

RESILIENCE OF A MINNESOTA BLACK BEAR POPULATION TO HEAVY HUNTING: SELF-SUSTAINING POPULATION OR POPULATION SINK?

BRIAN D. KONTIO,¹ Bell Museum of Natural History and Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA

DAVID L. GARSHELIS, Minnesota Department of Natural Resources, 1201 East Highway 2, Grand Rapids, MN 55744, USA, email: dave.garshelis@dnr.state.mn.us

ELMER C. BIRNEY, Bell Museum of Natural History and Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA, email: ecbirney@ecology.umn.edu

DAVID E. ANDERSEN, Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, USA, email: dea@finsandfur.fw.umn.edu

Abstract: We studied a heavily-hunted population of black bears (*Ursus americanus*) on the periphery of the bear range in east-central Minnesota in 1991 and 1992. This was one of the few areas in Minnesota where hunting pressure was not controlled by a quota on the number of hunting licenses. We hypothesized that the area supported high harvest levels because it was a population sink supplied by seasonal migrants, dispersing subadult male immigrants, or both from northern Minnesota. However, we captured 7 female and 5 adult male bears during late summer and from radiotracking found that all were residents of the study area. Also, the following evidence indicated that immigration of young males was not sustaining the population: (1) males made up a similar fraction of the harvest in the study area (53.6%) as statewide (53.1%); (2) the rate of decline in the ratio of males to females in each harvested age class, due to high harvest mortality that depleted male numbers faster than females, showed no sign of being retarded by an influx of males; and (3) yearling males, an age group not heavily represented among dispersers, composed a high proportion of the harvest. A simple deterministic model suggested that the population could remain stationary or grow with current harvest pressure. Thus, the area was not a population sink.

Ursus 10:139–146

Key words: black bear, hunting, immigration, population, reproduction, sink, source, *Ursus americanus*.

Bears exhibit low reproductive rates, and over-harvest of bear populations is a common concern (Smith 1985, Rogers 1987a, Miller 1990). Intentional reduction of bear numbers should then be a simple matter of increasing the harvest so that mortality exceeds reproduction. Sport harvest has been used to reduce black bear numbers and hence depredations on commercial forests in Washington (Poelker and Parsons 1980).

Since 1982 bear harvests in Minnesota have been controlled by a quota on licenses. As a result, the population has expanded both numerically and geographically through the mid-late 1980s and early 1990s (Garshelis 1990 In Press). The license quota was lifted in 1987 on the agricultural periphery of the bear range to reduce bear densities and crop depredation (Garshelis 1990). A portion of this so-called no-quota area in east-central Minnesota experienced intense hunting pressure for the 5 years following the removal of quotas, but the effectiveness of this management was equivocal. Harvests remained high, as did crop depredation complaints, according to local Minnesota Department of Natural Resources (MNDNR) conservation officers (P. Jensen and C. Rossow, Hinckley, Minn., pers. commun., 1991), suggesting that the population was not reduced by the increased hunting pressure.

This study was undertaken to ascertain how the bear population in east-central Minnesota could apparently withstand the intense harvest pressure. We hypothesized that the area might be a population sink supplied by immigration from the more forested primary bear range to the north, where harvests were limited by license quotas. The objective of this study was to determine if the principle source of recruitment to this population was either (1) immigration, in which case bears in the study area would be predominantly dispersing-age subadult males or seasonal migrants (i.e., adult bears making feeding excursions from the primary range to east-central Minnesota during the late summer) or (2) reproduction by residents in the study area.

We acknowledge the cooperation of B. Griffin, J.T. Nelson, and other employees of St. Croix State Park, and L. Hemness and K. Solberg of the MNDNR. Special thanks are owed to R.L. Ballantine, J.M. Evens, J.G. Ostheimer, and L. Schroeder for significant assistance with field work. P.L. Coy and K.V. Noyce of the MNDNR provided technical assistance. This project was funded by the Minnesota Legislature as recommended by the Legislative Commission on Minnesota Resources.

¹Present address: 723 NW 2nd Avenue, Grand Rapids, MN 55744, USA. Send reprint requests to second author, D. Garshelis.

STUDY AREA

Black bears occupy approximately the northern two-fifths of Minnesota. The 150-km² study area was located in east-central Minnesota (46°N, 92°W) at the southeastern fringe of the bear range, approximately 140 km north-northeast of Minneapolis-St. Paul (Fig. 1). This area had severe crop damage from bears since 1985. Long-time residents reported bears present since at least the 1950s, although apparently at much lower densities than in recent years.

The study area centered on a strip of agricultural land extending east of Hinckley, Minnesota. Heavily forested areas that adjoined the primary bear range in Minnesota and Wisconsin were east and north of this strip of agricultural lands; to the south, St. Croix State Park (SCSP) and Chengwatana State Forest formed a 260-km² triangle of forest. To the south and west, the landscape was densely populated and intensively farmed.

The principle crops were field corn, hay, oats, soybeans, and clover. Cattle, hogs, and sheep also were raised. The size and pattern of crop plantings ranged from small (<5

ha), isolated fields surrounded by forest to areas >500 ha almost completely cleared for agriculture. Non-agricultural lands on the study area were forested with fewer conifers and more oaks (*Quercus alba*, *Q. rubra*, *Q. ellipsoidalis*, and *Q. macrocarpa*) than forests in the primary bear range in Minnesota (Kratz and Jensen 1983).

The climate of the region was cool continental with mean annual precipitation of 72 cm. Mean January and July temperatures were -12.5 and 21.4 C, respectively. The growing season averaged 140 days, and snow cover lasted from around 20 November to 10 April. The topography was flat to gently rolling with elevations ranging from 105 to 340 m above sea level. Non-organic soils were mostly reddish sands and sandy loams formed on glacial deposits. There were a few small lakes in the eastern portion of the study area. The Kettle and the St. Croix were the main rivers in the region (MNDNR 1985).

The black bear hunting season extends from 1 September until mid October, although in recent years, >75% of bears harvested were killed before 15 September (MNDNR, unpubl. data). About 75% of hunters attracted bears with bait; hunters could begin baiting on 15 August. Hunting was prohibited in SCSP.

The density of the registered harvest (bears killed/area) in the no-quota hunting zone in east-central Minnesota exceeded that in the primary range. For the 5 years following the removal of harvest quotas (1987–91), registration block 159, a 1,454-km² unit that included the study area, had a mean annual harvest density that was higher (7.5 bears killed/100 km²) than in any other block in the state (next highest = 6.9 bears killed/100 km²; MNDNR unpubl. data; Fig. 1).

METHODS

Bears were captured in barrel traps baited with bacon scraps (Kohn 1982), except for 1 free-ranging bear fortuitously captured in its den and another treed by hounds and immobilized with a tranquilizer dart. Captured bears were immobilized with an intramuscular injection of tiletamine and zolazepam (Telazol®, Fort Dodge Laboratories, Fort Dodge, IA; \bar{x} = 6.5 mg/kg) administered with a jab-pole syringe. Age was estimated by sectioning an upper first premolar and counting cementum annuli (Wiley 1974). Bears <3-years old were categorized as subadults. The spacing of cementum annuli was used to estimate ages of first reproduction for adult females (Coy and Garshelis 1992). Bears were released where they were captured. All bears were ear tagged and most (72%) were fitted with radiocollars (Advanced Telemetry Systems, Isanti, Minn.). Radiocollared bears were visited in dens during winter to assess reproduction and weight changes

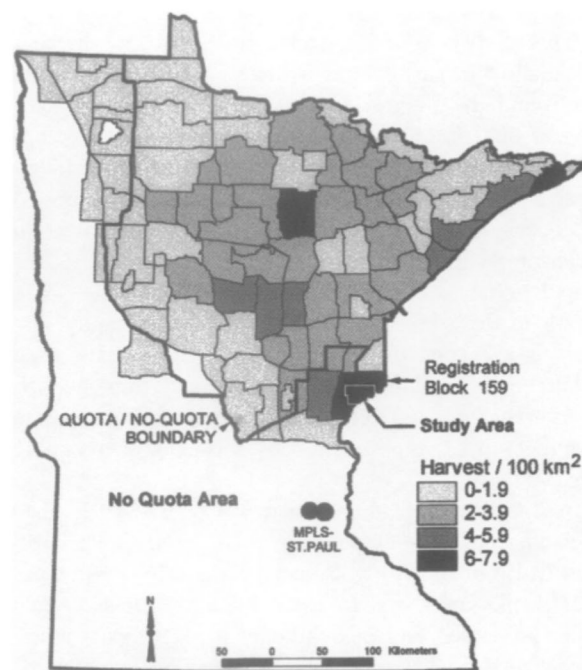


Fig. 1. Mean harvest/100 km² during 1987–91 in bear registration blocks in northern Minnesota. The study area (outlined in white) was located in registration block 159, a block within the no-quota area that had the highest harvest density in the state, partly because of its proximity to Minneapolis (Mpls)-St. Paul.

and to refit or remove radiocollars. Denning bears also were immobilized with Telazol ($\bar{x} = 4.5$ mg/kg).

We attempted to trap and mark bears uniformly across the study area. We trapped from 15 July until 24 August 1991 and from 15 May until 24 August 1992 on a 150-km² rectangular grid with trap sites approximately 3-km apart. We also captured bears adjacent to corn fields with bear damage during August 1992. Capture attempts were terminated 1 week before the opening of the bear hunting season because the use of immobilizing drugs for bears that might later be consumed by hunters was restricted.

We located radiocollared bears by triangulation from the ground with a hand-held, 3-element Yagi antenna or a 4-element antenna mounted on a vehicle. When a bear could not be located from the ground, we used an aircraft with 2 side-looking, 4-element antennas (Mech 1983). Locations of radiocollared bears were plotted in the field on 7.5-minute U.S. Geological Survey topographic maps and recorded as universal transverse mercator (UTM) grid coordinates. In 1991, bears were located at least biweekly from capture until they denning. In 1992, bears were located at least biweekly from den emergence until 15 July. From 16 July to 30 August, bears were located weekly, and during the hunting season (1 Sep–18 Oct) they were located twice weekly. Bears that dispersed from the study area were located approximately biweekly. We located bears during 0800–1700 hours except during the first 2 weekends of the hunting season, when we also obtained locations during 1700–1900 hours (when most bears were harvested).

We categorized female and adult male bears captured from 15 July until 24 August as residents if they remained within the study area through the fall and for denning, and as seasonal migrants if they were present only during late summer. Subadult males could have been dispersing from an unknown natal area, so their residency status was uncertain.

We investigated potential dispersal into the study area by comparing the age and sex composition of the harvest (MNDNR, unpubl. data) in registration block 159 (Fig. 1) to the composition of the harvest in the primary bear range. We pooled data from 1988–92 to minimize the effects of year-to-year variations in relative vulnerabilities of different sex and age classes, induced by fluctuations in natural food abundance.

To evaluate the potential influence of harvest, the resident bear population in the no-quota area of east-central Minnesota was simulated using a simple, deterministic model that begins with a population estimate in the past, and for each subsequent year subtracts documented and estimated mortality and adds estimated age-specific re-

production. Year-specific, non-hunting mortality was derived from MNDNR enforcement records of nuisance-killed and vehicle-killed bears (adjusted for estimated reporting rates), combined with sex–age specific rates of natural mortality observed in a telemetry study in north-central Minnesota (Garshelis et al. 1988). The tally and composition of each year's harvest was determined from mandatory registration of hunter-killed bears (adjusted for noncompliance and wounding loss) and tooth submission for age estimation. Reproductive inputs were based on data from radiomarked bears and reproductive histories gleaned from the spacing of annulations in teeth submitted by hunters statewide (Coy and Garshelis 1992). We initiated the model with various starting populations and selected the run in which the population size for 1991 matched the estimate obtained in a tetracycline mark–recapture study conducted that year (Garshelis and Visser 1997).

We estimated density on the study area in 1992 using the Petersen mark–recapture equation with Chapman's (1951) correction for sampling without replacement, because the recapture sample was obtained from bears killed by hunters. Hunters who registered a bear at a registration station in or adjacent to the study area indicated the bear's sex and plotted the location of their kill. The bear was weighed and a tooth was extracted for age estimation.

The recapture area used for calculation of density was delineated by circumscribing the contiguous home ranges of radiocollared bears located in the study area during 25 August–30 September. Home ranges were drawn as minimum convex polygons (Mohr 1947). Bears that left the recapture area or moved into SCSP (which was closed to hunting) were weighted in the Petersen equation in proportion to the amount of time they spent in the recapture area (Garshelis 1992). Separate density estimates (summed to obtain total density) were made for adult females, subadult females, adult males, and subadult males because probability of capture (harvest) likely differed by sex–age group.

We used remote cameras to estimate the proportion of marked bears in the unharvested SCSP (Garshelis et al. 1993). Camera stations consisted of 0.5 kg of bacon wired to a tree approximately 2 m above the ground, 3–5 m in front of a 35-mm autofocus camera equipped with a heat- and motion-sensitive triggering mechanism (Non Typical Engineering, Green Bay, Wis.). Photographed bears were identified as marked or unmarked based on presence or absence of ear tags and a radiocollar. When a bear visit was recorded, the station was moved to a new location to reduce the probability of

multiple photographs of the same bear. Stations were spaced approximately 3-km apart on a grid.

We could not estimate adult male density from harvest returns because no marked adult males were harvested. Thus, to estimate density outside SCSP, we estimated adult male density inside SCSP and applied this to the rest of the study area. We used the photographs of bears inside SCSP to differentiate adult males based on apparent size and body proportions (or individual identification in 1 photograph).

Hunting mortality for 1991 and 1992 was calculated for each sex-age class by dividing the number of marked bears harvested by the number of marked bears present on the study area during the hunting season.

RESULTS AND DISCUSSION

Immigration of Seasonal Migrants

No bears captured during this study appeared to be seasonal migrants. Of 43 bears captured, 7 females and 5 adult males were trapped during the late summers of 1991–92. Five females and all males were categorized as residents because they denned on the study area and remained there the following summer. Two of the females captured in August were radiotracked <6 months, so we were not certain of their residency status, although both remained on the study area.

That we captured no seasonal migrants was unexpected, given a tendency for southward feeding excursions among bears from northern Minnesota (Rogers 1987a, Garshelis et al. 1989) and the stable, rich food source provided by crops in and around our study area. In northeastern Minnesota, Rogers (1987a) reported that 42 (40%) of 105 female and 20 (67%) of 30 male bears traveled >7 km outside their usual home range; most movements were southward to a food-rich area. Garshelis et al. (1989) reported that 40 (85%) of 47 females moved at least 1.5 km beyond the perimeter of their spring-summer ranges in north-central Minnesota during a year of scarce natural food. As in northeastern Minnesota, most movements were southward to areas where mast-bearing oaks provided more abundant food.

Our data would have been biased toward resident bears if these movements tended to occur after 24 August, when we stopped trapping. However, Rogers (1987a:63–72) reported that 53% of females and 77% of males that made excursions from his study area left before late August. Thus, if bears did migrate into our study area, some should have been present by late August.

Natural food supplies may affect the extent of seasonal migrations by bears from northern Minnesota (Rogers 1987a, Garshelis et al. 1989), so the lack of seasonal migrants on our study area conceivably could have been attributable to abundant food to the north. However, food availability, assessed from an annual statewide survey (MNDNR unpubl. data), was about average in 1991 and below average in 1992. These data suggest that our results were not an artifact of circumstances during the study.

Immigration of Dispersing-age Males

We hypothesized that the study area might serve as a population sink for dispersing subadult males from the primary range. If this were true, the sex ratio of the harvest should have reflected male-biased recruitment and the sex-age structure should have been skewed toward dispersing-age males.

Harvest Sex Ratio.—From 1988–92, harvest sex ratios in registration block 159 (53.6% male) were similar to those in the primary range (53.1% male; $\chi^2 = 0.16$, 1 df, $P = 0.82$). In an area where most mortality is due to hunting, the sex ratio of the harvest should be close to the sex ratio of population recruits (Bunnell and Tait 1980, Garshelis 1993). In a closed population, the source of recruitment is births, so there will be roughly equal numbers of males and females in the harvest, although males will tend to be harvested at a younger age. In a dispersal sink, the source of recruitment is largely immigration, which is male-biased in black bears (Alt 1978, Le Count 1982, Rogers 1987b, Garshelis et al. 1988, Schwartz and Franzmann 1992), and the harvest sex ratio should reflect this male bias. Harvest sex ratios presented here did not indicate immigration into our study area.

Harvest Sex-Age Structure.—Males comprised 69% of yearlings harvested in block 159 during 1988–92, 57% of 2-year olds, 43% of 3-year olds, and 31% of ≥4-year olds. In the primary range, the decline in percent males by age group was somewhat more gradual: 69% of yearlings, 70% of 2-year olds, 59% of 3-year olds, and 27% of ≥4-year olds.

Males are more susceptible to harvest than females; therefore, in a closed population, the fraction of males in the harvest declines in each successive age-class until females outnumber males. The age at which this occurs is inversely related to the rate of harvest (Fraser et al. 1982, Fraser 1984). However, in a population where immigration of dispersing males is a significant source of recruitment, the influx of young males would retard the decline in the proportion of males in each succeeding age class. Our data suggest that the decline in proportion

of males in successive age classes in the area around our study area was not retarded by an influx of males.

Yearlings were the most frequent age class of males harvested in block 159 (50% of males). In the primary range, 1- and 2-year old males were harvested with nearly equal frequency (28 and 29%, respectively). If immigration were important, dispersing bears should be common in the harvest. Male bears in northern Minnesota generally dispersed at age 2 or 3 (Rogers 1987b, Garshelis et al. 1988), so the high proportion of yearlings harvested in block 159 was not due to immigration; it might be due to more intense hunting pressure, less hunter selectivity, or other factors. Regardless, the harvest sex-age structure does not indicate an influx of dispersing-age males.

Self-sustaining Resident Population

Our estimate of the pre-harvest density on the hunted portion of the study area in 1992 (excluding cubs) was 32.7 bears/100 km², which was higher than most other harvested black bear populations in North America (Garshelis 1994), including northern Minnesota. Extrapolating this estimate to the entire no-quota area of east-central Minnesota (Fig. 1) yielded a population size of approximately 1,600 bears, higher than the population estimate based on tetracycline mark-recapture (1,400 bears; Garshelis and Visser 1997; Garshelis unpubl. data). Even using the lower, tetracycline-based population estimate, the population model suggested that bear numbers in the no-quota area were stable or increasing under the observed harvest levels (Fig. 2). To ascertain whether the results of this modeling were reliable, we compared rates of reproduction and mortality in the model to those estimated from data obtained in this study.

Reproduction.—In our study, 3 of 10 (30%) females had first litters as 3-year olds and 4 of 5 (80%) females that did not produce cubs at 3 had litters as 4-year olds. However, for the model we estimated the age of first reproduction more conservatively, based on an extensive statewide database: 2–12% (yearly variation) of 3-year olds and 40–57% of 4-year olds produced first litters. We also used a more conservative 2.6 cubs/litter in the model than the observed mean litter size of 2.8 cubs/litter ($n = 8$) on our study area.

High reproductive potential in the no-quota zone fits with the good food supply there compared to the primary range. Habitat quality is the primary factor influencing the reproductive potential of bears (Jonkel and Cowan 1971, Rogers 1976, Beecham 1980, Garshelis 1994). In east-central Minnesota, oaks were much more common than in northern Minnesota (Rogers 1987a, Garshelis et al. 1989). Moreover, white oak, which produces a pre-

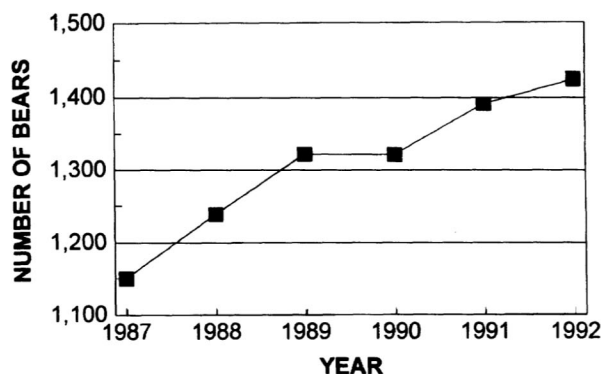


Fig. 2. Simulation of population trend for black bears in the no-quota zone in east-central Minnesota based on a 1991 initial population estimated from a tetracycline mark-recapture study. Mortality estimates were derived from known harvests and estimates of non-hunting mortality; reproductive parameters were from a radiotelemetry study and examination of annulations of teeth of female bears harvested statewide.

ferred, high-quality bear food (Garshelis and Pelton 1981), occurred on the study area, but was at the northern limit of its distribution in east-central Minnesota (Morley 1974). Bears also likely benefitted from several human-related food sources on the study area such as corn (Elowe and Dodge 1989) and hunters' baits (Kolenosky 1990), both of which were more common in the no-quota area than farther north. Bears harvested in the no-quota area were heavier than bears of the same sex-age class harvested in northern Minnesota (MNDNR, unpubl. data).

Mortality.—Mortality rates derived in our model (actual harvest/estimated population size) were similar to rates observed in our study for adult females and subadult males (Table 1). The model indicated lower mortality than we observed for subadult females (but with a very small sample) and a higher mortality than we observed among adult males (no marked adult males were harvested). Our data and the model suggested that subadults of both sexes had higher rates of harvest mortality than their counterparts in the primary range (MNDNR, unpubl. data), but despite the high harvest pressure (Fig. 1), adults in the no-quota area experienced somewhat lower harvest mortality than adults farther north.

The relatively low harvest mortality among adults may have several explanations. First, bears in east-central Minnesota have more human contact due to intense hunting pressure and relatively high rural human population density (Borchert 1980). Thus, surviving adult bears may exhibit cryptic behaviors that enable them to evade hunters. Cryptic behavior has been reported in black bears in Colorado (McCutchen 1990) and in brown bears (*U.*

Table 1. Harvest mortality (percent) observed among marked bears on the study area in east-central Minnesota in 1992 versus mortality estimated by modeling the population in the no-quota area.

	Subadult females	Adult females	Subadult males	Adult males
Empirical data	33 (1/3 ^a)	20 (2/10 ^a)	31 (4/13 ^b)	0 (0/8 ^a)
Model	19	15	36	17

^a Number harvested in study area/number present on study area at the onset of the hunting season.

^b Number harvested/number marked and presumed alive at the start of the harvest (most subadult males dispersed from the study area).

arctos) in Europe (Roth 1983). Many hunters in the study area reported night visits to their baits (hunting is restricted to daylight hours). Second, in parts of Minnesota where the number of hunters is limited by a quota, hunters may be more likely to pass up subadult bears in favor of adults because hunters wait a number of years before obtaining a bear license and because yearlings in the primary range are smaller and thus less desirable. Finally, hard mast and corn, both high quality bear foods (Elowe and Dodge 1989), are well-distributed in east-central Minnesota, whereas bear food in the primary range is less abundant and less evenly distributed (MNDNR unpubl. data). Thus, bears in the primary range may have fewer options to hunters' baits.

Conceivably, refugia such as SCSP, several other large blocks of public land with poor access to hunters, and some private land closed to hunting could protect some bears from hunting. However, movements and mortality of radiocollared bears area did not support this hypothesis. Of 8 radiocollared females that were usually located in SCSP during June–July, 6 were located outside of the park and thus vulnerable to hunters at the start of the hunting season in September. Perhaps they were attracted to hunters' baits or corn fields. Three of these bears moved back into the park between September 8 and 11, but most of the harvest occurred earlier in the season (in 1992, 70% of bears harvested in block 159 were killed by 6 Sept). Additionally, female bears at the edge of SCSP during the hunting season seemed more likely to be killed (2 of 7) than females further outside the park (0 of 3). Kill locations suggested that hunters concentrated their efforts along the park's edge: 1 bear/3.8 km² were harvested from the sections along the northern edge of SCSP, whereas harvest in the study area excluding this strip was about 1 bear/10 km². Although SCSP was the largest unharvested area in the no-quota zone, it was not big enough to protect bears from hunting (bears could be no more

than 3 km from a boundary), and thus may be more of an attraction to hunters than a refuge for bears.

MANAGEMENT IMPLICATIONS

Despite the study area's position near the periphery of the bear range in Minnesota and the unrestricted number of hunters, the study area did not appear to be a population sink for black bears. We initially hypothesized that the area attracted both seasonal migrants and immigrating subadults, explaining how it could support extraordinarily high harvest pressure and yet continue to have high nuisance activity and apparently high numbers of bears. However, no evidence of an influx of seasonal migrants or dispersing subadult males was detected. The population model, which used conservative estimates of reproduction, suggested that the population was stationary or increasing under observed harvest levels.

These findings have several implications for management. First, because local reproduction appears to be the primary source of population recruitment in the study area, management of bear–human conflicts in this area needs to be directed locally. Efforts aimed to slow recruitment from the primary bear range (i.e., increasing the harvest or managing habitat) will probably have little effect in east-central Minnesota.

In addition, greater flexibility in harvest methods may be required in east-central Minnesota. For example, hunting with hounds (currently illegal) would allow hunters to better target nuisance bears and bears not attracted to hunters' bait stations during legal shooting hours. Moreover, hound hunters would not have to use bait, which provides a significant food source in the study area and possibly enhances reproduction and encourages nuisance activity. However, hound hunting is likely to be unpopular with many bear hunters, land-owners, and animal-welfare advocates, and thus might not be a viable option in east-central Minnesota. Another improvement might be to open the season earlier, when bears begin feeding in cornfields. Finally, programs could be developed to give hunters greater access to public and private lands in the area. Gated public forest roads could be opened during bear season, and programs could be developed to improve hunter access to private lands. If reducing bear numbers in east-central Minnesota is desirable, strategies in addition to the current no-quota harvest will be required.

Finally, there is potential for continual crop depredation and other bear–human conflicts in the study area. The high incidence of crop depredation witnessed in the mid-1980s, which spurred the MNDNR to lift harvest quotas in the agricultural periphery of the bear range, was

due in large part to scarcity of natural food, conditions that we did not observe during the 2 years of our study. It is just a matter of time before such conditions occur again; the incidence of bear-human conflicts may then return to levels equaling or even exceeding those encountered during the last decade.

LITERATURE CITED

- ALT, G.L. 1978. Dispersal patterns of black bears in northeastern Pennsylvania—a preliminary report. East. Workshop Black Bear Res. and Manage. 4:186–199.
- BEECHAM, J.J. 1980. Some population characteristics of two black bear populations in Idaho. Int. Conf. Bear Res. and Manage. 4:201–204.
- BORCHERT, J.R. 1980. Atlas of Minnesota resources and settlement. Univ. Minnesota Press, Minneapolis. 309pp.
- BUNNELL, F.E., AND D.E.N. TAIT. 1980. Bears in models and reality—implications to management. Int. Conf. Bear Res. and Manage. 4:15–23.
- CHAPMAN, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. Univ. Calif. Publ. in Statistics. 1:131–160.
- COY, P.L., AND D.L. GARSHELIS. 1992. Reconstructing reproductive histories of black bears from the incremental layering in dental cementation. Can. J. Zool. 70:2150–2160.
- ELOWE, K.D., AND W.E. DODGE. 1989. Factors affecting black bear reproductive success and cub survival. J. Wildl. Manage. 53:962–968.
- FRASER, D. 1984. A simple relationship between removal rate and age–sex composition of removals for certain animal populations. J. Appl. Ecol. 21:97–101.
- , J.F. GARDNER, G.B. KOLENOSKY, AND S. STRATHEARN. 1982. Estimation of harvest rate of black bears from age and sex data. Wildl. Soc. Bull. 10:53–57.
- GARSHELIS, D.L. 1990. Minnesota status report. East. Workshop Black Bear Res. and Manage. 10:44–48.
- . 1992. Mark–recapture density estimation for animals with large home ranges. Pages 1098–1111 in D.R. McCullough and R.H. Barrett, eds. Wildlife 2001: Populations. Elsevier Appl. Sci., London, U.K.
- . 1993. Monitoring black bear populations: pitfalls and recommendations. West. Black Bear Workshop. 4:123–144.
- . 1994. Density-dependent population regulation of black bears. Pages 3–14 in M. Taylor, ed. Density-dependent population regulation of black, brown, and polar bears. Int. Conf. Bear Res. and Manage. Monogr. Series No. 3.
- . In Press. Minnesota status report. East. Workshop Black Bear Res. and Manage. 12.
- , P.L. COY, AND B.D. KONTIO. 1993. Applications of remote animal-activated cameras in bear research. Proc. Int. Union Game Biol. 21(1):315–322.
- , K.V. NOYCE, AND P.L. COY. 1988. Ecology and population dynamics of black bears in north-central Minnesota. Pages 43–53 in B. Joselyn, ed. Summaries of wildlife research project findings, 1987. Minn. Dep. Nat. Resour., Wildl. Populations and Res. Unit Rep., St. Paul.
- , ———, AND ———. 1989. Ecology and population dynamics of black bears in north-central Minnesota. Pages 36–49 in B. Joselyn, ed. Summaries of wildlife research project findings, 1988. Minn. Dep. Nat. Resour., Wildl. Populations and Res. Unit Rep., St. Paul.
- , AND M.R. PELTON. 1981. Movements of black bears in the Great Smoky Mountains National Park. J. Wildl. Manage. 45:912–925.
- , AND L.G. VISSER. 1997. Enumerating megapopulations of wild bears using an ingested biomarker. J. Wildl. Manage. 61:446–479.
- JONKEL, C.J., AND I.M. COWAN. 1971. The black bear in the spruce-fir forest. Wildl. Monogr. 27. 57pp.
- KOHN, B.E. 1982. Status and management of black bears in Wisconsin. Wisconsin Dep. Nat. Resour. Tech. Bull. No. 129. 31pp.
- KOLENOSKY, G.B. 1990. Reproductive biology of black bears in east-central Ontario. Int. Conf. Bear Res. and Manage. 8:385–392.
- KRATZ, T.K., AND G.L. JENSEN. 1983. Minnesota landscape regions. Nat. Areas J. 3:33–44.
- LECOUNT, A.L. 1982. Characteristics of a central Arizona black bear population. J. Wildl. Manage. 46:861–868.
- MCCUTCHEN, H.E. 1990. Cryptic behavior of black bears (*Ursus americanus*) in Rocky Mountain National Park, Colorado. Int. Conf. Bear Res. and Manage. 8:65–72.
- MECH, L.D. 1983. Handbook of animal radio-tracking. Univ. of Minnesota Press, Minneapolis. 107pp.
- MILLER, S.D. 1990. Population management of bears in North America. Int. Conf. Bear Res. and Manage. 8:33–56.
- MINNESOTA DEPARTMENT OF NATURAL RESOURCES. 1985. Moose Lake Area Forest Resource Management Plan. Minn. Dep. of Nat. Res., Division of Forestry, St. Paul.
- MOHR, C.O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223–249.
- MORLEY, T. 1974. Spring flora of Minnesota. Univ. of Minnesota Press, Minneapolis. 283pp.
- POELKER, R.J., AND L.D. PARSONS. 1980. Black bear hunting to reduce forest damage. Int. Conf. Bear Res. and Manage. 4:191–193.
- ROGERS, L.L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Trans. North Am. Wildl. and Nat. Resour. Conf. 41:431–438.
- . 1987a. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl. Monogr. 97. 72pp.
- . 1987b. Factors influencing dispersal in the black bear. Pages 75–84 in B.D. Chepko-Sade and Z.T. Halpin, eds. Mammalian dispersal patterns. Univ. Chicago Press, Chicago, Ill.
- ROTH, H.U. 1983. Activity of a remnant population of European brown bears. Int. Conf. Bear Res. and Manage.

- 5:223–229.
- SCHWARTZ, C.C., AND A.W. FRANZMANN. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *J. Wildl. Manage.* 56:426–431.
- SMITH, R.P. 1985. Are we taking too many bears? *Mich. Out-of-doors.* 39:64–67.
- WILLEY, C.H. 1974. Aging black bear from first premolar tooth sections. *J. Wildl. Manage.* 38:97–100.