

THE EFFECTS OF HUNTING ON AN ONTARIO BLACK BEAR POPULATION

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Abstract: The effects of hunter harvest on a tagged sample of black bears (*Ursus americanus*) (198 males, 144 females) in east-central Ontario were investigated from 1969 to 1980. Hunters annually removed an average of 18% of available males and 10% of available females during spring hunts and 5% of available males and 2% of available females during fall hunts. During the 12 year period, hunters shot 32% of all tagged males and 28% of all tagged females. Mean and maximum elapsed times between tagging and hunter kills were 2.1 and 6 years, respectively, for males and 3.4 and 11 years, respectively, for females. Males aged 2–6 years were more vulnerable than younger or older males. For females, 3- to 6-year-olds were more vulnerable than the younger or older age classes. Females older than age 6 appeared relatively invulnerable, as only 13 of 35 different bears at risk for a total of 292 years were harvested. Eight of those kills occurred during the final 3 years, when spring hunting pressure on the study area increased by 700% over the 1969 level. The frequency of movements > 20 km between capture and kill sites was greater for males than females. More males (72%) than females (20%) were killed outside the study area. The major effects of hunting were to reduce population size and lower the mean age of captured males. The prolonged period of maturation for black bears in Ontario, and the increased vulnerability of adult females, with increased hunting pressure emphasized the need for conservative provincial harvest quotas.

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Sport hunting is frequently regarded as 1 of the major factors limiting black bear populations in regions with heavy hunting pressure (Wakefield 1972, Lindzey et al. 1976, Gilbert et al. 1978, Beecham 1980). Returns from hunter harvests are often used to assess population abundance and structure (McIlroy 1972, Willey 1978, Lindzey and Meslow 1980). Although it is widely recognized that males are generally more vulnerable to hunters than females (Bunnell and Tait 1980, Fraser et al. 1982) the degree of vulnerability is rarely known because no marked sample is available for comparison.

This paper discusses the availability of different sex and age classes of tagged black bears and their removal by hunters. Objectives of the study were to investigate the proportion of tagged bears removed seasonally and annually, determine the relative vulnerability of specific age and sex groups, assess changes in vulnerability with changes in hunting pressure, and estimate annual nonhunting mortality for specific age and sex groups. Data were collected as part of a comprehensive ecological study of the species conducted in east-central Ontario from 1969 to 1980.

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STUDY AREA

The primary study area of 233 km² is in east-central Ontario at approximately 46° 45' North latitude and 79° 20' West longitude (Fig. 1). Underlain by the Canadian Shield, the area is characterized by exposed outcrops of granites, gneisses, and basalts interspersed with sections overlain by glacial and lacustrine deposits (Boissonneau 1968). Much of the western portion is composed of sandy or silty till of low relief; the eastern section varies from gentle undulating and interlobate moraines to precipitous cliffs surpassing 30 m in height. Soils are shallow and consist largely of a mixture of sand, gravel, and boulders. Approximately 11% of the study area consists of small, deep, clear lakes.

Situated within the Great Lakes-St. Lawrence Forest Region (Rowe 1972), the area represents an ecotone between the deciduous forest farther south and the boreal forest to the north. On upland sites, the original forest dominated by red and white pine (*Pinus resinosa*, *P. strobus*) has been largely replaced by a mixture of poplars (*Populus tremuloides*, *P. grandidentata*), white birch (*Betula papyrifera*), jack pine (*P. banksiana*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and maples (*Acer saccharum*, *A. rubrum*, *A. spicatum*) as a result of logging and fires. In lowland sites, black spruce (*P. mariana*), larch (*Larix laricina*), white cedar (*Thuja occidentalis*), and speckled alder (*Alnus rugosa*) are common species. The complex interspersed of deciduous and coniferous trees ranging 0–70 years in age has produced a diverse habitat highly suitable for bears.

The climate of the area is humid continental (Dep. of Mines and Technical Surveys 1957) with cool sum-

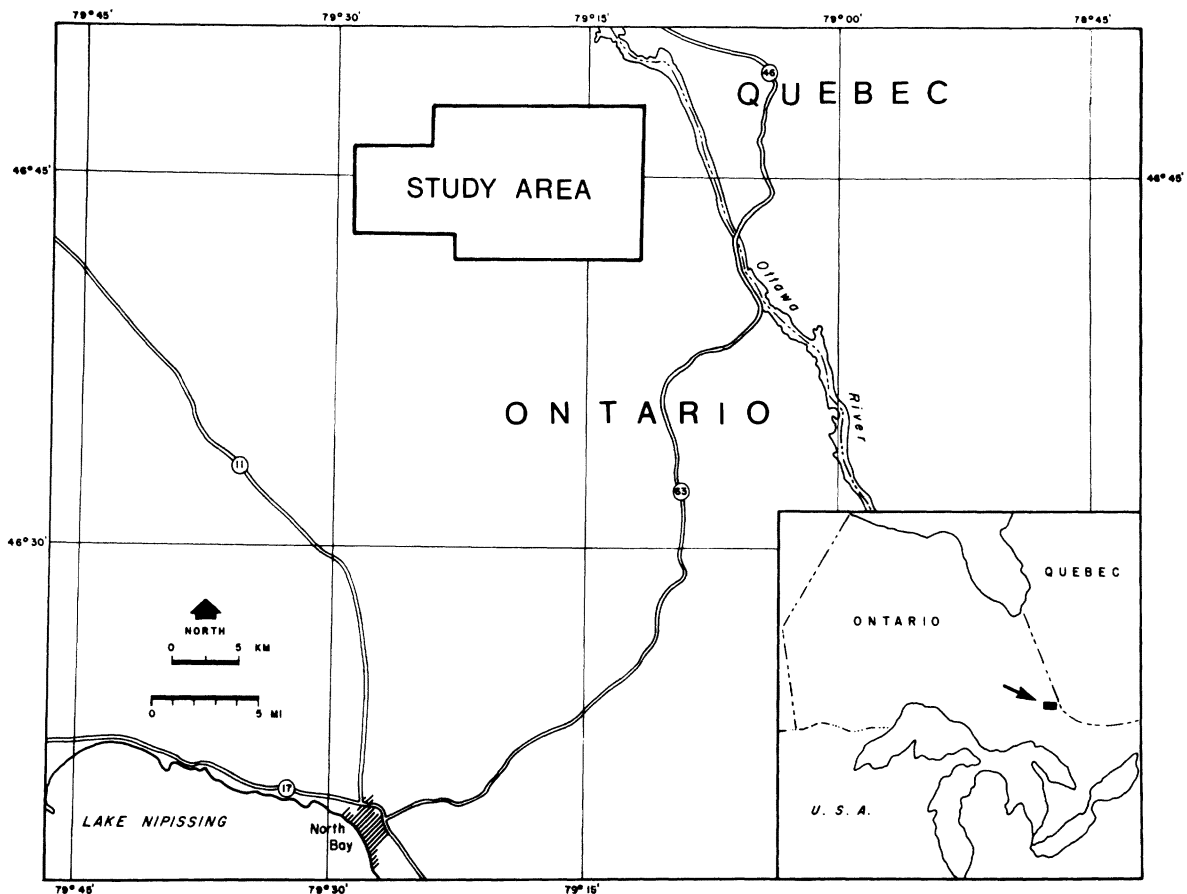


Fig. 1. Location of the North Bay study area.

mers and no dry season. Mean monthly temperatures during January and July for North Bay, approximately 40 km south of the study area, were -12.8 C and 18.3 C, respectively. Average total precipitation was 98.8 cm annually (Annual Meteorological Summary, North Bay Airport, 1978).

METHODS

During all years from late May to early September we captured bears in Aldrich leg snares or occasionally with barrel traps. We immobilized each captured bear (Addison and Kolenosky 1979) and then weighed, measured, and extracted a premolar tooth to determine bear age (Stoneberg and Jonkel 1966). We placed a numbered aluminum ear tag bearing the inscription ONT MIN NAT RES in each ear. In 1969 and 1970, we tattooed each captured bear in the lower lip. Cubs that we extracted from dens during winter denning studies from 1976 to 1980 (Kolenosky and Strathearn, unpubl. data) were tagged

with smaller aluminum ear tags. Commencing in 1970, we fitted selected individuals with radiocollars marked with a reward offer, address, and telephone number (Voigt and Lotimer 1981). Radiotracking gave us additional information about the survival of individuals not recovered. In 2 instances adult females were known to be alive and on the study area even though they were never recaptured.

From fall 1969 to spring 1973, the hunting season for black bears extended from 1 September to 30 June of the following year. In 1973, the fall season was shortened (15 Sep–30 Nov), as was the 1974 spring season (15 Apr–15 Jun). The latter dates remained in effect through the rest of the study. Thus, during the 1st 4 years the season was 303 days long, whereas the combined spring (63 days) and fall (77 days) seasons during the latter 7 years were only 140 days. However, the effective season was similar for all years because most bears were in winter dens between early November and early April and therefore were generally unavailable to hunters.

Use of rifles, shotguns, black powder, and archery weapons was allowed, as were baiting, stalking, still-hunting, and dogs. Any bear was legal, including cubs and females with cubs. Only 1 bear per license could be taken, but hunters could purchase more than 1 license in either spring or fall. Multiple purchases of licenses were infrequent. During the spring, most hunting was done by nonresidents still hunting over baits, whereas in the fall most bear kills were incidental to white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) hunting. Use of dogs within the study area and vicinity was infrequent and did not occur until the late 1970s.

We annually requested outfitters and hunters within the study area and immediate vicinity to report any tagged bear that had been shot. Whenever possible, we examined the harvested bear and informed the hunter of its history. We determined hunter effort on the study area from direct contact with the local outfitter and casual hunters. A single access road into the study area ensured that all hunters could easily be monitored. We expressed hunting effort as hunter-days (1 hunter hunting for 1 day = 1 hunter-day) (Fig. 2). We based hunting effort in the regions surrounding the study area on the number of registered outfitters and local license sales. Accuracy of our estimates was verified by a questionnaire sent to outfitters in the spring of 1977. Additional checks of selected outfitters were conducted by research personnel and conservation officers.

We estimated maximum nonhunting mortality by 2 methods. In method 1, the maximum nonhunting mortality rate was derived by dividing the number

of tagged bears never recovered by the total number of different bears tagged (Jonkel and Cowan 1971:40). This method could be applied only to bears tagged from 1969 to 1974 because it required a minimum of 6 years to assure maximum recovery of tags (Fig. 3). In method 2, the maximum nonhunting mortality rate was derived by dividing the number of tagged bears never recovered by the number of tagged bears assumed to be available at the start of each year. Each yearly sample consisted of bears tagged before that year and known to still be alive. For example, a bear tagged in 1969 and subsequently recovered in 1972 was considered part of the sample available for recovery in 1970 and 1971. If it was never recovered after 1972, it was assumed to have died or disappeared in 1972. Recoveries included all bears handled or reported subsequent to initial capture. We consider estimates of nonhunting mortality to be maximum rates because of our inability to differentiate between death and dispersal of tagged animals never recovered.

The number of tagged individuals for each age class available to hunters before annual spring and fall hunts was equal to the total number of bears tagged minus the calculated maximum nonhunting mortality and known deaths from all causes. All individuals tagged during a particular year were considered available for the fall hunt of that year but not the spring hunt. Cubs were not considered available for the spring hunt but were available for the fall hunt if tagged that year.

We determined age-specific vulnerability to hunting by comparing kill rates of age classes. Kill rate per age class represented the proportion killed of the

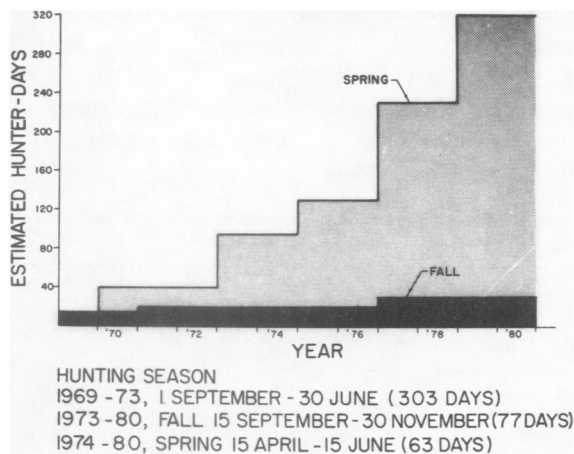


Fig. 2. Bear-hunting effort during spring and fall on the North Bay study area, 1969-80.

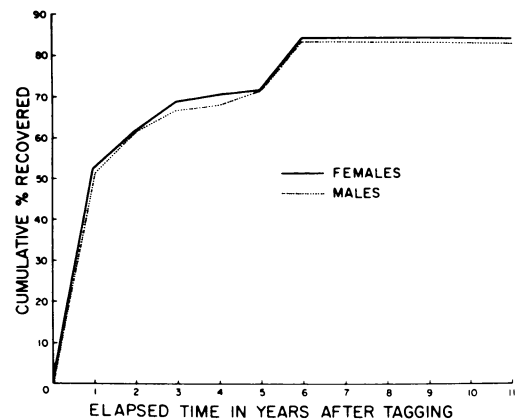


Fig. 3. Cumulative percentage of tagged bears recovered by all methods at yearly intervals after tagging, North Bay study area, 1970-80.

total available. Numbers available included all tagged bears of that age class available for at least 1 hunt. For example, a bear tagged as a cub in 1975 and subsequently known to be alive in the summer of 1978 was considered available as a cub in the fall of 1975, a 1-year-old in 1976, a 2-year-old in 1977, and a 3-year-old in the spring of 1978. Bears ≥ 4 years of age were classified as adults and those < 3 years of age as subadults. The latter included cubs unless indicated otherwise.

Statistical analyses were according to Zar (1974). A t-test was used to compare the ages of adult females killed from 1970 to 1976 with those killed from 1977 to 1980. Chi-square tests were used for all other statistical comparisons. The 5% level of probability was considered significant.

RESULTS

Bears Tagged

Between 1969 and 1980 we captured, tagged, and released 342 bears (198 males, 144 females). Table 1 shows the number of captured individuals within specific age classes. Tag loss was not considered to have affected results, because fewer than 2% of tagged bears older than winter tagged-cubs lost 1 tag and no recovered bear examined had lost both tags (1,100 handlings). Ear tags were known to persist a minimum of 12 years for females and 8 years for males. Although some tag loss was recorded for cubs tagged in the den, all recaptured winter-tagged cubs were

Table 1. Age-class distribution of black bears captured on the North Bay study area, 1969–80.

Year	Cubs		Yearlings (1–3 yrs)		Adults (≥ 4 yrs)	
	Males	Females	Males	Females	Males	Females
1969	0	0	2	4	16	9
1970	0	0	4	3	14	7
1971	2	0	1	2	10	11
1972	2	1	3	4	7	7
1973	3	1	7	6	13	14
1974	2	1	12	8	14	19
1975	10	8	28	8	16	27
1976	9	4	19	10	11	24
1977	10	10	14	8	11	25
1978	5	7	15	15	9	24
1979	3	0	18	14	3	24
1980	5	5	18	14	11	18
Totals	51	37	141	96	135	209
Ratio M:F	138:100		147:100		65:100	

retagged. Those not captured and retagged were not included in calculations.

Failure of hunters to report tagged bears was considered negligible. The offer of a reward for the return of radio-collars, the publicity surrounding the study, and the natural curiosity of hunters seeking information about the history of the tagged bear they had just killed all contributed to an extremely high reporting rate, if not 100%.

Hunting effort on the study area and surrounding vicinity was greatest during the spring season. Effort during the fall hunt was considerably less because most bears were taken incidentally by residents whose primary interest was in moose and deer. Spring hunting effort on the study area, virtually nonexistent at the study's inception, increased by 700% over the 12-year study period (Fig. 2). From 1969 to 1976, this increase occurred primarily because the local outfitter catered to more hunters. During the last 4 years, the number of hunters operating through the local outfitter increased slightly, but most of the increase in hunting pressure during that period resulted from a greater number of independent hunters.

Off the study area, most outfitters were in operation before the study began and maintained that level of effort throughout the study.

Nonhunting Mortality

Rates of nonhunting mortality varied among groups and years (Table 2). Although the 2 methods yielded slightly different estimates, differences among groups were similar. Throughout the study, nonhunting mortality rates were lowest for adult females and adult males, followed by subadult females and subadult males. Nonhunting mortality estimates for adults and subadults of each sex were similar 1970–75. From 1976 to 1980 nonhunting mortality estimates for adult and subadult females remained similar, but rates for subadult males were greater ($P <$

Table 2. Calculation of maximum nonhunting mortality of subgroups of black bears, North Bay study area, 1970–80.

	Females		Males	
	Adults (≥ 4 yrs)	Subadults (≤ 3 yrs)	Adults (≥ 4 yrs)	Subadults (≤ 3 yrs)
Method 1				
1970–75	0.15	0.18	0.15	0.20
Method 2				
1970–75	0.11	0.17	0.10	0.18
1976–80	0.12	0.21	0.22	0.38

0.02) than those of their adult counterparts. Although mortality estimates for all groups were higher from 1976 to 1980 than from 1970 to 1975, only those for adult ($P < 0.03$) and subadult ($P < 0.02$) males were significant. The observed increase between the 2 periods and the difference between the 2 sexes was at least partially a function of the manner in which the estimate was derived. Because the estimate was predicated on total recoveries and there is a positive correlation between time and rate of recovery (Fig. 3), we would expect to recover a higher proportion of those bears tagged earlier. Similarly, proportionately fewer males than females would be recovered during the latter years because of their slower recovery rate (Fig. 3).

Hunting Mortality

Kill rate by hunters was derived by dividing the number of tagged bears killed by the number available. Numbers annually available to hunters represented minimum values because only tagged individuals recovered during or after a particular hunt were included. To adjust for lack of recovery time during the last 5 years, numbers available were adjusted upward to the maximum recovery level of 83% for males and 84% for females (Fig. 3). For example, females tagged in 1975 had only 5 recovery years rather than the required 6. Because the average female recovery rate after year 5 was only 85% of year 6, the total 1975 sample subsequently recovered (9) was adjusted upward ($9 \times 0.15 = 1.4$) to allow for potential recoveries from years 5–6. An adjustment of 1 was added to a minimum of 38 for a total of 39 available in the spring of 1976 (Table 3).

In the spring, hunters removed an average of 18% and 10% of available males and females respectively, and 5% of available males and 2% of available females in the fall (Table 3). We used geometric means rather than arithmetic means to partially overcome the problem of variable yearly sample sizes. In all instances, arithmetic means differed by less than 1 percentage point. More males than females were removed in the spring ($P < 0.03$) and fall ($P < 0.04$). Spring removal of males ($P < 0.001$) and females ($P < 0.001$) exceeded fall removal. The percentage of available males and females removed in the spring was consistently higher each year than the corresponding fall removal rate except for 1972, when proportionately more males were killed in fall than spring (Table 3). Also, except for the spring of 1980, when the kill of females exceeded that of males, the

percentage of males removed during both seasons was consistently higher than that of females.

Vulnerability

Between 1969 and 1980, hunters shot 32% of all tagged males and 28% of all tagged females. During all years, 85% of the female kills occurred during the spring vs. 72% of male kills, but differences were not significant. Percentages of both sexes shot during the year of tagging were almost identical, but thereafter tagged males were removed more rapidly (Fig. 4). All males eventually shot were taken ≤ 6 years after tagging, whereas females continued to be removed by hunters as long as 11 years after release. Mean elapsed time between tagging and hunter kill was 2.1 years for males and 3.4 years for females. Between 1970 and 1977, the ratio of males to females in the kill varied from 1:1 in 1972 to 5:1 in 1971 and averaged 2.5:1 (Fig. 5). From 1978 to 1980, however, the ratio declined to 0.9:1 and reached a low of 0.7:1 in 1980. During the final 3 years, more females than males were shot on the study area ($P < 0.02$).

Males first became vulnerable at age 2 and remained at approximately the same level of vulnerability until age 6 (Table 4). Numbers shot within those year classes were higher than those taken in either younger ($P < 0.01$) or older age classes ($P < 0.05$). Females older than age 6 appeared relatively invulnerable to hunters as only 4.5% ($N = 292$) were harvested. Three- to 6-year-old females were more vulnerable than the combined younger and older age classes ($P < 0.03$) (Table 4). Yearly loss of resident adult females averaged 5.6% before 1977 (Table 5); however, during the next 4 years, yearly losses within this group increased dramatically and reached an unprecedented high of 33% in 1980. Differences between the 2 periods were highly significant ($P < 0.005$). Also, the mean age of resident adult females

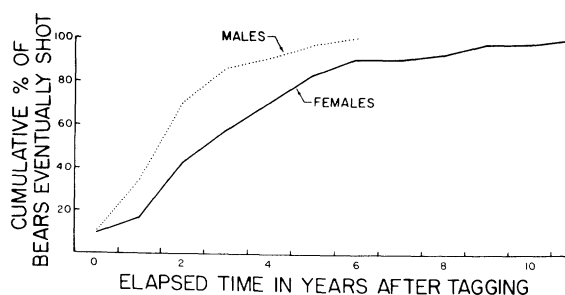


Fig. 4. Cumulative percentage of bears shot at yearly intervals after tagging, North Bay study area, 1969–80.

Table 3. Number of available tagged black bears removed by hunters during spring and fall hunts, North Bay study area, 1969–80.

Year	Spring				Fall			
	Males		Females		Males		Females	
	No. avail*	No. killed	No. avail	No. killed	No. avail	No. killed	No. avail	No. killed
1969	—	—	—	—	15	0	16	0
1970	12	2	13	0	19	0	16	0
1971	17	3	15	0	16	2	20	1
1972	12	0	16	2	20	3	20	1
1973	14	5	18	1	25	1	26	1
1974	22	2	21	1	34	0	36	0
1975	30	7	32	3	64	3	50	1
1976	40(3)	4	39(1)	2	50	2	48	1
1977	35(4)	6	43(2)	3	49(1)	3	50(1)	0
1978	39(5)	5	45(4)	3	41(3)	0	52(2)	1
1979	32(5)	7	43(5)	8	37(2)	1	40(1)	0
1980	29(5)	7	33(4)	11	28(1)	1	28(1)	0
Tot.	282	48	318	34	398	16	402	6
Geometric mean		17.7		9.9		4.5		1.7

* Number available = minimum number available each year + annual adjustments from 1976 to 1980 to bring annual recovery up to the 6-year maximum of 83% for males and 84% for females. Numbers in parentheses are adjustment values. No adjustments were made for fall 1969–76 and spring 1970–75.

was greater during the last 4 years ($\bar{x} = 8.8$ yrs) than during the earlier 7 years ($\bar{x} = 5.5$ yrs; $t = 2.23$, $P < 0.05$). Differences were considered largely due to the increasing age of resident adults during the latter years of the study. The increased overall kill of adult females during the latter 4 years was attributed mainly to the significant increase in hunting pressure that occurred within the study area proper.

Distribution of Hunter Kills

The distribution of bears tagged in the study area between 1969 and 1980 and subsequently recovered by hunters is shown in Figure 6. Distances between final capture sites and kill sites were greater for males than females as indicated by the higher frequency of >20 km straight-line movements for males (56%) than females (15%) ($P < 0.001$). Only 5% of the females had moved distances greater than 60 km

compared to 17% of the males. Although more females were killed off the study area in spring (83%) than in the fall (9%) ($P < 0.001$), there was no difference for males.

Straight-line distances between final locations on the study area and fall kill sites for males varied 23.4–91.2 km ($\bar{x} = 55.8$ km), whereas respective values for spring kills ($N = 32$) were 5.8–215.0 km ($\bar{x} = 41.2$ km). Differences were not significant. Mean elapsed times between final records on the area and kill dates for fall kills (16.4 months) and spring kills (20.0 months) were similar. Seven of 14 fall kills occurred within 1 year of the last sighting of the bear on the area vs. 13 of 32 for spring kills. Maximum elapsed times for spring and fall kills were 57 and 73 months, respectively.

Straight-line distances travelled by females taken beyond study area boundaries ranged 19.5–90.0 km in the fall ($N = 5$) and 10.3–73.6 km in the spring ($N = 3$). Mean distances of 41.3 km for spring and 49.2 km for the fall were similar. Elapsed times between final occurrences on the study area and kill dates were similar for spring ($\bar{x} = 16.3$ months) and fall ($\bar{x} = 12.2$ months). Three of the 5 fall kills occurred within the same year that they were recorded on the study area compared to only 1 of the 3 spring kills.

Ages of females killed off ($N = 8$) and on ($N = 32$) the area averaged 5.3 years (range 0.5–10) and 6.5 years (range 1–14) respectively, whereas ages of

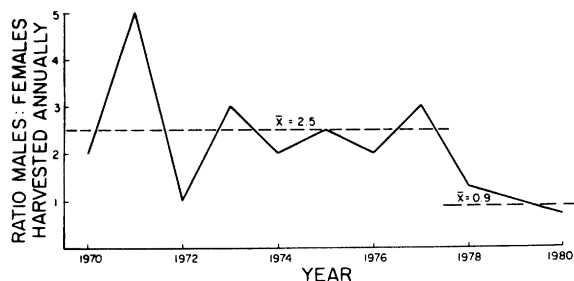


Fig. 5. Ratio of tagged males and females annually removed by hunters, North Bay study area, 1970–80.

Table 4. Age-specific vulnerability of male and female black bears to hunting, North Bay study area, 1970–80.

Age class	Males			Females		
	No. avail ^a	No. shot	% shot	No. avail	No. shot	% shot
Cub	54	0	0.0	43	1	2.3
1	90	2	2.2	65	1	1.5
2	72	12	15.3	52	2	3.8
3	69	10	11.6	53	4	7.5
4	57	9	12.3	58	6	10.3
5	55	8	14.5	65	7	10.8
6	49	8	16.3	61	6	9.8
7	51	3	6.9	54	2	3.7
8	36	6	16.7	56	1	1.8
9	25	2	4.0	53	2	3.8
10	21	2	9.5	38	2	5.3
11	12	0	0.0	25	1	4.0
12	9	0	0.0	21	1	4.8
13	8	1	12.5	15	1	6.7
14	3	1	33.3	13	2	15.4
15	0	0	0.0	9	1	11.1
16	0	0	0.0	4	0	0.0
17	0	0	0.0	2	0	0.0
18	0	0	0.0	2	0	0.0
Total	611	64		689	40	
Mean			10.5			5.8

^a Bear years at risk; includes all bears available for at least 1 hunt. All bears captured during summer were assumed available for that year's fall hunt. Bears available for spring hunt include only individuals known to be alive at some later date.

males killed off the area ($\bar{x} = 5.3$ years, $N = 46$) were 40% greater than those killed on the area ($\bar{x} = 3.8$ years, $N = 18$). However, differences in mean ages of bears killed on and off the study area were not significant.

As total hunting pressure on the study area increased, hunters killed a greater proportion of the tagged bears available. During 1969 to 1976 when hunting pressure was low, annual hunter kill was 0.3% for subadult males, 0.5% for subadult females,

and 0.7% for adult males and adult females. During the final 4 years, when hunting pressure was high, the proportion killed increased by a factor of 4.4 for subadult females and 10.3 for subadult males. The proportion of adults killed increased by a factor of 5.4 for adult males and 6.0 for adult females. Although the sample of bears killed in each sex and age category was relatively small, the pronounced increase in kill rates indicated the vulnerability of black bears to heavy hunting pressure.

Table 5. Yearly loss of resident female black bears (≥ 4 yrs) to spring hunting, North Bay study area, 1970–80.

Year	Estimated prehunt no. ^a	Number shot	Percent shot
1970	10	0	0.0
1971	16	0	0.0
1972	17	3	17.6
1973	21	1	4.8
1974	26	1	3.8
1975	28	2	7.1
1976	26	1	3.8
1977	26	3	11.5
1978	25	3	12.0
1979	24	4	16.7
1980	18	6	33.3

^a Females captured that year or assumed to be on the study area for that year if captured both before and after that year.

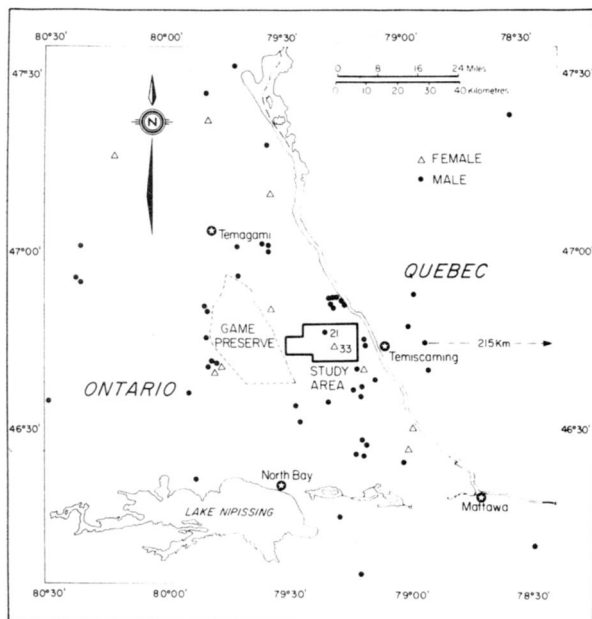


Fig. 6. Locations of tagged black bears killed by hunters, North Bay study area, 1969–80.

Changes in Age Structure of Study Population

The mean age of captured males declined from approximately 6.2 years during the early 1970s to less than 3.5 years during the late 1970s (Fig. 7). In contrast, ages of females fluctuated only slightly about the overall mean of 5.5 years. A comparison of the ratio of captured adults to subadults (Table 6) indicates why fluctuations in mean age were greater for males than females. Although the proportion of adult females in the female population declined during the

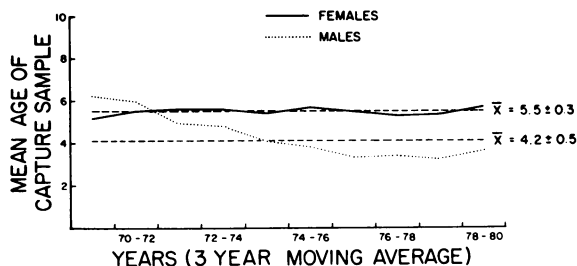


Fig. 7. Mean age of captured black bears, 3-year moving average, North Bay study area, 1969–80.

last 3 years, adults always outnumbered subadults. The total number of adult females did not start to decline until the last 2 years, when increased hunter removal of that segment commenced to exert its effect. For males, adults were more numerous during the 1st 6 years, but subadults predominated thereafter. The reduction in mean age of males was attributed to a combination of hunter harvest, which removed many of the adults and increased productivity that started in 1975 (Kolenosky, unpubl. data). As discussed earlier, tagged males were removed at the outset of the study and that removal continued throughout the investigation. In contrast, few females were removed during the early years when hunting pressure was low. Females, however, especially resident adults, became more vulnerable as hunting pressure increased.

Although annual production of male and female cubs was significantly greater from 1975 to 1980 than during the earlier years, the addition of younger females was offset by the advancing age of the resident adults. These adults, initially tagged as 4- to 6-year-

Table 6. Ratio of adult (≥ 4 yrs) to subadult (1–3 yrs) black bears captured on the North Bay study area, 1969–80.

Year	Females*	Males
1969	3.0:1 (16)	8.0:1 (18)
1970	2.3:1 (10)	3.5:1 (18)
1971	5.5:1 (13)	10.0:1 (11)
1972	1.8:1 (11)	2.3:1 (10)
1973	2.3:1 (20)	1.9:1 (20)
1974	2.4:1 (27)	1.2:1 (26)
1975	3.4:1 (35)	0.6:1 (44)
1976	2.4:1 (34)	0.6:1 (30)
1977	3.1:1 (33)	0.8:1 (25)
1978	1.6:1 (39)	0.6:1 (24)
1979	1.7:1 (38)	0.3:1 (21)
1980	1.3:1 (32)	0.6:1 (29)
Totals	308	276

* Numbers in parentheses are total number of captures, including recaptures of previously marked bears.

olds in 1969, were now present as 13- to 15-year-olds. Thus, the female segment consisted of a much wider age spectrum than during the earlier years, when few old or young were captured. The male segment also consisted of a wider age spectrum, but there the younger age groups dominated because few males survived to the more advanced ages of the females.

DISCUSSION

Natural annual mortality rates for subadult black bears range 0.15–0.35 and total mortality rates for adults range 0.17–0.26 (Bunnell and Tait 1981). In this study, nonhunting mortality rates varied from 0.10 for adult males to 0.38 for subadult males. The highest mortality estimate for the latter group was anticipated because the method of calculation includes dispersal plus mortality, and subadult males are the most frequent dispersers in a black bear population (Jonkel and Cowan 1971, Young and Ruff 1982). Nonhunting mortality estimates for subadult females, which varied 0.17–0.21 between the 2 time periods, may be inflated because their more restricted travel patterns (Rogers 1977; Kolenosky, unpubl. data) may reduce their likelihood of recapture.

Different mortality estimates between the 1st and 2nd half of the study appeared to be related to differences in the size and composition of the existing populations during those periods. From 1969 to 1974, the study population consisted primarily of adults at densities that varied from 0.2 to 0.4 bears/km² (Yodzis and Kolenosky 1986). Competition for space and resources within and among age groups was probably minimal. In 1975, the population increased to more than 0.6 bears/km² as a result of greater cub production and ingress of subadult males. Although influx of subadults declined, continuing yearly cub production ensured high recruitment of young. Thus the combination of higher densities and a greater proportion of young resulted in a more stressed and less stable population. The combination of these factors would contribute directly and indirectly to the higher mortality rates observed.

Reduction in numbers as a consequence of hunting was reported by McIlroy (1972), McCaffrey et al. (1976), Lindzey et al. (1978) and others. The major impact of hunting in this study was not only to reduce total numbers for both sexes but also to lower the mean age of captured males. Population estimates derived from Jolly-Seber calculations indicated peak densities of males (0.36 bears/km²) and females (0.28

bears/km²) occurred in 1975. Female numbers declined 21% and male numbers 29% over the next 3 years. During the final 2 years, male numbers stabilized at approximately the 1978 level, but the female segment, because of increasing hunter pressure, continued to decline. Kemp (1972, 1976) and Young and Ruff (1982) demonstrated a substantial increase in the number of subadult male black bears at Cold Lake, Alberta, after removal of 23 adult males. McCullough (1981) suggested a similar phenomenon occurred for grizzly bears (*U. arctos*) in Yellowstone National Park. The substantial removal of adult males by hunters, during the early years of this study, may have been partially responsible for the large ingress of subadult males that occurred. Also, failure of much of the berry crop outside the study area in 1975 may have precipitated more movement than usual. Most of the subadults tagged that year were transients because few were ever recovered on the area. In addition to considerable ingress of subadult males, increased cub production on the area after 1974 contributed to the lower adult:subadult ratio (Kolenosky, unpubl. data). In contrast the mean age of females did not decline despite the increased productivity, undoubtedly because of the removal rate of older females and the relatively high vulnerability of females aged 3–6. Although our data up to 1980 indicated little change in the mean age of captured females, hunter removal of old females in 1979 and 1980 indicated a lowering of mean age was imminent. The average age of females likely was lower by 1982, but termination of sampling precluded definite verification.

Males generally use larger areas than females (Poelker and Hartwell 1973, Rogers et al. 1976, Alt et al. 1980). This difference was reflected by the removal of a higher proportion of females within the study area boundaries; most males were taken outside. Tagged males were removed at a relatively constant rate throughout the study, whereas females, especially adults, were taken infrequently until the later years. Increased vulnerability of the females at that time was attributed mainly to a significant increase in hunting pressure within the study area. This increase did not affect male vulnerability as directly, because most males either dispersed from the study area boundaries or often traveled well beyond them.

Although we considered hunting effort to have been severe during the final years of the study, several indicators suggested it was still relatively light compared to a number of areas in the United States. In

Wisconsin, 20% of adult bears were shot in the same year they were tagged (Kohn 1982). In Virginia, hunters killed 70% of tagged males and 46% of tagged females within 3 years of tagging (Carpenter 1973). Forty-six percent of the males and 19% of the females were killed in the same year they were tagged. In the Catskills of New York, 91% of the bears tagged were killed by hunters within 3 years of tagging (McCaffrey et al. 1976). In contrast, only 32% of the males and 28% of the females tagged in this study were documented hunter kills after intervals of up to 11 years.

Another indicator of hunter pressure is the age structure of a population (Beecham 1980). Unhunted and lightly hunted populations usually contain a higher proportion of older individuals than do hunted populations (LeCount 1982). In this study, the mean age of all captured bears was 4.8 years, whereas the average age of heavily hunted populations in the United States varied from 2.5 to 3.0 (Collins 1973, Lindzey et al. 1976, McCaffrey et al. 1976). Between 1969 and 1974, when hunting pressure was regarded as light, 66% of captured males and 70% of captured females were > 4 years old. During the final 4 years, when hunting pressure was classified as severe, adults comprised only 29% and 54% of the captured male and female samples, respectively.

Age-related vulnerability is a function of availability, hunting pressure, and hunting method. In North Carolina, Collins (1973) found that 1- and 2-year-old males comprised the bulk of the annual harvest. Alt (1980) in Pennsylvania indicated older bears were less vulnerable than younger ones and that yearlings were the most susceptible group. In the North Bay area, males first became vulnerable at age 2 and females at age 3. The greater vulnerability of females aged 3–6 was probably related to greater movement precipitated by sexual maturation and associated search for a mate or territory or both (Rogers 1977). Some females on the study area became sexually mature at age 4 and reproduced at age 5, but most failed to reproduce until age 6 or older (Kolenosky, unpubl. data). For males, the onset of dispersal activity at age 2 (Jonkel and Cowan 1971, Rogers 1977) undoubtedly contributed to their greater vulnerability.

The more rapid removal of males is related to larger home ranges (Bunnell and Tait 1980), less cautious behavior (Alt 1980), or differences in feeding patterns (Willey 1978). The use of different hunting techniques (Harger 1978) or changes in hunting pressure (Bunnell and Tait 1980) could alter the usual pattern of male vulnerability. With light-to-moderate pressure,

males predominate in the kill, but as pressure increases, females constitute an increasingly larger component (Fraser et al. 1982). In this study, females, especially resident adults, remained relatively invulnerable during the 1st several years, when hunting pressure was low, but became increasingly vulnerable as hunting effort intensified. We postulate that the continuing removal of resident adult females is 1 of the 1st indicators of excessive exploitation and must ultimately lead to a population decline. Once a bear population is overharvested, it may take a decade or more to recover (Hilton 1981). Recovery is slow because of the species' inherent low rate of reproduction (Jonkel and Cowan 1971) and lengthy period of maturation. In Ontario, no females produced cubs before age 5 (Kolenosky, unpubl. data), whereas bears farther south may reproduce at age 3 (Sauer 1975, Alt 1981). Differences in rates of maturation are probably a function of available nutrition (Rogers 1976). Allowable harvest levels for bears in Ontario will have to be more conservative than those of populations farther south because growth rates are lower and the onset of sexual maturation is later.

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