

ESTIMATING HARVEST RATES OF BEARS FROM SEX RATIO CHANGES

RICHARD B. HARRIS,¹ Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812
LEE H. METZGAR, Department of Zoology, University of Montana, Missoula, MT 59812

Abstract: Using simulation modeling, we assessed the potential for estimating harvest rates for generalized bear (*Ursus* spp.) populations from changes in kill sample sex ratios (Paloheimo and Fraser 1981, Fraser 1984). Models underlying these techniques require assumptions that may be violated in the field. We found that both estimators were sensitive to violations of 4 critical assumptions, and that bias was generally most pronounced when applied to bear populations with low harvest rates, moderate differences in hunting vulnerability between sexes, and complex age structures. Additionally bears typically occur in low densities and yield small harvests, producing limited data from which harvest estimates are produced. Chance deviations from the expected patterns occurred with small (20-180) samples of harvested bears, producing substantial variability in year-to-year estimates.

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Data analyses based on mathematical models are now commonplace in wildlife studies. Models inevitably make simplifying assumptions that will be violated in nature to some degree. In addition, many models are deterministic, thereby providing no way to assess the variability of the technique when applied to field data. When possible, analytical methods are validated under controlled field conditions where the parameters of interest are known, quantifying bias and variability directly. Empirical assessments of this sort are now common in the literature; e.g., Robinette et al. 1974, Greenwood et al. 1985, Conner et al. 1986.

However, some analyses are intended to help biologists estimate parameters in situations where controlled field conditions are difficult or impossible. In such cases a biologist must either apply a technique in which unmet assumptions produce unknown consequences, or dispense with the technique entirely. Many will proceed with the analysis, adding a note that assumptions may be violated. Managers and administrators often place credence on the results of such studies, ignoring accompanying qualifiers and disclaimers regarding assumption violations or insufficient sample size.

Simulation modeling can identify some consequences of unmet model assumptions with realistic amounts of data. In this paper we use simulated grizzly (*Ursus arctos*) and black bear (*U. americanus*) populations to assess a harvest rate estimator developed by Fraser (1976, 1984). Obtaining precise population estimates for bears,

especially grizzlies, is exceedingly difficult in practice, making field verification of harvest rates virtually impossible.

The analysis, originally developed by Fraser (1976) for moose (*Alces alces*), considers a cohort that starts with equal numbers of males and females, in which males are consistently more vulnerable to harvest. As the cohort ages and the more vulnerable males are depleted by hunting, the standing age structure increasingly favors females. In more intensely harvested populations, females predominate more quickly. Fraser (1976, 1984) found that the reciprocal of the age at which females 1st predominate approximated the composite harvest rate (\bar{x} of M and F harvest rates) over a broad range of harvest rates and differential vulnerabilities. Consequently, harvest rate could be estimated by regressing percent males on age. Four assumptions underlie the model: (1) males and females are equally represented in the age class prior to the 1st age of harvest or, alternately, that sex ratios can be determined empirically; (2) no systematic changes occur with age in the relative male and female vulnerabilities to hunting; (3) both sexes experience equal non-harvest sources of mortality; and (4) harvest effort is constant during the period analyzed. Other than the last, these assumptions also underlie the more general model (Paloheimo and Fraser 1981) on which this analysis is based.

These 4 assumptions may be violated in bear populations. Production of cub (age 0.5 year) grizzly bears in Yellowstone National Park was biased toward males (Craighead et al. 1974, Knight and Eberhardt 1985), violating Assumption 1. Conversely, sex ratios of preharvest age

¹ Present address: Alaska Fish and Wildlife Research Center, 101 12th Ave., Fairbanks, AK 99701.

classes may be biased toward females if aggression from adult males is directed disproportionately at young males (Bunnell and Tait 1981, Young and Ruff 1982, Stringham 1983). Violations of Assumption 2 may occur if young males travel more widely and have greater vulnerability to hunting relative to females than do older males (Carlock et al. 1983). Conversely, the decline in percent males in the kill may slow or even reverse if relative male vulnerability increases with age; e.g., from regulations prohibiting killing of females with attendant young (Fraser et al. 1982). Violations of Assumption 3 may be caused by differences in male and female natural mortality rates. Assumption 4 may be violated by changing harvest regulations through the time period (Carlock et al. 1983), or by harvests that remove other than a constant proportion of the population each year.

Both Paloheimo and Fraser (1981) and Fraser et al. (1982) discussed these assumptions and suggested designs to minimize violations, cautioning against indiscriminate use of the methods. Paloheimo and Fraser (1981) generated variances for their nonlinear estimator under various harvest and vulnerability rates using a stochastic simulation model, but they used larger sample sizes (cohorts of 1,000 animals) than characterize most bear kill data.

Here we use deterministic and stochastic simulation models to generate data sets resembling those from harvests of black and grizzly bears. We identify biases and variability in Fraser's (1984) harvest rate estimator (hereafter referred to as the "linear estimator") when assumptions are violated and killed samples are small. We conducted similar analyses using the non-linear estimator of Paloheimo and Fraser (1981) and found similar results, a select few of which are presented here for comparison.

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METHODS

To explore the effects of assumption violations on the linear estimator, we used a deterministic population projection computer program (L. H.

Metzgar, unpubl. manual, Univ. Montana, Missoula). Cohorts in this model are reduced each year by age-specific natural mortality rates. Additionally, hunting removes a constant proportion of the population each year, with kills allocated among sex and age classes according to constant relative vulnerability coefficients (RVC's). The number removed from each sex/age class each year is thus a function of the overall harvest rate, the RVC of that class, and the abundance of the sex/age class relative to the total population. Upon depleting a class, any remaining harvest is allocated among the other sex/age classes according to their RVC's and abundance.

For the deterministic simulations, we modelled survivorship schedules that typify 21 age classes of black bears (Haroldson 1987). Consequences of violating assumptions 1, 2, and 3 were tested using constant natural mortality rates. Assumption 4 was evaluated using equilibrated populations, which necessitated density-dependent rates. All deterministic simulations projected the population through 21 years.

To assess deviations from Assumption 1, we followed cohorts in which the sole source of mortality was from the hunt. We applied the linear estimator to cohorts that began with sex ratios ranging from 40 to 60% males. Male:female RVC's were set at 6:4 and 7:3, values falling within the range specified by Fraser (1976), and similar to those calculated by Bunnell and Tait (1980) for North Carolina black bears (Collins 1974), and by Nagy et al. (1983) for Northwest Territory grizzlies. Populations were modelled with 5 and 10% harvest rates.

For examining Assumption 2, we used the same model as for Assumption 1, except that males and females in the initial age class were equally abundant and the RVC's of males and females were altered at age 5. Male:female RVC's for age classes 0-4 ranged from 6:4 to 8:2, and for age classes 5+ from 8:2 to 6:4. Populations were harvested at 5 and 10% yearly.

To evaluate biases produced by unequal natural mortality (Assumption 3), we set constant female nonhunting mortality rates, and male rates as multiples of the female rates. For females <1 and >16 we used 0.15; for females 1-2 years, 0.10; and for females 3-15 years, 0.10. The set of male age-specific death rates was obtained by multiplying the female rates by a variable ranging from 0.5 to 1.5 in 0.1 increments.

Table 1. Mean annual rates of natural mortality and relative vulnerability to hunting of a generalized grizzly bear population, as used in the stochastic model using specified recruitment parameters..

	\bar{x} mortality		Relative vulnerability	
	F	M	F	M
Age 0 with mother	0.04	0.04	0.05	0.05
Age 0 without mother	0.92	0.92	2.00	2.00
Age >0 with mother	0.04	0.04	0.20	0.20
Age 1-2	0.33	0.40	2.00	7.00
Age 3-4	0.16	0.24	2.00	7.00
Age 5-12	0.09	0.11	0.80	1.00
Age 13-20	0.14	0.16	0.80	1.00
Age 21-24	0.29	0.31	0.80	1.00
Mother with young (yg)			0.20	—

^a **Recruitment:** 1st reproduction at ages 5-8 = 65, 26, 9, and 1%, respectively; \bar{x} age at 1st reproduction = 5.50 years; % litters of sizes 1, 2, or 3 cubs = 19, 55, and 26, respectively; \bar{x} litter size = 2.07 cubs; % of breeding intervals of years 2-5 = 14, 63, 20, and 2, respectively; \bar{x} breeding interval = 3.09 years; \bar{x} cubs/reproductive F/year = 0.67.

^b Natural mortality rates for F did not distinguish those with yg and without yg.

To evaluate deviations from Assumption 4, we applied the linear estimator to vertical harvest data from individual years and altered harvest rates during the simulations. We used the same model structure as for Assumption 3, adding birth rates typical of black bears to the death rates (Haroldson 1987): Both birth and death rates were made density dependent so that populations would achieve an equilibrium with sustainable harvests. We conducted 20-year simulations with 5 and 10% harvest rates and 6:4 and 7:3 male: female RVC values. The age structure from year 20 of each simulation was then retained as the initial age structure for a 15-year simulation at the alternative harvest rate. For example, after 20 years at 10%, the harvest rate was changed to 5% and simulated for an additional 15 years. We also used a population structure that had equilibrated under a 5% harvest, and projected it for 21 years under successive harvest rates of 2.5, 5, and 7.5% for 7 years each.

We used a stochastic simulator to examine the variability of the linear estimator with small samples. This simulator traces individual animals rather than cohorts. Age-specific survival and reproductive rates derive from probabilities applied to each individual in a series of Bernoulli trials. Only females without attending offspring breed. The number removed by hunting each year is constant and allocated among all individuals according to RVC's that reflect age, sex, and whether or not the animal belongs to a

family group. The program examines each individual in turn, either removing it or allowing it to survive.

We used 25 age classes, and natality and survival rates typical of Rocky Mountain populations of grizzly bears (Table 1). Natality and survival rates came from data on unhunted populations in Glacier National Park, British Columbia (Mundy and Flook 1973), Glacier National Park, Montana (Martinka 1974), and Yellowstone National Park (Craighead et al. 1974, Knight and Eberhardt 1985); as well as hunted populations in southeastern British Columbia (McClellan 1983) and northwestern Montana (Jonkel 1982, Aune and Stivers 1983). We also made reference to unpublished data gathered from bear researchers by an Inter-agency Task Force charged by the U.S. Fish and Wildlife Service with assessing grizzly bear population status in Montana. Our intent was not to mimic the behavior of a particular population, but rather to create a "representative" population by combining the best available data from ecologically similar areas. The resulting model is generally similar to those described by McCullough (1981) and Knight and Eberhardt (1985). Further descriptions of the stochastic model and rates used are available in Harris (1984, 1985).

We generated data sets typical of grizzly bear populations, in which annual harvests ranged from 20 to 60 bears/year (6% of standing populations ranging from 333 to 1,000). We used 10 independent starting populations possessing age distributions that varied randomly about their theoretical stable distributions, and calculated the linear estimator from each year's vertical sample of sex/age frequencies. Populations were projected through 24 years. The 10 replicated simulations of 24 years produced 240 estimates, from which we calculated means and standard deviations. To increase numbers of bears in each sample, we also performed analyses with pooled data from non-overlapping groups of 3 consecutive years. (Because 3 years is the most frequent breeding cycle of grizzly bears, combining data this way helps reduce variability arising solely because of synchronized breeding.) We anticipated an independence problem in using kill samples of age structures from consecutive years, but the resulting harvest rate estimates among consecutive years were not significantly ($p < 0.05$) correlated.

In all cases we calculated the linear estimator by regressing sex ratio (weighted by sample size)

Table 2. Harvest rates produced by the estimator under unequal abundances of males and females in the 1st harvestable age class of a generalized bear population. Values are the arithmetic mean of male and female harvest rates.

Estimator	True harvest rate (%)	M:F vulnerability	Estimated harvest rate (%) under initial sex ratio (M:F)			
			60:40	55:45	45:55	40:60 ^a
A ^b	5	6:4	2.4	3.3	9.6	
		7:3	3.0	3.8	6.8	10.0
	10	6:4	5.1	6.9	18.4	
B ^c	5	6:4	2.6	3.5	9.7	
		7:3	3.6	4.3	7.1	10.1
	10	6:4	5.4	7.1	18.5	
		7:3	8.9	9.2	14.3	19.6

^a Blanks indicate that rate not calculated because % was never $\geq 50\%$ (Estimator A) or because F rate was negative (Estimator B).

^b Analysis using Fraser et al. (1982).

^c Analysis using Paloheimo and Fraser (1981).

on age for each sample (Neter et al. 1983). Parameters for the nonlinear estimator (Paloheimo and Fraser 1981) were estimated using BMDPAR (Dixon 1981).

RESULTS

Assumption 1: Initial Sex Ratio

Unequal sex ratios of cubs strongly biased estimates of harvest rate, underestimating rates for male-dominated cohorts and overestimating rates for female-dominated cohorts (Table 2a). Biases were greater with lower hunting rates (5 vs. 10%) and lower male : female vulnerability to hunting (6:4 vs. 7:3). Paloheimo and Fraser (1981) and Fraser (1984) similarly demonstrated that sensitivity to unequal initial sex ratios was greatest when differential vulnerability was minimal. Rates for cohorts consisting of 60% females could not be calculated because males in the harvest did not predominate at any age class, resulting in failure of the fitted regression line to intersect 50% males. Compared to the linear estimator, underestimation of harvest rates using the nonlinear method of Paloheimo and Fraser (1981) was less severe when males outnumbered females, and more severe when females predominated (Table 2b).

Assumption 2: Vulnerability of Sexes

Changes in relative vulnerability at age 5 produced small biases in the linear estimator when cohorts were harvested at 10% yearly, but relatively large biases for those cohorts harvested at 5% (Table 3a). Decreases in female vulnerability with age allowed males to remain rela-

Table 3. Harvest rates, of a generalized bear population, produced by the estimator when the sex-related vulnerability to harvest changes at age 5. All relative vulnerabilities are within the range suggested to be accurate by Fraser (1976), and males are always more vulnerable than females. Values are the arithmetic mean of male and female harvest rates.

Estimator	Sex	Relative vulnerability at age (years)		Estimated harvest rate when true harvest rate is	
		0-4	5-20	5 %	10 %
A ^a	M	6	8		
	F	4	2	0.1	9.5
	M	6	7		
	F	4	3	2.4	9.2
	M	7	6		
	F	3	4	6.9	11.2
B ^b	M	8	6		
	F	2	4	7.5	11.6
	M	6	8		
	F	4	2	0.3	9.5
	M	6	7		
	F	4	3	2.5	9.4
	M	7	6		
	F	3	4	7.1	11.7
	M	8	6		
	F	2	4	8.2	12.8

^a Analysis using Fraser et al. (1982).

^b Analysis using Paloheimo and Fraser (1981).

tively numerous in the harvest, thus causing the regression line to underestimate the true harvest rate. Reductions in male vulnerability with age caused the percent males to drop precipitously, biasing the harvest rate upwards.

In virtually all cases, the nonlinear estimator produced a slightly higher harvest rate estimate, accentuating the overestimation when male vulnerability declined with age and reducing the overestimation when male vulnerability increased with age (Table 3b).

Assumption 3: Natural Mortality

Biases in estimated harvest rates were roughly proportional to the differences in natural mortality between the sexes (Fig. 1), and were less severe in those simulations with greater relative male vulnerability. The relative bias of the estimate was greater for populations harvested at 5 than at 10% (Fig. 1). For example, with male RVC of 0.7, natural mortality biased by 10% toward males increased the estimate of the 10% harvest rate to 11.6% (16% bias), but increased the estimate of the 5% rate to 6.7% (34% bias).

Assumption 4: Harvest Effort

Estimated yearly harvest rates during a 21-year period of altered harvest effort began closer

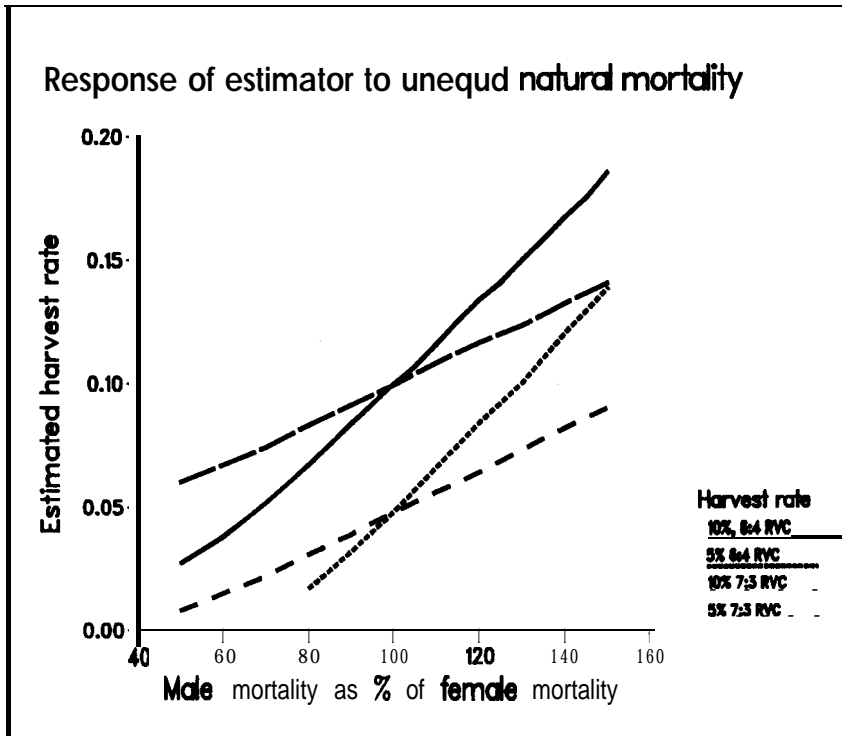


Fig. 1. Response of the estimator to unequal natural mortality in males and females in a generalized bear population. Harvest rates shown were produced by the estimator when true harvest rates were 5 and 10%, and natural mortality rates of male bears were 50–150% those of female bears. When natural mortality rates of both sexes are equal, the estimated harvest rates equal the true rates.

to the previous harvest rates used to generate the age structure than to the new harvest rates. The estimates gradually moved toward the current true harvest rate, converging only after 10–15 years (Fig. 2). Time lags were about equally long for simulations with harvest rates doubled and halved, as well as for both sets of RVC's. The simulation in which we changed harvest rates every 7 years produced estimated harvest rates that consistently lagged behind the true harvest rates (Fig. 3a).

If the kill sample is assumed to be the total kill, an estimate of population size may be generated by dividing the number of animals killed by the estimated harvest rate (Fraser et al. 1982). We calculated population sizes in this manner each year and compared them with the known, simulated population sizes. The estimated population appeared to make spectacular increases (Fig. 3b), because the altered harvest rate created sudden changes in the number of animals killed (numerator) without equally rapid changes in the estimated harvest rate (denominator).

These results suggest that vertical data can be used in place of cohort data only after the stable age distribution characteristic of the current harvest rate has been attained. Using a simulation with 21 age classes, 10–15 years were required before age structures stabilized enough that estimated harvest rates approximated true harvest rates.

Variability of Estimated Harvest Rates

Standard deviations of harvest rate estimates decreased as sample size increased from 20 to 60 bears/year, and decreased further when 3 consecutive years' data were pooled and analyzed together (Table 4). However, standard deviations of the estimated harvest rates were always considerably greater than those of the true harvest rates, in some cases by an order of magnitude. For example, the coefficient of variation (CV) of the true harvest rate for simulations with a yearly harvest of 40 bears was 6%. For the same group of simulations, the CV of the esti-

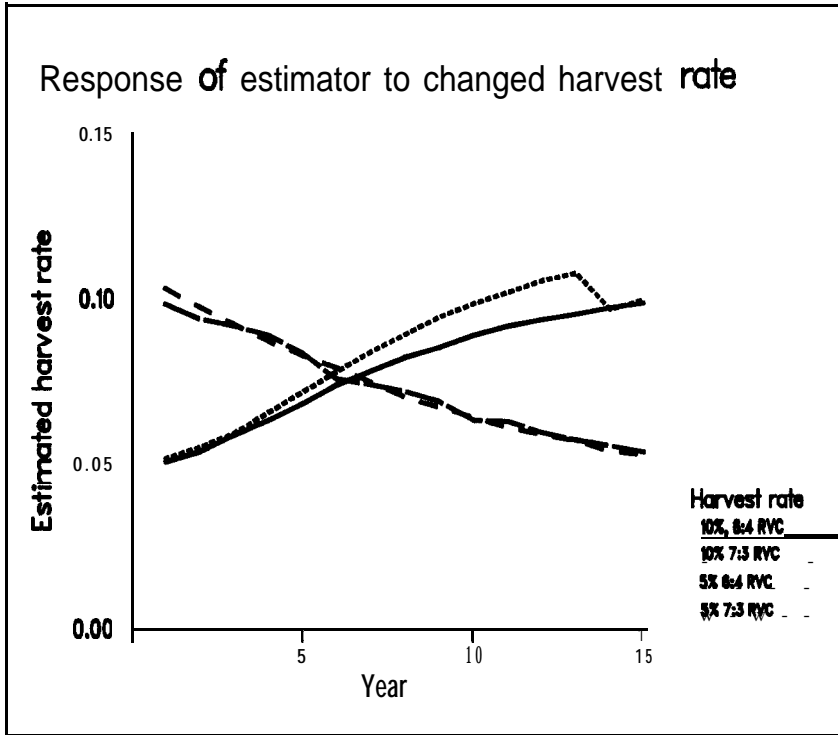


Fig. 2. Harvest rates, for generalized bear populations, produced by the linear estimator each year when the true harvest rate has been changed at Year 1 from 5 to 10% and from 10 to 5%.

mated harvest rate was almost 52%. The most variable estimates came from the smallest samples of harvest animals. With 20 bears/year harvested, true harvest rates varied between 5 and 7% yearly but estimated harvest rates ranged from <1% to >20% (Table 4 and Fig. 4). Even

with samples of 180 animals (60/year taken, 3 years pooled), the standard deviation of the estimated harvest rate was >2.5% (Fig. 5). Thus, for example, estimates computed from 3-year pooled data from grizzly bear populations of 1,000 animals harvested at exactly 6% each year

Table 4. True and estimated harvest rates, of a generalized bear population, from the stochastic simulations. Entries are the mean harvest rate, its standard deviation, the number of simulated years analyzed (N), and the proportion of samples from which an estimate could not be produced. Estimated harvest rates are higher than true harvest rates because subadult males had higher vulnerability to harvest relative to females than did adult males (violating Assumption 2), and natural mortality was greater for males than females (violating Assumption 3).

Analysis ^a	Bears killed yearly	Estimated harvest rate (%)			True harvest rate (%)			Proportion not calculated ^b
		\bar{x}	SD	N	\bar{x}	SD	N	
A	20	13.6	22.7	174	6.2	0.6	240	0.27
	30	12.3	5.8	198	7.8	0.9	240	0.17
	40	10.1	5.2	205	6.3	0.4	240	0.15
	50	10.0	4.4	216	6.5	0.4	240	0.10
	60	9.7	3.8	218	7.0	0.4	240	0.09
B	20	8.8	3.7	73	6.2	0.5	80	0.09
	30	10.4	3.4	76	8.1	1.2	80	0.05
	40	8.5	2.5	79	6.3	0.4	80	0.01
	50	9.0	2.7	79	6.5	0.4	80	0.01
	60	8.9	2.6	80	7.0	0.4	80	0.00

^a A = data from each year analyzed separately and B = pooled data from 3 consecutive years analyzed together.
^b An estimate was not possible when the fitted regression had a positive slope, or intersected 50% M at age <1.

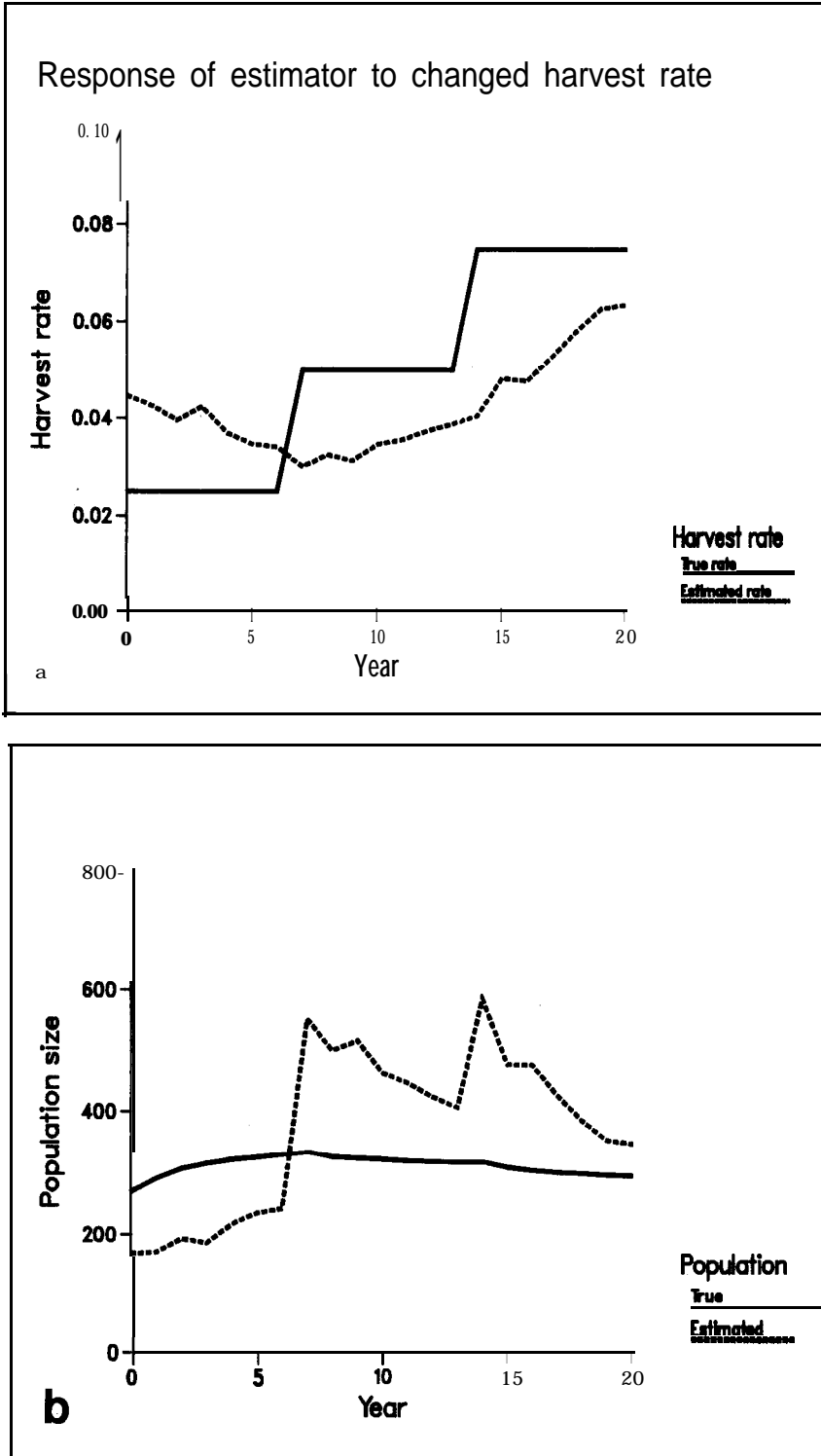


Fig. 3. Harvest rates and population sizes, for generalized bear populations, produced each year by the linear estimator for a population initially stabilized at 5% harvest, harvested at 2.5, 5, and 7.5% for 7 years each. Upper panel shows the estimated harvest rate and the true harvest rate for 21 years. Lower panel shows the estimated population (computed by dividing the no. killed by the estimated harvest rate) and the true population.

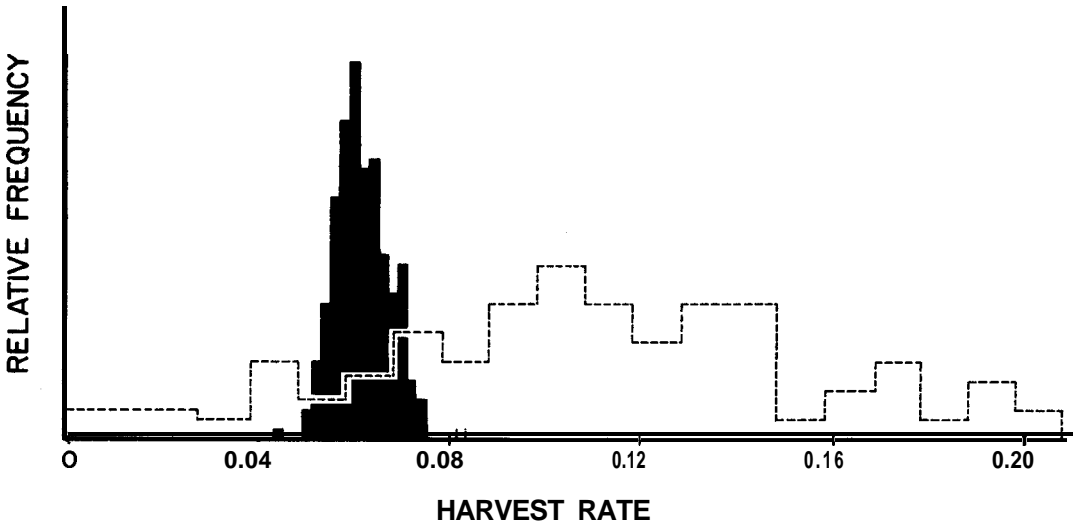


Fig. 4. Frequency distribution of harvest rates, in a generalized bear population, from 240 simulation years with 20 bears killed each year. The solid histogram represents true harvest rates; the dotted histogram represents results using the linear estimator. The stochastic simulator is described in the methods; rates are detailed in Table 1.

would lie between 3.5 and 8.5% in 68% of cases, and 1–11% in 95% of cases if estimated harvest rates were normally distributed and no other assumptions were violated.

DISCUSSION

Users of the method suggested by Fraser (1984) should be aware of the underlying assumptions. We found the linear estimator sensitive to violations of all 4 assumptions. The non-

linear estimator (Paloheimo and Fraser 1981) performed similarly in all cases where we performed parallel analyses. Additionally, we found that results obtained from vertical age/sex data reflected current harvest rates only when age structures had stabilized, a process that required 10–15 years in our simulated populations.

North American grizzly bears are most often managed in units providing yearly kill samples of approximately the size we modelled (20–60).

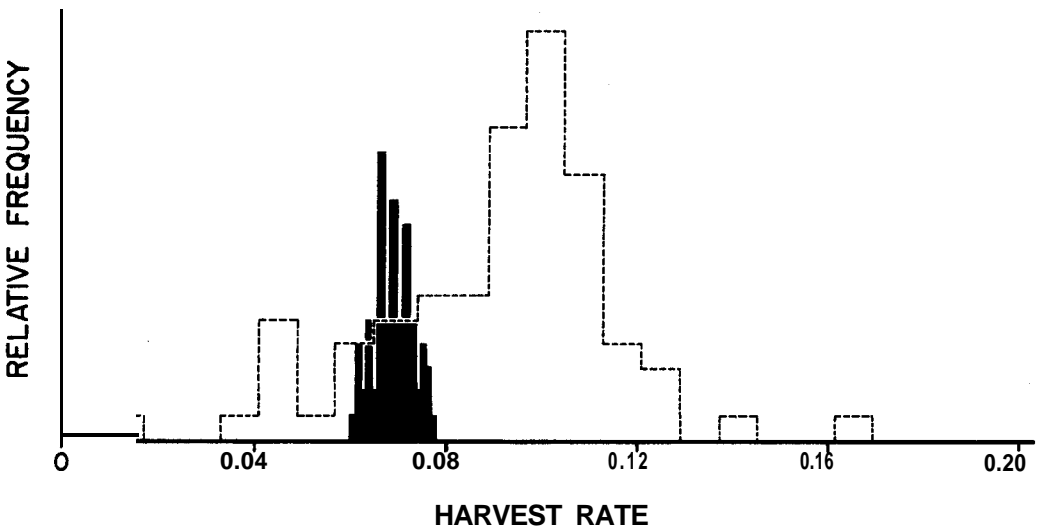


Fig. 5. Frequency distribution of harvest rates, for generalized bear populations, from 80 non-overlapping groups of 3 consecutive simulation years with 60 bears killed each year (180 bears in each sample). The solid histogram represents true harvest rates; the dotted histogram represents estimated harvest rates. The stochastic simulator is described in Methods; rates appear in Table 1. Means of true and estimated harvest rates differ because assumptions 2 and 3 (see text) were violated in the simulations.

Yearly kills averaged 18 in Montana (Dood et al. 1986), and 27-38 in Alaska Unit 13 (Miller 1984). In British Columbia during 1976-82, 3 blocks, each consisting of 12 contiguous hunting units, averaged 25, 34, and 52 grizzly bear kills/year (F. Tompa, B. C. Minist. of Environ., unpubl. data, 1984). Yearly kills in game management units from the Alaska peninsula during 1961-74 averaged from 16 to 56 yearly (Glenn 1975). The magnitude of variability we report here (for up to 180 total bears when 3 years' data of 60/year are pooled) should caution against using the method on individual game management units, even when no assumptions are violated. For example, knowing only that a harvest rate is between 1 and 11% may be of limited use, given the sensitivity of the trajectory of bear populations to slight changes in exploitation pressure (Knight and Eberhardt 1985). Unfortunately, the alternative of combining several units risks "averaging out" true differences in harvest rates.

We emphasize that many of the difficulties reported here are specific to long-lived, low density species such as bears. Both estimators are much more robust with species having more simple age structures and yielding relatively greater harvests. Also, species capable of sustaining higher harvest rates than bears are likely to be more abundant and generate larger kill samples. We do not discourage using these methods on the many harvested species for which they are useful, and consider the work of Fraser and colleagues a major contribution to population analyses. However, decision makers may not appreciate the likelihood of erroneous results when these analyses are applied to small samples from long-lived species.

Managers wishing to use bear population data should decide how much sensitivity they require. High accuracy will demand evidence that assumptions are not violated. For precision within 2 or 3% of the true value, only those populations yielding the largest sample sizes are candidates for these estimators of harvest rates.

Finally, we suggest that simulation models may be useful to examine the properties of analysis techniques when empirical assessment is not possible.

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