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Mortality Rates of North American Bears

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ABSTRACT. The age structures of 39 populations of three species of North American bears were analyzed. Estimated mortality rates of cubs in their first year were 30–40% for brown bears and 25–30% for black bears. Apparent subadult mortality rates derived from living animals (15–35% annually) were higher than those of adults. Apparent mean annual mortality rates of subadult and adult females combined were 17.2, 16.8, and 18.8% for black, brown, and polar bears respectively. Comparable values for males were 25.5, 23.0, and 22.6% annually.

Because hunting appears to be the major mortality factor in most North American bear populations, interpretation of age structures is facilitated by explicitly incorporating the effects of hunting and its associated biases in the analyses. The simple model proposed to accommodate the hunter-bear interaction clarifies differences in age distributions between species and between sexes within species. Most of the differences in sex-specific mortality rates are a product of differential vulnerability related to home range size and method of hunting.

Key words: age distribution, bears, mortality rates, North America, sex ratios, *Ursus* species

RÉSUMÉ. Les auteurs ont analysé la structure d'âge de 39 groupes d'ours représentant trois espèces nord-américaines. Les taux de mortalité calculés pour les oursons au cours de leur première année étaient de 30 a 40% chez les ours bruns et de 25 a 30% chez les ours noirs. Les taux de mortalité apparents parmi les jeunes, calculés d'après les animaux en vie (15 a 35% chaque année) étaient plus élevés que ceux des adultes. Les taux de mortalité moyens annuels apparents pour les femelles jeunes et adultes étaient de 17.2% chez les ours noirs, de 16.8% chez les ours bruns et de 18.8% chez les ours blancs. Les valeurs comparables pour les mâles étaient respectivement de 25.5%, 23.0% et 22.6%.

Puisque la chasse comporte les plus important facteur de mortalité dans la plupart de populations d'ours en Amérique du Nord, l'interpretation des structures d'âge est facilitée par l'inclusion dans les analyses des effets de la chasse et de ses tendances associées. Le modèle simple proposé en vue d'accomoder l'interaction entre chasseurs et ours signale plus clairement les différences dans la portée des groupes d'âge entre les espèces et entre les sexes d'une même espèce. Les différences dans les taux de mortalité calculés par sexe sont d'ordinaire un produit d'une vulnerabilité différentielle reliée à l'étendue du domaine et à la méthode de chasse.

Mots clés: distribution d'âge, ours, taux de mortalité, Amérique du Nord, proportion par sexe, espèce *Ursus*

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INTRODUCTION

Cowan (1972) suggested that numbers in most bear populations were limited by hunting mortality — that is, mortality rates commonly equaled or exceeded reproductive rates. Reproductive rates of bears were reviewed recently (Bunnell and Tait, 1981); here we review mortality rates. Estimation of mortality in bear populations is difficult. Although numerous sources of data are available, each represents a relatively small sample. Many observed age structures are based on hunter kill, which may be biased, some are samples of the living population, and a few are mixed samples of live and dead animals. Most populations are hunted, and in most instances hunting appears to represent a major component of the mortality. Estimation of mean mortality rates is further hampered by the reproductive behaviour of bears. Reproduction can become synchronized if the majority of females fail to reproduce in a particular year or a cohort of cubs experiences unusually high mortality. In either case most females become potentially reproductive the following year (for black bears see Jonkel and Cowan, 1971; Free and McCaffrey, 1972; Collins, 1974; Rogers, 1976; Lindzey and Meslow, 1977a; for brown bears, Martinka, 1974; for polar bears, Stirling *et al.*, 1975). The resultant "peaks and valleys" in the age distribution impede analysis by composite life tables.

Demographic variables such as mortality rates, age ratios, and sex ratios of "natural" populations are often estimated from harvest data. As several workers have noted (e.g., Caughley, 1977:93-95), the assumptions required for these estimations are seldom satisfied by a sample of harvest data.

We have two objectives: first, to review data on age structure and apparent mortality rates of bear populations; second, to evaluate the utility and generality of a simple model of hunter-bear relationships for interpreting age structures of bear populations subject to hunting.

We use a simple statistic that describes the shape of sample age distributions to evaluate the generality of the model. Bunnell and Tait (1980) proposed the model as a more informative means of evaluating age structures of bear populations. Paloheimo and Fraser (1981) demonstrated that an analogous approach was useful for species other than bears. Fraser *et al.* (1982) applied the approach to a population of black bears (*Ursus americanus*). We evaluate the model's generality using data from 39 populations of black bears, brown bears (*U. arctos*), and polar bears (*U. maritimus*).

METHODS

We recognize three age groups of bears (cub, subadult, and adult) but can treat only two of these adequately. Subadult bears disperse widely and become reproductive (adult) at different ages, dependent largely on nutrition (Bunnell and Tait, 1981). In most of our analyses subadults are treated jointly with adults. Animals under the protective care of their mother are termed cubs regardless of their age. Cub mortality is estimated simply from numbers of animals observed at different ages. For animals older than cubs we consider the population dynamics resulting from varying intensities of harvest.

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We compare and contrast shapes of the sample age distribution for living populations and harvest data within and between species of bears. Specifically, we are interested in a description of the shape of the age distribution for bears older than some minimum age. One could use the slope of a regression of the number of bears versus age, or the slope of log numbers versus age. Erratic age structures often render such approaches ineffective. Our approach is to examine the average number of years lived by a bear beyond some specified minimum age. Our statistic (Eq. 1) is the inverse of that average number of years plus a correction factor to accommodate small sample sizes:

$$\hat{q} = (1 - 1/n) \,/\, (\bar{x} - (a - 1) - 1/n) \qquad (1)$$

where $\hat{q}$ = the statistic representing the shape of the sample age distribution, referred to as "apparent mortality rate" (for reasons discussed below);

n = size of the sample used in the estimate;

$\bar{x}$ = mean age of animals aged "a" or older (age of cubs of year = 1);

a = the minimum age used in the estimate; and

$\bar{x} - (a-1)$ = the average number of years that a bear lives past the age of $a-1$.

The estimator $\hat{q}$ can be derived algebraically from Chapman and Robson's (1960:356) estimate of the annual survival rate (past some minimum age) of a population with a stationary age distribution and a constant annual survival rate (Eq. 2).

$$S = T/(n + T - 1) \qquad (2)$$

where S = annual survival rate or $1-\hat{q}$; and

$T = n(\bar{x}-a)$ where $\bar{x}$, a and n are as in equation 1.

At worst, $\hat{q}$ provides a simple statistic that characterizes the shape of sample age distributions. Large values of $\hat{q}$ correspond to distributions that decline rapidly with increasing age, whereas small values correspond to distributions with a relatively large number of older animals and a slow decline with increasing age. At best, if the age distribution is a random sample from a population with a stationary age distribution and constant mortality rate (above the specified minimum age), then $1-\hat{q}$ represents a minimum variance, unbiased estimator of the annual survival rate (Chapman and Robson, 1960). Because these conditions, particularly that of a random sample, are seldom met in samples of age distributions of bears, we refer to $\hat{q}$ as the "apparent mortality rate per year." The statistic $\hat{q}$ facilitates comparison between sexes and sampling method (hunter harvest versus live capture) within populations and can be used to compare age distributions, based on different minimum ages, between populations.

THE MODEL

The model provides an explicit means of incorporating interactions between hunter and bear. For it to be useful, hunting must be the major form of mortality. In its general form, it is applicable to many predator-prey interactions.

Consider a recently born cohort of animals with a 1:1 sex ratio. As a result of behavioural attributes of either the predator, prey, or both, males tend to be more vulnerable than females to predation. The predators remove males two to three times faster than they remove females. As the cohort ages, the sex ratio in the cohort becomes heavily skewed toward females. A point is reached when there are two to three times as many females as males left in the cohort. Individual males are still more vulnerable to predation, but there are fewer of them left. A predator is now just as likely to take a female as a male from the aging cohort. If we consider the sex ratio of the kill through time, or age of cohort, it begins heavily skewed in favour of males. As the ratio of males to females in the population decreases due to selective removal of males, the proportion of males to females in the kill steadily decreases, reaches 1:1, and continues to decrease. Eventually, both the cohort and the kill consist almost entirely of females.

Three points emerge from this simple model. First, if predation is the only source of mortality and if the predator selects males, then with time the living population should become predominantly female. Second, after some time the sex ratio in the kill, when all ages are combined, should be close to even. Essentially, all animals born eventually are killed. Third, if predation is not the near-exclusive form of mortality, other mortality factors do not discriminate with respect to sex, and males remain more vulnerable to predation, then, the sex ratio of the kill cannot be even. More females than males succumb to "other" mortality factors because females remain in the population longer. The latter two points remain valid if there is a pre-predation period during which other mortality factors that do not discriminate with respect to sex are operating.

A final attribute to be considered in the model is a change in vulnerability to predation with change in the animal's age. If the vulnerability increases with age, then proportionately more older animals would show up in the kill and proportionately fewer older animals would remain in the population. Estimates of mortality that assume a constant mortality rate (such as Eqs. 1 and 2) would differ depending on whether they used a sample of the population or a sample of the kill. They would underestimate mortality when based on the kill and overestimate when based on the living age distribution. The opposite holds if vulnerability decreases with age.

RESULTS AND DISCUSSION

Cub Mortality

The period during which young bears are under the protective care of their mothers varies both within and between species (Bunnell and Tait, 1981:Table 3). Black bear orphans on islands have been reported self-sufficient as early as 5 months (Erickson, 1959). The usual period with the mother is 1.5 years (Jonkel and Cowan, 1971), but some litters may remain with the mother for 2.5 years (Rogers, 1977). Brown bears show greater variability, with some family breakup taking place in the second year (1.5 years of age, Craighead *et al.*, 1969) and other litters not breaking up for at least 4.5 years (Reynolds, 1976). The earliest reported age of self-sufficiency in the brown bear is 7 months (Johnson and LeRoux, 1973). Among polar bears, family breakup occurs after 2.5 years in Alaska (Lentfer *et al.*, 1980). However, Stirling *et al.* (1975) cited two instances of three-year-olds still with the female on the Beaufort Sea, and Lønø (1970:83) stated that in Spitsbergen the young separated from the female at 1.5 years.

The mortality rate of young bears while under the protection of their mother usually has been assumed to be low. A number of authors (e.g., Troyer and Hensel, 1964; Hensel *et al.*, 1969; Lønø, 1970; Jonkel and Cowan, 1971; Mundy and Flook, 1973; Martinka, 1974; Pearson, 1975; Glenn *et al.*, 1976; Stirling *et al.*, 1978; Lentfer *et al.*, 1980) have estimated early mortality by comparing the average litter size for two or more age classes. Changes in mean litter sizes from cubs of the year to yearlings or mean corpora lutea counts to mean litter size of cubs of the year have been assumed to estimate mortality. However, changes in mean litter sizes can provide only a poor lower limit on estimates of mortality rates.

The average change in mean litter sizes of Table 1 suggests a mortality rate of 11.8% from age 0.5 to 1.5 years. In one case (Martinka, 1974), the computed mortality rate would be negative. Using the total numbers of bears as reported by Martinka (1974), the computed mortality rate is 8.5%. Note that using the litter size reported by Martinka (1974) in Table 1 and applying an annual mortality rate of 30% to individual cubs changes the average litter size at 1.5 years by only 15% after one year. Some litters of size 1.0 would disappear, some of size 2.0 would become 1.0, and some size 3.0 litters would become 2.0. The overall distribution of sizes need not change significantly. If there is a bias toward losing singleton cubs, which could have a selective advantage (Tait, 1980), then the average litter size may increase despite high mortality. Adoption of abandoned cubs would explain the rare large litters observed (Table 1; Tait, 1980).

The average change in total number of observed young from 0.5 to 1.5 years of age in the brown bear populations summarized in Table 1 suggests a 35% mortality rate for cubs of the year. Few studies have followed individual litters of brown bears. The observed first year mortality in Yellowstone was 39% (Craighead and Craighead, 1967, in Martinka, 1974). We calculate a 30% mortality for Yellowstone brown bear cubs based on the total number of observed cubs between 1959 and 1969 and the total number of observed yearlings between 1960 and 1970 (Craighead *et al.*, 1974:Table 1). At McNeil Falls, Glenn *et al.* (1976) reported a 38% mortality rate in the 13 litters identified in consecutive years. That estimate is consistent with the 13% reduction in average litter size observed between cub and yearling litters (Glenn *et al.*, 1976). Total numbers in different age classes appear to provide better estimates of cub mortality than do changes in mean litter sizes.

Jonkel and Cowan (1971) reported a first year mortality rate of 5% for black bears by excluding animals killed as a result of the study. If animals killed through research activities are included, the mortality rate is 13%. We estimated a 25% cub mortality for Minnesota black bears (data of Rogers, 1977:Table 3). That estimate is based on the total number of yearlings observed (1972-75) versus the total number of cubs observed (1971-74). In Alberta, Kemp (1972) reported a first year mortality rate of 27% for black bears. He later recognized (Kemp, 1976) that his population age structure was neither stationary nor stable and could not be used to estimate mortality. Among polar bears, we have found no satisfactory estimate of first year mortality. As with brown bears, the average litter size alone cannot be used to estimate mortality. Both Stirling *et al.* (1975) and Lentfer *et al.* (1980) observed more yearlings than cubs of the year. New family groups were still in maternity dens when the earliest surveys were made (Lentfer *et al.*, 1980).

Subadult Mortality

There are even fewer reliable statistics for mortality rates of yearlings and subadults. Subadult animals are often dispersing from the population, an unacceptable violation of mark and recapture assumptions. Jonkel and Cowan (1971) observed that subadult black bears (about 1.5 to 4 years old) disappeared rapidly from the population. Data of Rogers (1977:Table 3) for black bears show little change in the total number of two-year-olds from 1972 to 1975 compared to the total number of one-year-olds from 1971 to 1974, but they do show a sizeable decline between ages 2 and 3 years: 41 two-year-olds, 1971 to 1974, and 27 three-year-olds, 1972 to 1975, a 34% loss rate.

In the other two instances where subadult mortality rates

TABLE 1. Number of cubs in brown bear litters of different ages

Source	Age (yr)	Number in litter 1	2	3	4	5	Total litters	Total young	Mean litter size
Mundy and Flook, 1973	½	26	56	26	0	0	108	216	2.00
	1½	13	22	10	0	1	46	92	2.00
	2½	4	9	1	0	0	14	25	1.79
Martinka, 1974	½	15	16	4	0	0	35	59	1.69
	1½	10	16	4	0	0	30	54	1.80
Hensel *et al.*, 1969	½	22	37	33	6	0	98	219	2.23
	1½	27	50	25	1	0	103	206	2.00
Novikov *et al.*, 1969	½	11	22	9	3	0	45	94	2.09
	1½	13	4	0	0	0	17	21	1.24
Klein, 1958	½	18	27	16	4	0	65	136	2.09
	1½	10	26	14	0	0	50	104	2.08
Dittrich and Kronberger, 1963	½	56	97	54	6	0	213	436	2.05

could be segregated effectively from adult rates, they also were substantially higher than adult rates (data of Glenn, 1975, and Craighead *et al.*, 1974). The average annual mortality rate from age 1.5 to 4.5 years among brown bears in Yellowstone was 24% and 18% for males and females respectively (computed from Table 9 of Craighead *et al.*, 1974). Data of Glenn (1975) also indicated substantially greater subadult mortality rates in males than in females (Table 2).

Unlike cubs, subadults appear regularly in hunter harvest and trapped samples. For this reason, together with the fact that subadults become reproductive or adult at variable rates, we treated subadults jointly with adults in most of the analysis.

Adult Mortality

We consider the apparent mortality rates estimated from capture and harvest data (Table 2). Within the same population, estimated apparent mortality rates for females were con-

TABLE 2. Estimates[a] of apparent mortality of black, brown, and polar bears in North America based on capture and kill data

Location	Source	Minimum age used in estimate	Mortality rate (·yr⁻¹)				All ages total kill	
			Capture data		Kill data			
			Male	Female	Male	Female	Male	Female
Ursus americanus:								
Alberta	Nagy & Russell, 1978	2	0.33 (29)[b]	0.19 (13)	0.44 (5)	—	5	1
Oregon	Lindzey & Meslow, 1980	2	—	—	0.24 (190)	0.18 (204)	250	248
Washington	Lindzey & Meslow, 1977a	1	0.33 (9)	0.21 (13)	—	—	—	—
North Carolina	Collins, 1974	1.75	—	—	0.28 (75)	0.19 (69)	—	—
Alaska	McIlroy, 1972	1	—	—				
0-48 km from Valdez		1	—	—	0.15 (54)[c]		16	5[c]
64-112 km from Valdez		1	—	—	0.13 (30)[c]		9	4[c]
64 km from Valdez		1	—	—	0.09 (8)[c]		19	1[c]
80-128 km from Valdez		1	—	—	0.09 (14)[c]		25	1[c]
Minnesota	Rogers, 1977	3	0.27 (51)	0.19 (93)	—	—	—	—
New York — north	McCaffrey *et al.*, 1976	1	—	—	0.45[d](46)	0.33[d](44)	51	49
— south		1	—	—	0.61[d](38)	0.57[d](26)	40	27
Washington	Poelker & Hartwell, 1973	0	0.21[e](79)	0.13[e](56)	—	—	—	—
trapping							2419	1420
dog							730	930
sport							13582	9438
Ursus arctos:								
Yellowstone	Craighead *et al.*, 1974	5	0.10[f]	0.15[f]	—	—	165	122
		2-5	0.24[f]	0.18[f]	—	—	—	—
Alaska	Glenn, 1975	2	0.38 (113)	0.20 (222)	—	—	—	—
		0	—	—	0.23 (321)	0.16 (289)	321	289
		5	0.28 (23)	0.22 (120)	0.16 (97)	0.14 (136)		
	Wood, 1976	2	0.16 (8)	0.12 (28)	—	—	—	—
	Johnson, 1980	2	—	—	0.14[g](457)	0.15[g](164)	457	164
	Reynolds, 1981	2	0.13 (42)	0.11 (59)				
Yukon	Pearson, 1975	7	0.21 (37)	0.15 (15)	0.14 (113)	0.20 (86)	190	130
Alberta	Nagy & Russell, 1978	2	0.28 (9)	0.16 (10)	0.30 (9)	0.67 (5)	11	9
British Columbia	B.C. Fish & Wildlife Compulsory Records, Victoria, B.C.							
	— Accessible	2			0.17 (189)	0.15 (91)	303	144
	— Remote	2			0.14 (106)	0.15 (43)108	69	
Ursus maritimus:								
Can. Central Arctic	Stirling *et al.*, 1978	3	0.14 (116)	0.16 (142)	0.21 (51)	0.13 (38)	66	44
Can. High Arctic	Stirling *et al.*, 1978	3	0.18 (117)	0.12 (151)	0.20 (140)	0.19 (66)	161	91
Western Can. Arctic	Stirling *et al.*, 1978	3	0.20 (183)	0.20 (173)	0.30 (42)	0.25 (41)	67	52
Alaska	Lentfer *et al.*, 1980	6	0.32 (109)	0.24 (244)	—	—	—	—
	Lentfer, 1976		—	—	—	—	ca3400	ca1100
Hudson Bay	Stirling *et al.*, 1977							
Churchill area	(heavier hunting)	2	0.36 (37)	0.24 (29)	0.36 (18)	0.17 (12)	24	17
Outside Churchill area		2	0.25 (2)	0.14 (12)	0.28 (41)	0.23 (16)	51	23
Combined		2	0.36 (39)	0.20 (41)	0.30 (59)	0.20 (28)	75	40
James Bay area	Jonkel *et al.*, 1976							
James Bay		5	0.16 (11)	0.07 (9)	0.05 (8)	0.08 (6)		
Belcher Island	(heavier hunting)	5	0.10 (4)	—	0.14 (18)	0.14 (9)	—	—
Combined		5	0.14 (15)	0.08 (10)	0.10 (26)	0.12 (15)	30	23

[a] See equation (1) for derivation of "apparent" mortality.
[b] Numbers in parentheses represent sample sizes used in estimate.
[c] Sexes not separated except for one year of total kill.
[d] Used pooled age classes.
[e] Based on average ages; combined sample size, both sexes equals 135.
[f] Based on life table, assumed n = 100.
[g] Mean ages used, assumed cubs and yearlings rare in kill.

sistently lower than those for males when derived from either capture or kill data. Using capture data, the weighted averages ($\bar{x} \pm$ SE) of apparent annual mortality rates for females were 17.2 ± 0.2, 16.8 ± 0.2, and 18.8 ± 0.2% for black, brown, and polar bears respectively. Comparable rates for male bears were 25.5 ± 0.4, 23.0 ± 0.7, and 22.3 ± 0.3%. On average, apparent mortality rates of males are higher by 48, 37, and 19% of the female rate for black, brown, and polar bears respectively. Reynolds (1981) noted that only two bears had been reported as killed by hunters in his study population over the past 25 years. His population together with that in Yellowstone had the lowest apparent mortality rates (Table 2). Estimated mortality rates for male black and brown bears in all other populations were two to three times the rate estimated for the unhunted male bears in Yellowstone or the Brooks Range. This great disparity suggests that hunting accounts for at least 50% of the mortality in most North American bear populations and emphasizes the importance of treating hunting explicitly when estimating mortality. Implications of hunter-bear interactions are examined within the model.

Vulnerabilities

Factors determining the vulnerabilities by age and sex differ between species and also between and within populations, but some generalizations are evident. Males are more vulnerable to hunting than are females. That is consistently demonstrated by the larger number of males harvested, the higher apparent mortality rate of males in the capture data, and the higher apparent mortality rate of males in the kill data (Table 2). Apparent mortality rate is a function of the average age. Low average age or fewer old animals represent a high mortality rate. Factors that contribute to the greater mortality rates of males could be: 1) hunter selectivity (e.g., avoidance of mothers with cubs or selection of larger, hence male, bears), and/or 2) sexual differences in vulnerability (e.g., hunting practices such as bear baiting or shooting over gut piles that attract dominant males).

Other factors that determine bear vulnerability are the movement patterns of both the hunter and bear that affect the probability of encounter. Summarizing Bunnell and Tait (1980), the probability of an ambush-type predator encountering prey reflects the probability that the predator is in the prey's home range. For set guns, traps, or hunting parties attached to fixed camps, one would expect the relative vulnerability of males and females to be roughly proportional to the ratio of their home range sizes. However, if the predator or hunter moves along one dimension such as along a road, river, or trail, then the relative vulnerability of males and females is roughly proportional to the ratio of the square root of their home range sizes. Finally, if the predator moves freely in two dimensions, such as by flying or traveling a dense network of intersecting trails or roads, then the relative vulnerability of males and females approaches 1.0. Simply stated, two-dimensional motion of the predator moves the predator toward the prey independently of the prey's sex, while point source and one-dimensional motion of the predator has the prey moving toward the predator with the range of movement of each sex determining relative vulnerabilities.

Table 3 summarizes reported home range sizes by sex for black and brown bears. Although parturient females return to traditional denning areas, polar bears range widely. Differences in home range size of species exhibiting more discrete movements are broadly equivalent to differences in the amount of movement. For black and brown bears the mean values ($\bar{x} \pm$ SE) for the ratio of male to female home range sizes are 5.4 ± 1.4 and 3.6 ± 0.9 respectively. These values suggest that the sex differential between mortality rates as estimated from the kill data should be about 1.5 times as great for black bears as for brown. In fact, the mean ratio of male to female apparent mortality rates is about 1.3 for black and 1.0 for brown bears, or 1.3 times greater in black bears (Table 2). Indeed, much of the apparent difference in mortality rates between sexes can be accounted for by differences in home range size, implicating differential vulnerability.

TABLE 3. Mean size of home ranges of adult black and brown bears (km²)

Location	Source	Mean home ranges			
		Male	Female	Male/Female	$\sqrt{\text{Male}}$ $\sqrt{\text{Female}}$
Ursus americanus:					
Washington	Lindzey & Meslow, 1977b	5.05	2.35	2.2	1.5
Montana	Jonkel & Cowan, 1971	30.8	5.2	5.9	2.4
Michigan	Erickson & Petrides, 1964	51.8	25.9	2.0	1.4
Washington	Poelker & Hartwell, 1973	60.3	4.8	12.6	3.5
Idaho	Reynolds & Beecham, 1980	60.5	11.5	5.3	2.3
Idaho	Amstrup & Beecham, 1976	112.1	34.3-48.9	2.3-3.3	1.5-1.8
Minnesota	Rogers, 1977	129.4	11.4	11.4	3.4
Alberta	Nagy & Russell, 1978	138.5	93.6	1.5	1.22
Pennsylvania	Alt *et al.*, 1980	173	41	4.2	2.05
Grand mean ± SE				5.4±1.4	2.16±0.3
Ursus arctos:					
Alaska	Berns *et al.*, 1980	24.4	14.3	1.7	1.3
Wyoming	Craighead, 1976	150.3	85.7	1.8	1.3
S.W. Yukon	Pearson, 1975	287	86	3.3	1.8
N. Yukon	Pearson, 1976	414	73	5.7	2.4
Alberta	Nagy & Russell, 1978	1054	188.6	5.6	2.4
Grand mean ± SE				3.6±0.9	1.8±0.2

Relative vulnerability of males and females also reflects the specific movement patterns of the predator or hunter relative to its prey in a region. Poelker and Hartwell (1973) believed that the black bear in Washington were experiencing heavy, but sustainable, hunting pressure with less than 10% of adult bear mortality due to factors other than man. The sex ratio of their kill data varied with hunting technique. Both sport hunting and professional trapping killed significantly more males than females, while the use of dogs killed more females than males (Table 2). Bunnell and Tait (1980) suggested that dogs increased the mobility of the hunter relative to the bears, thus reducing the apparent differences between males and females. The kill from hunting with dogs would thus better reflect the actual sex ratio within the population.

Hunting of black bears in the Hakusan National Park, Japan, uses beaters to drive the bears from cover (Hanai, 1980). Adult sex ratio in the kill over four years was 26 males and 33 females, or 0.79:1.0. Sex ratios of hunted Japanese black bears in other areas were 2.04 and 1.25:1.0 (Torii, 1974; Watanabe, 1974). The latter two populations were trapped; their sex ratios probably reflect the different sizes of male and female home ranges, whereas the hunt by driving tends to eliminate that effect on vulnerability.

Indices of Overharvest

The model of differential vulnerability also suggests that the sex ratio of the kill should, to some extent, reflect the relative hunting pressure experienced by the population (Bunnell and Tait, 1980). As hunting pressure increases, the proportion of males in the harvest should decrease. Fraser *et al.* (1982) noted potential biases that could modify that pattern. We evaluate the apparent generality of the relationship.

McCaffrey *et al.* (1976) observed a decline of the average hunter harvest of black bears in the northern Catskill range of New York that they attributed to over-exploitation. Consistent with the model, the sex ratio of the kill was even and the age distribution exhibited a steeper decline for males than for females (Table 2). In contrast, the hunter harvest in the southern Catskill range of New York has been sustained for a number of years (McCaffrey *et al.*, 1976). The kill in the south was predominantly male. The higher apparent mortality rates in the south (Table 2) or, more explicitly, the larger proportions of young bears (principally yearlings) showing up in the harvest suggest that vulnerability of Catskill black bears to Catskill hunters declines with age.

McIlroy (1972) examined sex ratios and age distributions of black bears with respect to distance from Valdez, his indicator of hunting pressure in Prince William Sound, Alaska. Both the apparent mortality rate and the proportion of females in the harvest increased with increasing hunting pressure (Table 2). He did not divide his age distribution by sex.

The sex ratio of the kill of brown bears from the Alaskan Peninsula was close to even (Glenn, 1975). The population was heavily hunted, had a declining average age of kill, but was believed to be harvested at "maximum sustainable yield." Whether one uses capture or kill data, males disappear from the population at a faster rate than females (Table 2). The sex ratio of the captured animals, and thus presumably the population, is the inverse of the ratio of the apparent mortality rates within the population, thus matching the model ideally.

Although about 70% of the southeastern Alaska brown bear kill comes from the Admiralty, Baranof, and Chichagof Islands (Johnson, 1980), the bears do not appear to be experiencing as high a hunting pressure there as on the Alaskan Peninsula. Harvest on the islands is predominantly male (Table 2), but as the total harvest increases within a specific year, the percentage of males in the harvest declines (Fig. 1).

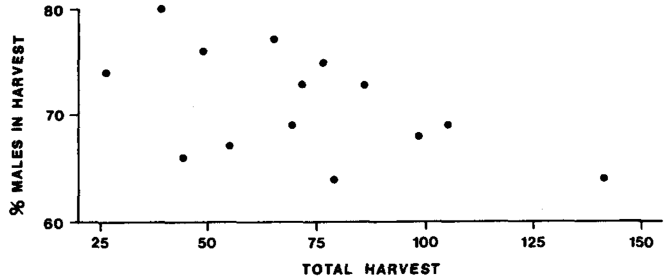

FIG. 1. Percentage of male brown bears in the harvest as a function of total harvest (data from Johnson, 1980:Table 3).

The slightly higher apparent mortality rate of females in the kill (Table 2), coupled with the fact that they represent only 36% of the kill, suggests that in this area as well, female vulnerability declines with age. Data of Wood (1976) from Admiralty Island are consistent with this suggestion. His captured sample is predominantly female, with the male segment having the higher apparent mortality rate (Table 2).

In British Columbia the sex ratio of brown bears harvested in the more remote coastal areas is 2.47:1.0 (male:female), and male and female mortality rates are about equal (Table 2). In the southeastern portion of the province, where hunting pressure is greater, the sex ratio is 2.08:1.0 and the apparent rate of male mortality is 21% greater than on the coast (Table 2). The sex ratio of the harvest still favours males more than Glenn's (1975) Alaskan data, 1.11:1.0.

Similar patterns are repeated among polar bears with few exceptions. Off the coast of Alaska, Lentfer *et al.* (1980) captured over twice as many females as males, and as predicted, the apparent mortality rate of the captured males was higher (by 37%) than the apparent female mortality rate (Table 2). Consistent with these capture data, males formed 80% of the total harvest (Lentfer, 1976). Hunting then was facilitated by use of aircraft over the ice, with the hunter selecting the largest polar bear not accompanied by cubs. Stirling *et al.* (1977) separated their data into bears from near Churchill, experiencing heavier hunting pressure, and bears from outside the Churchill area, experiencing lighter hunting. The sex ratio of the kill was not significantly different from 1:1 near Churchill but showed a preponderance of males outside Churchill (Table 2). The capture data also showed a higher apparent mortality rate for males than for females, and for bears near Churchill than for bears away from Churchill.

In the western Canadian Arctic, data of Stirling (1978) suggested that there were no significant differences in age structure, mortality, or vulnerability among polar bear sex classes. Unlike the Alaskan situation prior to 1972 when aircraft were used to hunt, the kill in the western Canadian Arctic was made by Inuit close to the shore line, the denning area of females (Stirling, 1978). A similar situation occurred near Barrow, Alaska, after hunting with aircraft was stopped (Lentfer *et al.*, 1980). The sex-specific areal distribution of bears appears to offset the reduced vulnerability enjoyed by females with cubs.

CONCLUSIONS

It appears that the frequent suggestion that young bears experience little mortality beyond that of the mother is in error. Reevaluation of available data suggests that brown bear cubs frequently experience mortality of 30–40% in their first year of life. Available data suggest a slightly lower rate, 25–30%, for black bears. Data for polar bears are more difficult to interpret but suggest lower rates than either black or brown bears.

Estimation of mortality rates of subadults is confused by the animals' dispersal but appears higher than among unhunted adults and in the order of 15–35% per year. Indices of harvest intensity suggested by Bunnell and Tait (1980) appear general but were examined *a posteriori*. Consistent explanations of the demographic measures in terms of hunting patterns and hunting pressures could be derived for each case summarized in Table 2. Presumably, they also can be used *a priori* as a diagnostic tool by a manager. For example, an equal sex ratio in a large kill suggests very heavy hunting pressure. An equal sex ratio also suggests that the hunter sample represents most of the population mortality.

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