particular individuals, irrespective of sex, age, or time spent in the study area. Bears that were initially radiocollared in dens, without being trapped, were less likely to be trapped in future years than those that were initially radiocollared via trapping. Radiocollared bears trapped or photographed 1 summer were more likely than others to be trapped or photographed again the next summer or to be shot by hunters in the fall. This linkage between the marked and recaptured samples caused population estimates to be biased low. When we treated previously radiocollared bears that were trapped or camera-trapped 1 summer as a "marked" sample, and bears so sampled the following summer or shot by hunters the following fall as a "recapture" sample, in 12 of 13 cases we underestimated the known size of the population of radiocollared bears by 12–47%. We discuss ways to reduce bias, but warn that bias is likely inescapable.

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Key words: black bears, camera sampling, capture heterogeneity, hunting, mark–recapture, population estimation, risk ratios, sample bias, trap vulnerability, *Ursus americanus*

Appropriate sampling design is essential for obtaining reliable population estimates of free-ranging animals. Choice of sampling methods, sites, and timing affect sampling efficiency (how quickly an adequate sample is acquired) and bias (how representative a sample is obtained). In bear population studies, animals have been sampled by trapping (Piekielek and Burton 1975, Young and Ruff 1982, Beecham 1983, Hellgren and Vaughan 1989, McLellan 1989, Garshelis 1992, Doan-Crider and Hellgren 1996), photographing with remote cameras (Garshelis et al. 1993; Mace et al. 1994*a,b*; Kontio et al. 1998), sighting from aircraft (Miller et al. 1987, 1997; Schwartz and Franzmann 1991) or on the ground (Garshelis et al. 1999), hunting (Garshelis and Visser 1997, Kontio et al. 1998), or, most recently, "catching" hair samples for genetic fingerprinting (Woods et al. 1997, 1999; Mowat and Strobeck 2000). A key requirement for estimating populations with such sampling is equal catchability of marked and unmarked individuals.

Eberhardt (1969) and Caughley (1977) described 3 causes of unequal catchability: (1) differences in the relative opportunity for capture, as a consequence of such things as immigration, emigration, death, seasonal or daily movements outside the study area, home range location relative to trap sites, and daily rates of travel; (2) innate variability in individual or sex–age-related behavior toward traps or other sampling devices; and (3) disparity in learned responses to sampling devices. The first 2 problems together result in what is known as capture heterogeneity (Pollock et al. 1990). The last situation, wherein the capture experience either predisposes an animal toward, or conditions it against, being recaptured, is referred to as trap response (Pollock et al. 1990). Both capture heterogeneity and trap response can cause a link between the probability of being marked and probability of being recaptured, which biases population estimates.

Radiotelemetry provides a means of detecting and compensating for capture heterogeneity caused by death or movements of bears outside a study area (Miller et al. 1987, 1997; McLellan 1989; Garshelis 1992). In the absence of radiotelemetry, permanent loss of animals from the population (lack of demographic closure) can be estimated using so-called open models with multiple sampling periods (Jolly 1965, Seber 1965, Pollock et al. 1990); however, these methods cannot account for short-term movements outside a study area (i.e., lack of geographic closure).

Capture heterogeneity due to differences in behavior or home range location presents a more formidable obstacle. Assessment of this type of heterogeneity requires knowing not just which individuals and classes of animals *were* sampled, but also which ones *were not*. Obtaining information about animals that were not sampled is an obvious difficulty.

Long-term telemetry studies provide a means for evaluating this type of capture heterogeneity. With a radiocollared sample population, each individual can be monitored across sampling events (Miller et al. 1987, Mace

et al. 1994*a*) and its relative likelihood of being sampled (versus other sex–age classes or individuals) assessed. Accuracy depends on radiocollaring a representative sample of the population, which is most feasible in studies of long duration. With long-lived animals like bears, trapping over a number of years increases the chances of catching (and thus including in the sample population) even the least vulnerable individuals. Also, radiocollared animals can assist in the detection and capture of other individuals, such as their offspring or breeding partners, which might not otherwise be caught.

Our goal was to identify biases in sampling bear populations using traps, camera-traps, and hunting. We accomplished this by monitoring a test population of radiocollared bears through a series of annual sampling events. Our test population was acquired over multiple (≥4) years and included individuals that were initially radiocollared via trapping as well as those initially radiocollared while in dens of their radiocollared mothers (i.e., not trapped). Specifically, we tested the following hypotheses: (1) vulnerability of bears to trapping, camera-trapping, and hunting varied by sex, age, family status (i.e., presence or absence of cubs), and proportion of time in the study area; (2) idiopathic differences in vulnerability existed, which were independent of sex, age, family status, or time in study area; (3) timing of sampling influenced the relative vulnerability of different classes of bears; (4) sex and age of bears trapped varied with changes in trap density; (5) bears prone to capture in traps or by cameras were also prone to harvest by hunters; and (6) bears initially radiocollared via trapping had, as a group, higher rates of recapture and hunting mortality than bears initially radiocollared as yearlings in their mother's den.

STUDY AREA

The study was conducted on approximately 360 km^2 of the Marcell District of the Chippewa National Forest and the adjoining George Washington State Forest (47°30'N, 93°30'W) in northcentral Minnesota. The area was >95% forested and included dozens of small and medium-sized lakes. Aspen forests (*Populus tremuloides*, with *Betula papyrifera* and *Abies balsamea*) were predominant on the uplands, along with lesser amounts of conifers (*Pinus resinosa, P. strobus, Picea glauca*) and northern hardwoods (*Acer saccharum, Tilia americana, Quercus rubra, Q. macrocarpa*). Lowland forests of black spruce (*Picea mariana*), tamarack (*Larix laricina*), northern white cedar (*Thuja occidentalis*), and black ash (*Fraxinus nigra*) comprised approximately 33% of the forested area. Terrain was shaped by Pleistocene glaciations and varied from poorly drained outwash plain to hilly terminal moraine. The area was heavily used for timber production, hunting, fishing, and other forest- and lake-centered recreation, so forest roads and trails provided good access throughout most of the study area. Fall bear hunting was legal throughout the area, and bear harvests/unit area were among the highest in the state (>6 bears killed/100 km^2).

METHODS

As part of a telemetry-based study of the population dynamics of black bears in northcentral Minnesota, we radiocollared as many bears as we could on our study area through intensive trapping (1981–89) and by handling yearlings in winter dens of radiocollared females (1981–96). With this long-term sampling effort, we acquired a sample that we felt was reasonably representative of the resident bear population. By the end of 1984, we had trapped all parts of the study area and it appeared that we had captured most of the full-time residents, as well as many of the part-time residents (bears living along the study area boundaries); after 1984, we caught only 1 unmarked adult female that resided entirely within the study area, and her home range filled the only space not already occupied by a radiocollared female in this territorial population. Moreover, because virtually all reproductive females were radiocollared, we were able to collar in dens (as yearlings) nearly all bears of both sexes born on the study area. We continued to trap new males each year through 1989; most were young (1–4 years old) and not the offspring of radiocollared females, so we assumed they were immigrants from elsewhere.

We estimated the number of bears on the study area by considering previously radiocollared bears as our "marked" sample and obtaining annual "recapture" samples by trapping (1985–89) or camera-trapping (1994–96). These population estimates, some of which are presented in another paper (Garshelis 1992), are not our focus here. However, this was the basis for the current study.

Because we radiocollared a large portion of the study area population, we recognized that we could use our data to help identify sampling biases that might occur when long-term marking is not feasible. To perform this analysis, instead of using the sample of radiocollared bears as a marked population, we used this sample as a known test population. We monitored the sampling history of each radiocollared bear across years to identify bias in each sampling event (i.e., annual trapping, camera-trapping, or hunting) and to look for shared bias in pairs of sampling events, such as might be encountered in classic single mark–recapture studies. We describe below the methods we used to acquire the test sample of bears, examine sampling data for bias, and construct mark–recapture simulations. We reiterate that the purpose of the simulations

was to provide information on sampling bias, not to produce actual population estimates for our study area.

Marking and Sampling the Test Population

We captured bears in baited barrel traps or foot snares, immobilized them, measured them, extracted a first upper premolar for age estimation, and attached radiocollars and plastic, colored ear tags. We also immobilized radiocollared bears in their dens during December–March each year, at which time we replaced radiocollars as needed and eartagged and radiocollared yearlings with adult females. After trapping and den visits during 1981–84, we acquired a sufficient sample of radiocollared bears (n = 31 by the beginning of trapping in 1985) to make up a test population for this study. We recorded physical features of these bears and their radiocollars that might be useful for identifying individuals in photographs obtained from camera traps (e.g., chest blazes, position of collar hardware, and length of extra collar belting). During den visits in 1995 and 1996, we epoxied a unique, colored design to the front of the transmitter casing of each radiocollar to enhance individual photographic identifications.

During 1985–89 we sampled the radiomarked test population by trapping. Each year we trapped for 8 weeks (mid-May to mid-July). In 1985, we trapped the entire study area, but trap density was not uniform. We changed this during 1986–89, when we systematically placed traps within a grid of 5-km^2 cells (1 trap/cell). We divided the study area into halves and alternated trapping between halves every 2 weeks, sampling 11 nights each session, with 2 sessions on each half.

We did not trap during 1990–95, but we continued to radiocollar yearlings in dens each winter. In 1996, we trapped to increase the number of marked males, as most males radiocollared as yearlings had dispersed from the study area at 2–3 years old, and most older males had died.

We sampled the population with cameras during June–early August, 1994–96. We placed cameras in 30–35 cells of our previous trapping grid, leaving 34–39 cells open at any time. Cameras were housed in a wooden case and nailed 4 m high on the trunk of a smooth-barked tree. A bait (0.5 kg bacon in a mesh bag), connected to the camera triggering device by a string, hung 120 cm from the camera lens and 50 cm from the tree trunk. To reach the bait, a bear had to climb the tree, lean backwards, and extend its neck across the camera's field of view. Bears took baits with their mouths, as their paws were clasped to the tree. By pulling on the bait, a bear triggered the camera to take a single flash photograph of its head and neck. In 95% of photographs thus obtained (189 of 200), we could determine whether the bear had a radiocollar. Those without a collar were not included in this analysis. We individually identified 98% of photographed radiocollared bears (105 of 107), based on distinguishing features of collars, ear tags, or the bears themselves. Because cameras required manual resetting and rebaiting after each photograph, and because we checked and reset cameras only weekly, our sample size was limited to ≤1 photograph/camera/week. To avoid repeat photographs of the same bear at a camera site, we moved cameras after each photograph of a bear to an empty grid cell that had not had a camera for ≥2 weeks. Thus, if 2 photographs were obtained at a site, they were separated in time by ≥2 weeks.

We obtained recapture samples from hunters (i.e., radiocollared bears that they killed) in the form of mandatory registration of all harvested bears. The hunting season extended from 1 September to mid-October every year across all of northern Minnesota. Most hunters (80%) used bait and scent to attract bears; these attractants could be put in the woods 2–3 weeks prior to the hunting season. Hunters were mailed information packets before the season in which they were instructed to treat ear-tagged and radiocollared bears as they would unmarked bears and to turn in radiocollars from harvested bears at registration stations.

Evaluation of Samples

We used bear captures/trapnight (1 trapnight = 1 trap set/night) as a measure of trapping success. We tested for differences in trapping success for weekly periods among years using 1-way ANOVA. We grouped bears into 8 sex–age groups: juvenile (1–2 years old) males and females; 3–5-year-old males, females without cubs, and females with cubs; and older (≥6 years) males, females without cubs, and females with cubs. Pooling years, we compared the median dates when bears of each sex–age group were first captured each year using a Kruskal-Wallis test. We used chi-square tests for homogeneity to examine differences among sex–age groups in timing of first captures across four 2-week periods and recapture frequencies within trapping sessions (SAS Proc CATMOD; SAS Institute, Inc. 1990). We tallied the frequency of consecutive captures at each site of the same bear versus different bears and compared these data obtained by trapping versus camera-trapping using a chi-square test for homogeneity.

We investigated the effects of trap density on sampling using data from 1986–89 (the years when trap density and trapping effort were most consistent). To simulate the effects of using half the trap density, we only used data from every other trap site (resulting in 2 subsets of data each year); for one-fourth the trap density we used data from every fourth trap site (4 subsets of data), and so forth. We compared mean captures/year, number of different

bears caught, proportion of the test population caught, and sex–age distribution of the captured sample among these simulated trap densities.

We used the test population of radiocollared bears to examine biases in data obtained by trapping (1985–89), camera-trapping (1994–96), and hunting (1985–89 and 1994–96). We restricted the test population to bears that were radiocollared at the beginning of each sampling session and (for trapping and camera sampling) were present on the study area during ≥10% of the sampling session. To determine presence on the study area, we flew the perimeter ≥10 times each session and used telemetry equipment to ascertain whether each bear was inside or outside that perimeter.

We compared the likelihood of sampling with cameras or traps by sex–age group and by percent of time in the study area (10–50% versus >50%) using a maximum likelihood logistic response model (SAS Proc CATMOD). Due to smaller sample sizes for camera-trapping, we condensed analyses of camera data to 4 sex–age groups: juveniles (both sexes, 1–2 years old), subadults (both sexes, 3–5 years old), adult females without cubs, and all females with cubs. When significant main effects were detected, we used pairwise contrasts to identify differences among groups. We used risk ratios (SAS Proc FREQ) to compare the likelihood of bears trapped or photographed 1 year, versus not sampled that year, to be sampled again the following year or killed by a hunter that fall. If a bear's status changed from 1 year to the next (e.g., juveniles became adults, females with cubs became females without cubs, bears shifted their ranges and thus spent more or less time within the study area), we reassigned it to the appropriate group for the second year. Also using risk ratios, we compared the vulnerability of bears that were already in our radiocollared test population to newly collared bears captured each year and compared bears that initially had been marked via trapping to those initially marked as yearlings in the dens of their radiocollared mothers. When risk ratios differed from 1, indicating that samples were not independent, we used 2- and 3-way logistic response models (SAS Proc CATMOD) to determine whether the lack of independence was a function of sex–age, time spent in the study area, or individual differences in vulnerability.

Mark–Recapture Simulations

We simulated various mark–recapture scenarios using pairs of actual sampling periods. We derived population estimates and compared estimates to the known size of the radiocollared sample population. Collared bears caught or photographed in the first period were treated as marked, and those sampled during the second period were considered as recaptured. All other bears in the test population were classified as unmarked. Scenarios included trapping in 2 consecutive years, camera-trapping in 2 consecutive years, trapping or camera-trapping followed by hunting the same year, and trapping or camera-trapping followed by the cumulative of 3 years of hunting. We derived population estimates using the Petersen equation with Chapman's (1951) modification, because each animal was counted only once in each recapture sample (sampling without replacement). We omitted bears that died or emigrated from the test population between sampling periods; because all bears in the test population were collared, this was known with certainty. Immigration was not a concern in these simulations because we estimated only the number of bears in the test population, not the whole population.

RESULTS

Trapping Success

Trapping success (captures/100 trapnights) showed no consistent pattern across weeks during the summers of 1981–89 ($F_{10,58}$ = 1.33, P = 0.24; Table 1; total n = 744 captures, 8,839 trapnights). However, a pattern emerged in the timing of new captures (bears not previously caught that year); number of new captures/100 trapnights was highest during 25 May–7 June and declined through the end of trapping in mid-July (χ^2_4 = 44.6, $P < 0.0001$, n = 368). This pattern was consistent for juveniles, subadults, and females without cubs ($P < 0.05$ for all classes; Fig 1a), but not for adult males and females with cubs, who were equally likely to be first caught late in June or early July ($P > 0.2$; Fig. 1b). Median date of first capture was earliest for juvenile females (6 June) and latest for adult males and females with cubs (21 June; Kruskal-Wallace H = 17.96, P = 0.01).

The frequency that bears were recaptured within a summer also varied by their sex and age; bears of sex–age groups that tended to be caught earlier in the year were more likely to be recaptured (Fig. 2). This trend held for all years of trapping (χ^2_{12} = 30.0, P = 0.003) and for the subset of years (1985–89) when trapping effort was most consistent (χ^2_{12} = 18.9, P = 0.09). Sixty-two percent of juvenile females caught in a given year were recaptured the same year. Forty-two to 54% of juvenile males, subadults, and adult females without cubs were caught more than once, compared to a recapture rate of only 25% and 32%, respectively, for adult males and females with cubs.

When we simulated changes in trap density, we found that halving the density decreased the total number of captures/100 km^2 by 50%, but the number of different bears caught/100 km^2 decreased by only 35% (Fig. 3). When we halved density again, total captures declined by an-

Table 1. Total number of black bear captures/100 trap-nights, by week, in north central Minnesota, 1981–89.

	Captures/100 trap-nights									
	1981	1982	1983	1984	1985	1986	1987	1988	1989	$\bar{x}$
11–17 May		4							4	4.0
18–24 May		2						6	4	4.0
25–31 May		4		24	6	8	16	10	4	10.3
1–7 Jun	18	4		16	8	8	17	6	15	11.5
8–14 Jun	9	7	4	15	9	8	12	9	4	8.6
15–21 Jun	5	7	9	8	12	10	13	9	19	10.2
22–28 Jun	3	3	15	8	11	5	5	15	14	8.8
29 Jun – 5 Jul	7	7		8	9	4	4	8	13	7.5
6–12 Jul	11			14	7	9	2	14	12	9.9
13–19 Jul	6		13	5	4	6	1			5.8
$\bar{x}$	8.4	4.8	10.3	12.3	8.3	7.3	8.8	9.6	9.9	

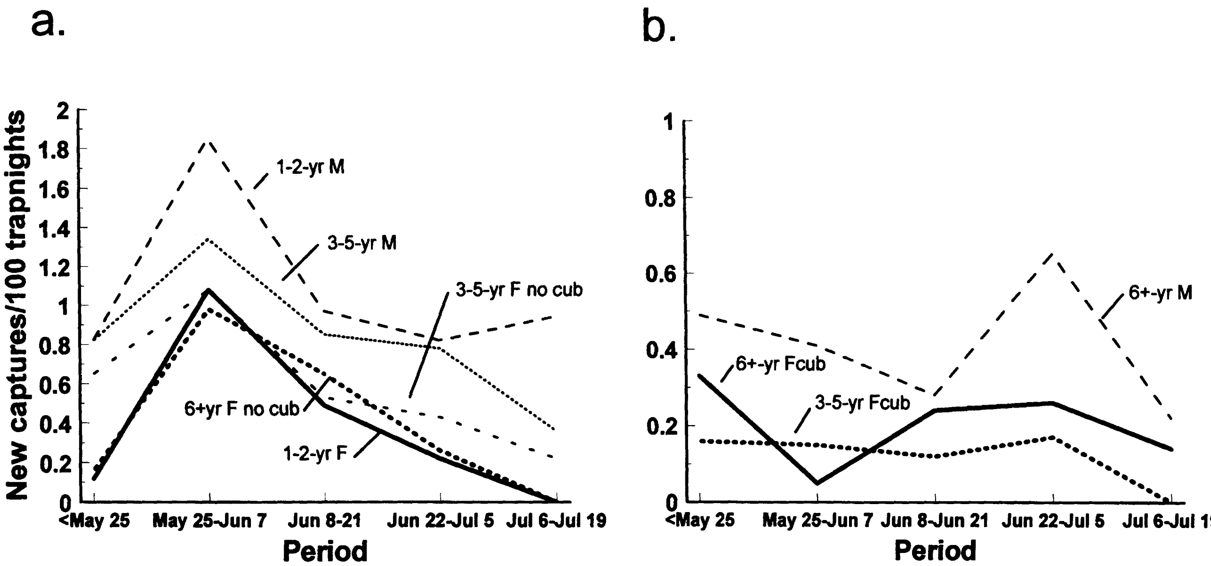

Fig. 1. Sex–age related differences in timing of first captures (for the year) of black bears in north central Minnesota, 1981–89. Adult males and females with cubs (panel b) did not exhibit the same pattern as other bears (panel a).

other 50%, but bears caught by 39%. Using data from all traps during 1986–89 (when trap spacing was uniform), captures/100 km² averaged 37 (SE = 3; *n* = 4 years), and we caught 53 ± 4% of the radiocollared population. Simulating one-eighth that density resulted in 4.6 captures/100 km² (one-eighth the number at full density), but we caught 12% of the known population (>20% of those caught with the full compliment of traps). Changes in trap density had no discernible effect on the sex–age distribution of bears trapped; we observed no differences in ratios of nonjuvenile (≥3-year-old) males:females (range 0.75–0.82, 4-yr means) or percent yearlings in samples (range 18–22%) for simulated trap densities ranging from 25–20/100km².

Vulnerability to Trapping and Camera Sampling

The first and second bears caught at any given trap site usually were different individuals (84% of cases, *n* = 204 sites with ≥2 captures); the third capture at a site usually was a third individual (61% of cases, *n* = 115), but the fourth typically was a recapture of 1 of the first 3 bears (71% of cases, *n* = 44). Similarly, the second bear photographed at camera sites was most often different than the first, but consecutive recapture of the same individual at camera sites was more common (38% of cases, *n* = 34) than at trap sites (16%; $\chi^2_1 = 7.5$, $P = 0.006$). Consecutive recaptures at individual trapsites remained the same when we made trap data more comparable to camera data by discounting captures <2 weeks apart.

We captured, on average, 51% (SE = 4, *n* = 5) of the test population each year during 1985–89. Thus, we expected that about half the bears not captured in any given year would be captured the next, if all bears were equally vulnerable to trapping. Instead, the observed mean capture rate for radiocollared bears not caught the first year was lower in successive years: 38% (SE = 8, *n* = 4), 36% (SE = 13, *n* = 3), and 33% (*n* = 1) 2, 3, and 4 years later,

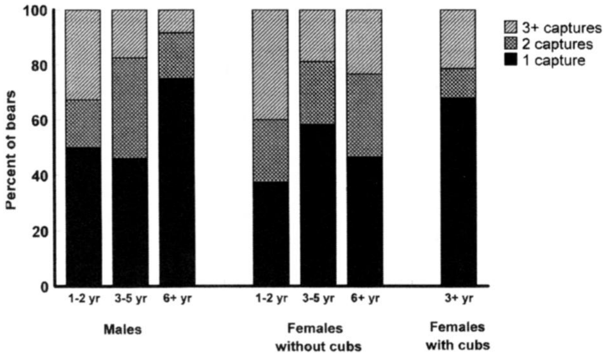

Fig. 2. Sex–age related differences in capture frequency of radiocollared black bears within annual trapping periods, 1981–89.

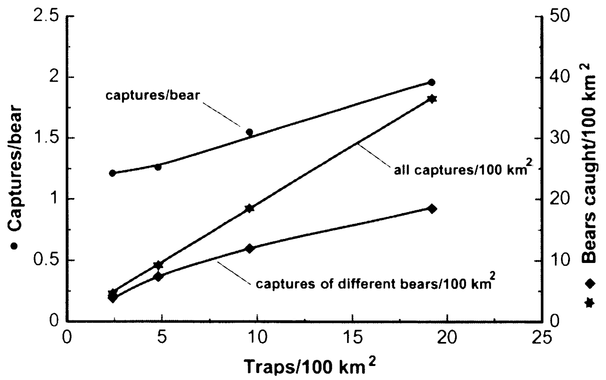

Fig. 3. Changes in capture rates of radiocollared black bears with simulated changes in trap density, north central Minnesota, 1986–89.

respectively. (Because trapping ended in 1989, and because by 1989 all bears in the 1985 test population not trapped during 1985–88 had died or dispersed, 2-year cumulative trapping data were available for only 4 test groups of bears [1985–88], 3-year data for 3 groups [1985–87], and 4-year data for 1 group [1986]). As a result of this decline, instead of catching an expected 88% of the population after 3 years (which would result from a constant annual capture rate of 51%) and 94% after 4 years, we caught 80% (SE = 4) and 85%, respectively (Fig. 4). The higher risk of capture for bears previously caught relative to bears not previously caught was apparent in each year's data and was statistically significant for 2 of the 5 individual years examined (1986: $\chi^2_1 = 7.02$, $P = 0.02$; 1987: $\chi^2_1 = 8.80$, $P = 0.008$). For all years pooled, bears trapped 1 year were 2.1 (95% CI = 1.4–3.2) times more likely to be caught again the next year than bears not caught the first year ($\chi^2_1 = 16.8$, $P < 0.0001$). As an example, in 1985, 15 (45%) of 31 radiocollared bears were captured; 10 of those 15 were present and 6 (60%) were captured again the second year. In contrast, of 9 bears not caught the first year and present the second year, only 3 (33%) were caught.

Vulnerability to trapping was related to how much time bears spent on the study area ($\chi^2_1 = 5.03$, $P = 0.01$) and to their sex and age ($\chi^2_1 = 16.9$, $P = 0.01$; $n = 31$–58 radiocollared bears available for capture each year [234 total]). Bears located within the study area >50% of the time were more likely to be trapped than those present 10–50% of the time (Table 2). Juvenile females and adult males were least likely to be caught, whereas subadult males and adult females without cubs were most prone to capture. Adult females with cubs were less likely to be caught than those without cubs ($\chi^2_1 = 4.04$, $P = 0.04$).

These biases could not explain, however, the propensity for bears that were caught one year to be caught again the next year. We considered the simultaneous effects of sex–age, time spent on the study area, and trapping history (whether or not a bear was caught the first year) for bears that were available for capture in 2 consecutive years: most of the variability in probability of capture the second year was explained by trapping history ($\chi^2_1 = 19.02$, $P < 0.0001$), not by sex–age ($\chi^2_7 = 12.47$, $P = 0.09$) or time on the study area ($\chi^2_1 = 2.61$, $P = 0.11$).

As with trapping, vulnerability of bears to camera-trapping ($n = 111$ photographs of radiocollared bears) was significantly related to each bear's time on the study area ($\chi^2_1 = 6.37$, $P = 0.01$) and sex–age group ($\chi^2_3 = 20.12$, $P = 0.0002$; Table 3). Juveniles were less likely than other

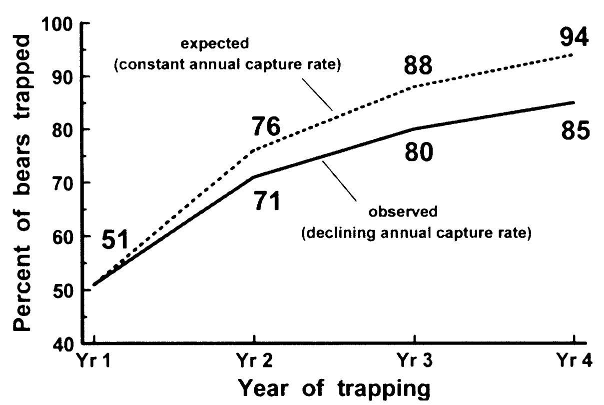

Fig. 4. Cumulative percent of radiocollared black bears captured during consecutive years of trapping in north central Minnesota. Each point represents a mean of up to 5 test populations of radiocollared bears. Test populations consisted of all bears radiocollared prior to the start of trapping in each of 5 years, 1985–89. Because trapping ended in 1989, and because by 1989 all untrapped bears in the 1985 test population had died or dispersed, 2-year cumulative trapping data were available only for 4 test groups (1985–88), 3-year data for 3 groups (1985–87), and 4-year data for 1 group (1986). Points on the lower curve represent observed values, averaged for the test groups available. Points on the upper curve represent expected values, if probability of capture was the same (51%) for bears that had been caught as well as those not previously caught.

Table 2. Sex–age specific vulnerability of black bears to trapping, measured in terms of percent of the radiocollared population trapped, north central Minnesota, 1985–89. Significant differences between sex–age groups are indicated.

	Radiocollared bears in trapping area						
	>50% of time		10–50% of the time		10–100% of time		
Sex–age group	Trapped (%)	(*n*)	Trapped (%)	(*n*)	Trapped (%)	(*n*)	Difference between groups[a]
Males							
1–2 yr	62	(29)	25	(12)	51	(41)	a,b,c
3–5 yr	80	(10)	75	(4)	79	(14)	c
6+ yr	50	(6)	29	(14)	35	(20)	a,b
Females without cubs							
1–2 yr	40	(42)	18	(11)	36	(53)	a
3–5 yr	60	(25)	70	(10)	63	(35)	b,c
6+ yr	75	(20)	62	(13)	70	(33)	c
Females with cubs							
3–5 yr	67	(9)	33	(3)	58	(12)	a,b,c
6+ yr	53	(19)	29	(7)	46	(26)	a,b

[a] Sex–age groups having the same letters did not differ in capture rates (χ^2 pairwise comparisons, SAS Proc CATMOD, $P \leq 0.05$).

Table 3. Sex–age specific vulnerability of black bears to camera detection, measured in terms of percent of the radiocollared population photographed, north central Minnesota, 1994–96. Significant differences between sex–age groups are indicated.

	Radiocollared bears in camera sample area						
	>50% of time		10–50% of time		10–100% of time		
Sex–age group	Photographed (%)	(*n*)	Photographed (%)	(*n*)	Photographed (%)	(*n*)	Difference between groups
Juveniles (1–2 yr M + F)	16	(38)	6	(16)	13	(54)	a
Subadults (3–5 yr M + F)	60	(10)	0	(4)	43	(14)	b,c
Adult females without cubs	76	(17)	50	(4)	71	(21)	b
Females with cubs	50	(16)	17	(6)	41	(22)	c

[a] Sex–age groups having the same letters did not differ in rates of camera detection (χ^2 pairwise comparisons, SAS Proc CATMOD, *P* 0.06).

classes to be photographed ($P \leq 0.02$ in all pairwise comparisons), adult females with cubs differed marginally from those without ($\chi^2_1 = 3.53$, $P = 0.06$), and subadults did not differ from either group of adult females ($P > 0.1$). Adult females with and without cubs appeared as likely to be photographed as trapped (Tables 2 and 3), whereas younger bears tended to be photographed less frequently. Overall, bears photographed one year were 2.2 (CI = 1.2–4.3) times more likely to be photographed again the next year than bears not photographed the first year ($\chi^2_1 = 6.3$, $P = 0.012$).

Each year during trapping, we caught some bears that were not previously radiocollared and thus were not part of our test population. These bears were no more vulnerable to capture the next year than bears already in the test population that were caught the same summer ($\chi^2_1 = 0.29$, $P = 0.6$). However, in 1996, 12 bears trapped for the first time immediately prior to camera sampling were 3.8 (CI = 1.8–7.9) times more likely to be photographed than bears that were already radiocollared ($P = 0.001$).

Bears that were originally radiocollared via trapping (n = 109) were 1.4 (CI = 1.1–1.8) times more likely to be trapped sometime in the future than bears that were first radiocollared as yearlings in maternal dens ($n = 124$; Table 4). To determine if this was due to differences in the sex–age composition of these 2 groups (most adults were first handled at traps, whereas most juveniles were first radiocollared at dens), we considered the simultaneous effects of sex–age and type of initial handling. Adjusted for sex–age effects ($\chi^2_7 = 15.08$, $P = 0.04$), likelihood of capture in traps was still strongly related to whether bears were initially captured in traps or handled in dens (χ^2_1 = 7.05, $P = 0.008$).

Relationship between Summer Trapping and Hunting

Bears that were captured in the summer were shot at a higher rate during the following fall hunting season (P = 0.08, risk ratio = 1.7, CI = 0.9–3.1) and the following 3 fall hunting seasons ($P = 0.02$, risk ratio = 1.4, CI = 1.1–1.9; Table 5) than bears that were not captured. This pattern was apparent nearly every year during 1985–89. Testing for the simultaneous effects of sex–age and trapping history, only capture history was significantly related to a bear's likelihood of being shot ($\chi^2_1 = 5.6$, $P = 0.02$ for capture history; $\chi^2_1 = 9.26$, $P = 0.23$ for sex–age group);

Table 4. Annual capture rates of black bears initially radiocollared via trapping versus those initially radiocollared as yearlings in dens, north central Minnesota, 1985–89.

	Radiocollared via trapping		Radiocollared in den	
Sex–age group	Trapped (%)	(*n*)	Trapped (%)	(*n*)
Male				
1–2 yr	75	(8)	45	(33)
3–5 yr	75	(12)	50	(2)
6+ yr	35	(20)		(0)
Females without cubs				
1–2 yr	50	(2)	36	(50)
3–5 yr	91	(11)	50	(24)
6+ yr	70	(27)	67	(6)
Females with cubs				
3–5 yr	80	(5)	43	(7)
6+ yr	46	(24)	50	(2)
All [a]	61	(109)	44	(124)

[a] Significant difference between bears initially radiocollared in traps versus in dens ($\chi^2 = 7.46$; $P = 0.006$).

that is, some bears were more vulnerable than others to both trapping and hunting not because of sex, age, or family status, but due to other unidentified factors.

The relationship between camera-trapping and hunting was not as clear. In 2 of 3 years and in the across-year pooled sample, there appeared to be a hunting bias toward bears that had been photographed the previous summer; this bias was of similar magnitude to the bias toward bears that had been trapped (Table 6). However, sample size for camera trapping was smaller than for trapping, so, whereas results were statistically significant for the trapping sample (all years pooled), they were not for the camera sample ($\chi^2_1 = 1.27$, $P = 0.31$). After 3 years of cumulative hunter harvest, results were clearly different from the trapping sample; the probability of being shot was no different for bears previously photographed versus those that were not ($\chi^2_1 = 0.33$, $P = 0.56$).

Estimates of Population Size

Mark–recapture samples underestimated population size in 17 of 21 (81%) simulated scenarios (Table 7). The largest errors occurred with consecutive years of trapping or camera-trapping. Samples obtained with 2 different techniques—trapping or camera-trapping to mark bears, hunting to recapture—produced less biased estimates, even though these samples were obtained the same year. The least biased estimates were obtained with an accumulation of data from 3 hunting seasons instead of just a single season.

DISCUSSION

Influence of Sampling Design on Sample Composition

Placement of sites and timing and duration of sampling are important considerations in designing a mark–recapture program. The potential benefits of moving sam-

Table 5. Percent of bears that were shot during the first or first 3 fall hunting seasons after trapping, comparing those that had been trapped versus not trapped, north central Minnesota, 1985–89.

	1985		1986		1987		1988		1989		All years	
	Shot (%)	(*n*)	Shot (%)	(*n*)	Shot (%)	(*n*)	Shot (%)	(*n*)	Shot (%)	(*n*)	Shot (%)	(*n*)
First hunting season												
Radiocollared bears trapped during summer	14	(14)	21	(19)	17	(30)	23	(30)	31	(26)	22	(119)
Radiocollared bears not trapped during summer	24	(17)	13	(23)	12	(17)	18	(22)	3	(29)	13	(108)
Previously uncollared bears trapped during summer	16	(19)	30	(20)	30	(23)	38	(16)	23	(22)	27	(100)
3 hunting seasons												
Radiocollared bears trapped during summer	54	(13)	44	(18)	54	(28)	59	(27)	64	(25)	59	(111)
Radiocollared bears not trapped during summer	47	(17)	29	(21)	40	(15)	50	(22)	33	(27)	39	(102)
Previously uncollared bears trapped during summer	71	(17)	81	(16)	62	(21)	62	(13)	44	(18)	64	(85)

pling devices (traps, cameras, hair-snags), in terms of potentially capturing more individuals, must be weighed against the effort of doing so. We found that the first 3 captures at each trap site were usually different bears, so moving traps immediately after a capture likely would not have significantly increased the number of individuals caught. Repeat visits by the same individual were more common at camera sites, even though we moved cameras after each capture (photograph) and did not reuse these sites for 2 weeks. This suggests that bears were more prone to revisit sites where they obtained bait without being physically trapped, thus supporting our strategy of moving cameras, but not traps, after each bear visit.

Timing of trapping can influence the sex–age distribution of bears that are caught. In our study, females with cubs and adult males tended to be caught later in the year (Jun–early Jul) than other sex–age groups. Adult males apparently reduce their feeding during the breeding season (Herrero 1983, Rogers 1987, Coy and Garshelis 1992, Noyce and Garshelis 1998), which peaks in mid-June in Minnesota (Garshelis and Hellgren 1994). Thus breeding males may be less attracted to baits during this time of

Table 6. Percent of bears that were shot during the first or first 3 fall hunting seasons after camera sampling, comparing those that had been photographed versus not photographed, north central Minnesota, 1994–96.

	1994		1995		1996		All years	
	Shot (%)	(*n*)	Shot (%)	(*n*)	Shot (%)	(*n*)	Shot (%)	(*n*)
First hunting season								
Radiocollared bears photographed during summer	23	(13)	35	(17)	0	(7)	24	(37)
Radiocollared bears not photographed during summer	18	(33)	25	(16)	2	(28)	16	(77)
3 hunting seasons								
Radiocollared bears photographed during summer	58	(12)	56	(16)	44	(9)	54	(37)
Radiocollared bears not photographed during summer	64	(22)	63	(8)	54	(13)	61	(43)

Table 7. Estimates of the number of radiocollared black bears (estimated population) compared to the known number of radiocollared bears (actual population) in north central Minnesota. Petersen mark–recapture estimates were made by sampling the radiocollared population, either by trapping, with cameras, or by hunting. For recapture samples obtained by trapping and camera-trapping, marked bears were those captured the summer of the previous year; for recapture samples obtained by hunting, marked bears were those trapped or camera-trapped that summer. All other radiocollared bears trapped, photographed, or killed by hunters in the indicated year were considered unmarked. Bears without collars were not part of this analysis.

	Capture–recapture			Capture–hunt (1 season)			Capture–hunt (3 seasons)[a]		
Year	Actual population	Estimated population	Relative bias (%)	Actual population	Estimated population	Relative bias (%)	Actual population	Estimated population	Relative bias (%)
Traps									
1985	19	13	- 32	31	34	10	30	27	- 10
1986	26	20	- 23	42	31	- 26	39	31	- 21
1987	32	24	- 25	47	40	- 15	43	39	- 9
1988	33	27	- 18	52	46	- 12	49	45	- 8
1989	b	b		55	29	- 47	52	39	- 25
$\bar{x}$			- 25			- 18			-15
Cameras									
1994	26	18	- 31	46	34	- 17	34	35	3
1995	17	10	- 41	33	27	- 18	24	25	4
1996	b	b		c	c		22	23	5
$\bar{x}$			- 36			- 18			4

[a] Cumulative harvest of radiocollared bears over 3 hunting seasons.
[b] No estimate possible because a recapture sample was not obtained the next summer.
[c] No estimate possible because no bears in the "marked" sample (photographed that summer) were shot during the fall hunting season.

year than later in June or July. Females with cubs may be less likely to encounter traps early in the year because cubs limit their daily movements and also may prompt mothers to be more wary of sites with odors of humans or other bears. Miller et al. (1987) noted that females with young cubs also were less visible from aircraft in the spring than in summer. Had we trapped only in May and early June, we would have caught 42% fewer young bears, but 65% fewer adult males and females with cubs.

We expected that changes in trap density also would affect the sex–age distribution of bears caught. We hypothesized that if traps were spaced widely enough that some small home ranges contained none, sex–age groups that tended to have small home ranges (e.g., yearlings and females) would be under-represented in the capture sample. However, this was not borne out in our simulations; when we increased trap spacing (decreased trap density) by censoring data from 50, 75, and 88% of the trap sites, sex–age distribution of bears sampled was remarkably consistent. One could argue that because we did not actually remove traps (we just manipulated the trapping data), captures of bears at censored sites may have affected the simulated sample composition by precluding capture of those bears at uncensored sites. However, because daily probability of capture for bears in this study was low (2–3% of known bears captured each night of trapping), the likelihood of this occurring, and of there being discernible sex–age bias among such cases, also was low.

We believe that sex–age biases related to trap density may take time to develop, particularly when daily probability of capture is low. The fairly short duration of our trapping (two 11-day sessions for each half of the study area) may have precluded these effects, even in our simulations. To illustrate, consider an area with 10 males having home ranges twice the size of those of 10 females and a trap distribution of 2/male and 1/female. If the daily rate of travel was similar for males and females, then trap encounter rates would be similar, and, barring differences in behavior toward traps, probability of capture also would be similar (Boulanger and Krebs 1996). If the daily probability of capture was 0.1 for both sexes, 65% of males and 65% of females would be expected to be captured in a 10-day trapping session ($[1- 0.1]^{10}$ = probability of not being caught). If trap density was halved, then all males, but only half the females, would have 1 trap in their home range. Daily probability of capture for males would drop to 0.05; mean daily probability of capture for females would also be 0.05, because half the females would have a probability of capture of 0.1 (those that still have 1 trap in their range) and half would have a probability of capture of 0 (those without traps). With this trap spacing, after 10 days we would expect to catch 40% of the males, 65% of the females with a trap in their range, and none of the females without traps, yielding a sample sex ratio of 1.23 M:F. If trapping continued for 20 days, we would expect to catch 64% of the males and 88% of females with traps, and again none of the females without traps, which yields a more skewed sex ratio of 1.46 M:F. The higher the daily probability of capture, or the greater the difference between sexes in capture probability, the sooner this bias would become evident.

Although simplistic, this example demonstrates the combined effects of trap density, duration of trapping, and probability of capture on the composition of the trapped sample. It also illustrates the importance of ensuring that every bear has a reasonable probability of being trapped. The distance between traps should not exceed the minimum width of a home range traversed by a bear of any sex–age group during the trapping period. Ideally, traps should be spaced at about half this distance, to ensure that each bear has access to >1 trap. The trap spacing that we used in our study was selected so that all bears had 1 trap within their home range; adults had ≥2. Otis et al. (1978:77) recommended ≥4 traps/home range, but this was directed mainly at small mammal mark–recapture studies where animal densities and probabilities of capture are high, so multiple traps/home range are necessary to prevent trap clogging (one animal's capture precluding the capture of another). This is unlikely to be a significant problem in bear studies.

The trap density we used may not have ensured that all bears with very small home ranges came in contact with a trap site during the trapping period; this may have contributed to the sampling bias we observed against juvenile females, in particular. Increasing trap density might lessen the effects of capture heterogeneity related to home range size or daily movement patterns; this is something that should be tested. However, it is unlikely that increasing trap density would eliminate the individual capture heterogeneity that was so pervasive in our sampling. Moreover, the potential benefits of providing more traps/unit area must be weighed against the disadvantages of lower sampling efficiency (fewer individual bears caught with the same trapping effort) and often of a smaller sampling area, constrained by logistics or budgets.

Capture Heterogeneity and Resulting Biases in Population Estimates

Some of the sampling biases we detected related to sex and age in trapping and camera-trapping were consistent with results from other studies (Miller et al. 1987, Mace et al. 1994*a*,*b*); females with cubs in our study were more difficult to sample with traps or cameras than other females. Contrary to expectation, however, adult males in our study were among the least likely to be trapped. Mace

et al. (1994*a*) reported that adult male grizzly bears were detected most readily at camera sites because of their wide-ranging movements. The difference between our study and theirs may have been related to the earlier timing of our trapping season (a higher proportion of our trapping period was during the breeding season) and closer spacing of our traps. In Mace et al.'s (1994*a*) study, 21% of the bears had no cameras within their ranges, which, as shown above, could bias the sample toward bears with large home ranges.

The strongest bias in our sampling methods, however, was caused by individual differences among bears; that is, some bears were more trappable than others for reasons unrelated to their sex, age, time spent in study area, or any other factor we could discern. Similarly, Miller et al. (1997) concluded that most of the heterogeneity that they observed in a mark–resight study of bears was caused by individual variation in sighting probabilities, not variation related to sex, age, or reproductive status. In other bear studies, investigators failed to detect capture heterogeneity (Kemp 1972, 1976; Yodzis and Kolenosky 1986; Clark and Smith 1994), based on chi-square comparisons of capture frequency distributions to various theoretical distributions (Caughley 1977, Seber 1982). Roff (1973), however, demonstrated that these tests are insensitive and often fail to detect heterogeneity even when it is known to occur.

We suspect that significant capture heterogeneity is more the rule than the exception in bear studies, posing a nagging problem for estimating population size. Several authors have dealt with capture heterogeneity related to sex and age by computing separate population estimates for sex–age groups of bears thought to have different rates of capture (Beecham 1983, Yodzis and Kolenosky 1986, Hellgren and Vaughan 1989, Garshelis 1992). Unfortunately, our results and those of Miller et al. (1997) demonstrate that it is difficult to guess *a priori* how to make sex–age groupings that best match actual differences in vulnerability. Though it is tempting to use recapture frequencies as a basis for making sex–age groupings *a posteriori*, this is also unreliable, as sex–age groups with the highest recapture frequencies are not necessarily those with the highest sampling rates; in our study, juvenile females were the least likely to be caught during our 8-week trapping period (Table 2), but those that were caught had the highest same-year recapture rates of any sex–age group (Fig. 2). Also, if animals display significant trap response, recapture rates would be a poor reflection of initial probability of capture.

The program CAPTURE, developed by Otis et al. (1978; also see White et al. 1982), has routines for dealing with various sorts of heterogeneity among capture probabilities and has been applied in cases where capture probabilities varied by individual (Boulanger and Krebs 1994, Manning et al. 1995). Bear capture studies typically have not employed this program because it requires population closure, multiple (≥4, preferably 7–10) and hence short (given the closure assumption) sampling periods, and high capture probabilities (>0.3) within these short sampling periods. Pollock et al. (1990) proposed an open model, derived from the Jolly–Seber estimator, that allows for capture heterogeneity. However, to incorporate capture heterogeneity, it applies the CAPTURE routine to multiple short sampling sessions within a longer primary sampling period; thus it, too, requires high capture probabilities and a closed population for the duration of each primary sampling period. The CAPTURE routine has 2 further stipulations that make it untenable for most bear studies (except in special circumstances, e.g. Mowat and Strobeck 2000). The first is geographic closure, which in bear studies can be more of a problem than demographic closure. Bears have large home ranges relative to most study areas and routinely move across study area boundaries. The CAPTURE routine cannot distinguish bears that live in the study area only part-time from those with low capture probabilities living there full-time; the effect is to overestimate population size. Garshelis (1992) and Miller et al. (1997) used radiotelemetry to detect deaths or movements of bears outside the study area and thereby account for lack of closure. However, this telemetry-based solution is not directly amenable for use in CAPTURE. The second stipulation is that all sampled animals must be individually distinguishable. This assumption cannot be met when sampling is done with cameras or aircraft sightings because unmarked animals remain unmarked and hence unidentifiable when sampled again.

The Petersen equation yields the simplest mark–recapture population estimate, but its use is tightly constrained by its assumptions of a closed population and independence between mark and recapture samples. Fortunately, the technique is readily compatible with telemetry-based solutions to the closure problem. The question is whether the single recapture Petersen estimator performs adequately in the presence of capture heterogeneity. Discussions of this procedure often emphasize the assumption of equal probability of capture (i.e., no capture heterogeneity; Eberhardt 1969, Caughley 1977, Begon 1979, Seber 1982, Pollock et al. 1990, Pollock 1991, Neal et al. 1993). However, Seber (1982), citing Robson (1969) and Junge (1963), clarified that "variation in catchability due to, say, trapping selectivity could exist for both initial and recapture samples without introducing bias if the sources of selectivity in the 2 samples were independent." (Seber 1982:86). Pollock et al. (1990:10) noted parenthetically, "If capture probabilities are heterogeneous in each sample

but independent from sample to sample, then no bias results". In other words, neither sex–age bias nor individual bias per se poses a problem if the biases are not common to both the initial and recapture sample. Simulations designed to assess bias in population estimates stemming from capture heterogeneity generally assume that differences in capture rates among groups or individuals persist for all sampling periods (Menkens and Anderson 1988, Boulanger and Krebs 1996)

We used radiocollared animals to empirically test for shared bias between mark and recapture samples, and, where it existed, to measure the relative risk of capture for bears previously sampled versus those not sampled; we then looked at the resulting effects on population estimates. The strongest link that we observed between 2 samples was in 1996, between the previously uncollared bears trapped and collared that spring and those detected at camera sites during the following 2 months. Bears trapped just prior to camera sampling were nearly 4 times as likely to be photographed as the rest of the radiocollared population; a Petersen estimate based on these 2 samples would have underestimated population size by 55%. Sampling with traps or cameras in consecutive summers also was strongly linked, underestimating population by 18–41% (Table 7). This bias likely would have been worse in the absence of hunting; each fall, by cropping the most vulnerable bears, hunters likely killed a disproportionate number of the bears that also were most vulnerable to trap capture, in effect removing them from our mark–recapture scenarios.

Linkages between summer trapping or camera-trapping and hunting were not as strong; shared bias resulted in population underestimates averaging 18% (Table 7). The relative vulnerability of individual bears and of different sex–age groups apparently varied more between summer and fall (i.e., between trapping and hunting), making those samples more independent, than between years (i.e., between trapping sessions in consecutive years). Previously, we found that vulnerability to hunting varied markedly from year to year with changes in fall food supply and that relative vulnerabilities among sex–age groups also changed yearly (Noyce and Garshelis 1997). Because early summer and fall food supplies tend to be fairly independent (Noyce, unpubl. data), and because sex-age-specific capture vulnerabilities remain consistent during trapping, vulnerabilities to summer capture and fall hunting tend to be more weakly linked than vulnerability to capture in consecutive summers.

Population estimates improved when we lengthened the hunting sampling period from 1 to 3 years (i.e., tallied all radiocollared bears killed over 3 hunting seasons; Table 7). This suggests that the first hunting season following any summer's marking removes the most vulnerable individuals; in the second and third year after trapping, less vulnerable individuals are harvested, so the combined 3-year harvest comprises a more representative sample of the population, thus yielding less-biased (higher) population estimates. Likewise, and posing the same explanation, Garshelis and Visser (1997) observed that bear population estimates derived from tetracycline-marking in summer followed by fall harvest recaptures increased as recapture samples accumulated over several years.

Samples obtained from camera-trapping followed by hunting were the least linked of all mark–recapture couplets that we examined (Table 6), though the bias in population estimates from these samples was as great as with conventional trapping followed by hunting (Table 7). Our failure to detect a statistical link between these samples may have been due to the low power of 2 x 2 tables (risk ratios), given our sample sizes. For example, with 25 marked and 25 unmarked bears (i.e., radiocollared bears that were and were not photographed) and a recapture rate of 20% (similar to our harvest rate), marked animals would have to be 4 times more likely to be harvested than unmarked animals to observe a statistically significant link ($P = 0.05$) between the 2 samples. Increasing the marked sample to 50 bears (well more than we had, Table 6), would still require that they be twice as likely to be harvested as unmarked bears to detect linkage between the samples. We caution that for bear studies like ours, apparent independence of 2 samples may be an artifact of low power (i.e., Type II error). The least biased population estimates were produced with camera-trapping and 3 seasons of hunting returns, as there was no evidence of any linkage between these 2 samples. In fact, bears *not* photographed made up a slightly larger proportion of 3-year harvest samples than bears that had been photographed (Table 6).

RESEARCH IMPLICATIONS

The linkage between marked and recaptured samples, and the consequent bias that this engenders in population estimates, is not easily averted. It might be argued that the linkages that we observed between consecutive years of trapping were to be expected given that we used the same kinds of bait, the same kinds of traps, and even generally the same trap sites each year. However, biases also were apparent with cameras that were frequently moved to different sites, and with the hunter-killed sample (which was statewide). The common thread to all of these sampling techniques was bait; a recapture sample obtained without bait, such as with hounds (Akenson et al. 2001) or sightings from the air (Miller et al. 1997) might also be biased, but if it was biased differently than the sampling technique used for marking, population estimates would

be unbiased. Unfortunately, researchers may have limited choices insofar as techniques that can be used. We did not have the option of using hounds (which were illegal for hunting in Minnesota), and attempts to obtain a resight sample from the air failed (Garshelis 1992).

We did learn things, though, that reduced bias in our estimates, which might be helpful to other researchers. First, we found that by using 2 techniques to mark bears (trapping and radiocollaring yearlings in dens), we acquired a more representative sample than by relying on a single method. Trapping was biased against very young bears, which were precisely the bears we marked in dens. Trapping also was biased toward easy-to-catch individuals. Radiocollaring yearlings in dens of radiocollared mothers did not necessarily prevent such bias, as yearlings are linked behaviorally, through genetics and learned behavior, to their mothers. If just a few easily-trappable mothers were radiocollared, then continued sampling of their offspring would likely not be representative of the population as a whole. Nevertheless, in most cases bears procured in dens would represent a broader spectrum of behaviors than their mothers, and hence a less biased sample with regard to vulnerability to capture. In our case, we eventually radiocollared virtually all adult females, so the yearlings we radiocollared were not really a sample, but a complete cohort absent any biases. Biases crept in as cohorts aged, however, because males eventually dispersed (100% in our study) and were replaced by immigrating young males. Trapping provided the only means of maintaining a marked sample of males.

Second, it was apparent that several years of trapping were required to generate a fairly representative sample of marked bears. We trapped bears in summer and radiocollared yearlings in dens for 4 years (1981–84) before we attempted to obtain our first population estimate. Even then, we likely missed resident bears that were particularly hard to catch (Fig. 4) and possibly overloaded our sample with new male immigrants, which tended to be easy to catch (Table 2). In partial solution to this latter problem, we partitioned our mark–recapture data by sex–age group to produce real population estimates for our study area (Garshelis 1992), although before conducting the analysis here, we did not really know what those age groupings should be.

Third, we found that a recapture sample accumulated over several years (i.e., the 3 seasons of hunting recaptures) helps alleviate bias. This reaffirmed the results of Garshelis and Visser (1997), who reported that their mark–recapture estimates increased (thus becoming less biased) with additional years of bear harvest (recapture) data corresponding to each year of marking (with tetracycline). However, these authors found that population estimates continued to climb even with 6 years of accumulated recaptures. Unfortunately, accumulation of recapture samples across years is not possible for most conventional mark–recapture studies using either trapping or harvest (Garshelis and Visser's tetracycline-marking study being an exception). Without a closed population, the immigration of unmarked animals would dilute the proportion marked, so estimates of this proportion for any given year would not be valid if samples were collected several years later. In our study, where we used a fixed (demographically closed) test population of radiocollared bears, the proportion marked in any given year could be estimated using harvest samples (of collared bears) in that year plus any year thereafter. The point in our using the 3-season hunting recapture samples (Tables 5–7) was to demonstrate the source and magnitude of bias, not to suggest that this procedure could be employed in an actual study.

An important finding, already well-documented in the population estimation literature but not widely acknowledged in the bear literature, is that mark–recapture tends to underestimate population size. This may provide a sort of safeguard in terms of conservatively managing populations. However, we warn that our investigation here centered only on the types of biases that produce population underestimates. In some situations, marked animals may become *less* prone to capture than the unmarked segment, and thereby bias population estimates upward. For example, hunters may avoid shooting bears wearing radiocollars. Likewise, previously-captured bears may become trap shy, or more likely for bears, trap wise (i.e., learn how to obtain bait but avoid capture), biasing recaptures against marked individuals. To circumvent this problem in our study, we deployed snares when there was evidence that bears visiting trapsites were avoiding capture in barrel traps, and when that did not work, we used cameras to photographically identify the animal. In all such cases, the untrappable photographed bear was already radiocollared or ear-tagged, indicating that it had been handled previously (Garshelis et al. 1993). Another situation that could tilt the bias in the other direction is the ingress of a large number of dispersing young males, possibly responding to the loss (e.g., harvest) of resident adult males. As young males are typically easy to trap relative to other sex–age groups, population estimates would be inflated if these young, unmarked bears were pooled with less capture-prone bears and if their time on the study area was not taken into consideration (Garshelis 1992, 1994).

The intent of this investigation was to make bear biologists, including ourselves, more aware of the potential and likely biases in population estimates. We hope that our results spur greater efforts to consider and employ sampling designs that minimize bias, and more research, like

this, to uncover sources of bias.

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