What can harvest data tell us about Montana’s black bears?

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Abstract: Harvest data provide readily available and relatively inexpensive information about populations of game species. However, these data are not necessarily representative of standing populations and may have limited applicability in management. We applied a method of harvest data analysis based on the changing sex ratio of the harvest with age to American black bear (Ursus americanus) harvest data from 1985–2005 in Montana. We assessed the ability of this method to identify assumption violations and the extent of resulting bias. A change in the relative vulnerability of females at primiparity due to protection of mothers with cubs from harvest was observable as a drop in the proportion of females in the harvest at the age of maturity. A changing harvest rate produced changing harvest rate estimates, but the estimates lagged up to 10 years behind the actual rate. Other assumption violations, such as unequal non-harvest mortality between sexes and stochasticity in the harvest rate, are not apparent in the harvest data themselves. If total harvest is known and the harvest rate is estimable, it may be possible to use harvest to identify population declines. However, we found with simulations that, in many cases, 10–15 years of harvest data are needed to identify a statistically significant decline. If all assumptions are met, we estimated harvest rates in Montana as 4.6% for females and 10.4% for males; these are overestimates if males have higher non-harvest mortality than females. Montana’s harvest data did not show an apparent decline in the relative vulnerability of females at maturity, despite nominal protection of mothers accompanied by cubs. Analyses of harvest data also contradicted the hypothesis, based on meta-analysis of demographic data, that black bears were declining in Montana.

Key words: American black bear, catch-at-age, harvest, Montana, population trend, relative vulnerability, sustainable harvest, Ursus americanus

Wildlife managers are often charged with managing populations of game species that are rare or secretive, such as many furbearers and carnivores, using very limited resources. Many jurisdictions require hunters to bring harvested individuals through check stations where age and sex data are collected (Rupp et al. 2000), and in many cases, harvest data are the best or only source of information about the status of these populations. A variety of techniques, relying on different assumptions about population and harvest processes, can be used to estimate both harvest rates and population status or vital rates from these harvest data (Skalski et al. 2005). However, it is surprisingly common for harvest data to be collected and not used or applied to management. For instance, in eastern North America, just 13 out of 26 jurisdictions that have a legal American black bear hunt used harvest data to estimate population size in 2011 (Noyce 2011). Likewise, Rupp et al. (2000) found that while almost all surveyed jurisdictions collected white-tailed deer (Odocoileus virginianus) harvest data, fewer than half of them used the harvest data for population models. Four respondents stated that harvest data were collected but not actually used in decision-making, and most of the agencies used harvest data to estimate the total harvest but not harvest rate or population size and trend (Rupp et al. 2000). More generally, harvest management is often developed from a patchwork of interests and implemented piecemeal over a sometimes long time

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frame (Milner-Gulland and Rowcliffe 2007), making application of harvest data in decision-making that much more idiosyncratic. Basing decisions on harvest data may also not be a top priority when managers must consider budget priorities and constraints and incorporate public interests and input.

One reason harvest data are not used more thoroughly may be the limitations of available harvest data analysis methods. Methods with various assumptions and requirements have been used to estimate harvest rate and population status from harvest data (Roseberry and Woolf 1991). Methods such as population reconstruction and change-in-ratio use the age and sex structure of the harvest to infer information about the population. Others, such as index removal and catch per unit effort, rely on combinations of surveys and harvest data. Roseberry and Woolf (1991) reviewed 9 methods and reported that half require data in addition to information on the harvested animals, such as harvest effort or a concurrent field study. Managers often lack such auxiliary information. Of methods that do not require auxiliary data, several use the age structure of the harvest to infer information about survival rates or population trend (Skalski et al. 2005). However, the composition of the harvest may not be representative of the living population (Litvaitis and Kane 1994), and the relative numbers of different ages may reflect hunter selectivity, age- and sex-specific vulnerabilities to harvest, or the effect of harvest regulations more so than the population trend (Bunnell and Tait 1980, Noyce and Garshelis 1997). Estimates of harvest rates derived from harvest data are also more reliable when a large proportion of the population is removed each year (Harris and Metzgar 1987, Roseberry and Woolf 1991), which is thought not to be the case for many carnivores.

In this paper, we examined the robustness of a combination of the methods presented by Paloheimo and Fraser (1981) and Fraser (1984) for estimating harvest rate of black bears. The method we applied avoids some problems of other methods, such as the need for additional data, and explicitly models the differential vulnerability to harvest across groups. However, information on hunter effort is needed if it has not been constant, and the method we used relies on a number of assumptions: the initial sex ratio is even, the differential vulnerability of the sexes is constant across ages, the harvest rate is constant across time, and the natural mortality rates are equal for both sexes. Assuming these are met, if one sex is more vulnerable to harvest than the other, the ratio of males to females in sequential harvests of a cohort will change as that cohort ages. Fraser (1984) showed that the inverse of the age at which the sex ratio of the harvest is even will approximate the average harvest rate. This simple estimate works best when the harvest rate is near 0.5 or the differential vulnerability is much less than the harvest rate. Paloheimo and Fraser (1981) used the same principle, but relaxed these requirements by using generalized least squares to estimate harvest rate and relative vulnerability using a model of harvest sex ratio at each age. Harris and Metzgar (1987) explored the utility of these methods for bears in general and especially grizzly bears (Ursus arctos), and found that violations of the assumptions biased estimates of harvest rate more when the harvest rate, differential vulnerability, or both were low and when harvest samples are small.

In many jurisdictions, black bear harvests exceed the samples simulated by Harris and Metzgar (1987) by an order of magnitude or more, meaning the method may be more appropriate for black bears than initially suggested. We used stochastic simulations to not only explore how assumption violations bias harvest estimates, but also to assess qualitatively whether the harvest data can indicate when assumptions are violated. We then applied the method to harvest data for black bears in Montana and examined the expectation that adult female black bears experience lower harvest than immature females because it is illegal to harvest a female when she is accompanied by young. Our expectation was that the vulnerability of female black bears in Montana decreased by 50% at primiparity because adult females spend about half their time accompanied by cubs (Mace and Chilton-Radandt 2011).

When total harvest is known, it is possible to estimate the population size based on harvest rate estimates. We used simulations to determine whether we would be likely to detect population declines under constant harvest rate using total harvest and estimated population size. We then applied this concept to Montana's black bear harvest data to evaluate the hypothesis that black bears were declining in Montana, an unexpected result from a meta-analysis of demographic studies (Beston 2011). The meta-analysis indicated that, on average, black bears were declining in the western United States, at
Black bear hunting In Montana

In Montana, black bear range is restricted to the mountainous western portion of the state, and hunting is permitted in all 5 Montana Fish, Wildlife and Parks (MFWP) regions where black bears occur. Bears were hunted in 2 seasons: in spring from April 15 through mid-May–mid-June, and in fall from September 15–late November. Black bear licenses for residents cost $15–19 and permit the take of 1 black bear/calendar year. Hunting bears using bait or dogs has been illegal in Montana since the first half of the twentieth century. It was also illegal to harvest cubs (black bears <1 year old) and mothers with young. Because family break-up occurs during the summer, a female with yearlings was illegal to harvest in the spring but legal to harvest in the fall of the same year. In addition to direct protection when accompanied by cubs, females tend to enter hibernation earlier and remain in hibernation later than males, especially when pregnant or nursing (Beecham et al. 1983). They may be in dens by mid-October and remain until late May (Jonkel and Cowan 1971, Beecham 1983), missing most of both hunting seasons. Tag sales in Montana were relatively constant for the 20 years prior to this analysis (MFWP, Helena, Montana, USA, unpublished data), and evidence from hunter surveys suggests the harvest effort, measured in hunter days, was consistent for the period for which data are available (MFWP, Helena, Montana, USA, unpublished data, 1996–2003). Therefore, we did not include hunter effort in our estimation approach. Hunters were required to bring harvested black bears through check stations, where each bear was sexed and a tooth collected for aging. Based on the callback survey, check station compliance was believed to be nearly complete, and thus we used the numbers of bears brought through check stations as the total harvest size.

Methods

Estimation of harvest rate

Given an average harvest rate of \( k \) and a difference in vulnerability \( 2v \), such that the harvest rate of males is \( k + v \) and the harvest rate of females is \( k - v \), then the ratio of males in the harvest, \( H_m \), to females in the harvest, \( H_f \), at age \( i \) can be written as

\[
\frac{H_{m,i}}{H_{f,i}} = \frac{M_1(1-(k+v))^{i-1}s_m^{-1}(k+v)}{F_1(1-(k-v))^{i-1}s_f^{-1}(k-v)},
\]

where \( M_1 \) and \( F_1 \) are the numbers of males and females, respectively, in the cohort when it enters the harvestable population, and \( s_m \) and \( s_f \) are the natural survival rates of males and females. This is essentially the same equation used by Paloheimo and Fraser (1981), replacing their vulnerabilities and hunter efforts with constant harvest rates.

Two methods can be used to estimate \( k \) and \( v \) based on this equation. We took the natural logarithm of both sides and used generalized least squares estimation to find \( k \) and \( v \), following Paloheimo and Fraser (1981). Alternatively, we used regression to estimate the age when the harvest sex ratio is 1 and coupled this with information from the youngest harvest age to create a system of 2 equations. We then solved these equations for the 2 variables, which was essentially the approach used by Fraser (1984). At the youngest age of harvest (1 year old for black bears), the sex ratio of harvest can be written:

\[
\frac{H_{m,1}}{H_{f,1}} = \frac{M_1(k+v)}{F_1(k-v)},
\]

and at age \( y \), the male and female harvests are equal, yielding:

\[
y = \frac{M_1(1-(k+v))^{y-1}s_m^{-1}(k+v)}{F_1(1-(k-v))^{y-1}s_f^{-1}(k-v)}.
\]

Note that we assumed \( M_i = F_i \) and \( s_m = s_f \) in order to solve for \( y \). We found that both methods produced
similar results, so we present results from the latter method.

**Analysis of assumption violations**

We used simulations to assess the effects of assumption violations on the structure of the harvest data and the resulting estimates of harvest rate. For each analysis, we simulated 2,500 replicate stochastic populations for 20 years using a 60 x 60, pre-birth pulse, sex and age-based matrix model (Caswell 2000). Bears were divided into 4 stages: cubs (0 years old), yearlings (1-yr), subadults (2–5 yr), and adults (6–30 yr). Males and females had the same survival rates, except in simulations that specifically considered deviations from equal natural mortality. Adult females produced cubs in a 1:1 sex ratio. We parameterized the model with survival rates and variances from the western half of North America (Beston 2011). Harvest rates for each sex, fecundity, and their variances, as well as age at primiparity, were based on data from Montana. Each year a harvest rate for each sex was selected from beta distributions with mean equal to the initial estimates from Montana’s harvest data and variance based on the variance seen in the total harvest assuming constant population size. After simulating harvest, vital rates were selected from beta distributions for survival, and a lognormal distribution for fecundity and the population was multiplied by that year’s matrix model.

One assumption made when using the method described above to estimate harvest rate is that the relative vulnerability of the sexes does not change as a cohort ages. In Montana, however, we expected the relative vulnerability of female black bears to decrease at primiparity because mothers accompanied by cubs are illegal to harvest. To assess biases due to varying relative vulnerability, we simulated populations with adult females harvested at half the rate of subadult females. We assessed whether the resulting harvest data could indicate that the assumption had been violated and compared estimated rates of harvest with the actual total female harvest rate.

Application of this method of harvest rate estimation also assumes that the natural mortality is the same for both sexes. Male black bears may have higher natural mortality than female black bears, especially as subadults (Hellgren and Vaughan 1989, Koehler and Pierce 2005). However, some studies have failed to find a significant difference between the mortality rates of males and females (Kasworm and Thier 1994, Wooding and Hardisky 1994). Results are also confounded because harvest mortality is included in most mortality estimates (Hellgren and Vaughan 1989, Kasworm and Thier 1994, Wooding and Hardisky 1994, Koehler and Pierce 2005). We simulated populations as above, with male natural mortality equal to up to 130% of female natural mortality, and assessed bias in harvest estimates and changes in harvest sex- and age-structure to determine whether violations of this assumption are apparent in the harvest data themselves.

Another assumption that many harvest data sets may violate is that harvest remains constant across the years analyzed. Two types of violations, stochasticity and trends in survival and harvest rates, can affect results. If there are no temporal trends, combining several years of harvest information should ameliorate the annual variability and increase the precision of estimates. To assess how the length of harvest dataset affects the precision of estimates of harvest rate, we conducted stochastic simulations of harvested populations using the model described above. We estimated harvest rate from the harvest age and sex structure beginning in year one. For each consecutive year, we estimated harvest rate using the sums of all bears harvested to date in each age and sex class.

When harvest rates changed, Harris and Metzgar (1987) pointed out that annual harvest estimates lagged several years behind. Their analysis explored a change from a stable population harvested at 5% to a 10% harvest rate, or vice versa. To explore the effect of a more continuous trend on the data structure and the resulting bias in harvest estimates, we conducted simulations with an increasing trend in the harvest rate over a 20-year timeline. We assessed the resulting harvest age and sex structure and the length of lag in the harvest rate estimates.

**Using harvest to detect declines**

If the harvest rate can be estimated and the total harvest is known, this information can be used to calculate population size through time. However, due to stochasticity and variation in harvest rate estimate, the power to detect changes in population size may be low. To assess the ability of abundance estimates derived from harvest data to reflect population declines, we used the above simulation harvested at 4% for females and 8% for males to
assess the power to detect a statistically significant decline in total population size as the length of the harvest dataset increased. Additionally, because managers sometimes lack information on the sex and age structure of the harvest, we also assessed the power to detect a statistically significant decline in total harvest from these simulations as an index for population size.

Initial population sizes were 10,000, 30,000, and 50,000 bears, which covers the likely range for Montana’s actual black bear population size based on the estimated harvest rates (see Results) as well as the best guess of managers as of 2001 (Hristienko and McDonald 2007). For each simulation, we fit a linear regression to either the estimated total population size or the total number of bears harvested each year, starting with 3 years of harvests and adding consecutive years through the end of the dataset. Each year, we checked for a statistically significant decline by assessing whether the coefficient of year was \( b < 0 (P = 0.05) \). This is likely a conservative scenario because the spatial variation incorporated in population growth rate (via vital rate distributions from Beston [2011]) probably overestimated the temporal variation in any one population (because management and habitat varied widely among populations across western North America).

Montana black bear data

We estimated the harvest rates for male and female black bears in Montana using the method described above. We estimated \( y \), the harvest in which the sex ratio is 1:1, using black bear harvest data collected in Montana from 1985–2005. We assumed low natural mortality over the winter (Hebblewhite et al. 2003) and combined the fall harvest with the following spring harvest to calculate the total harvest for each age class. To find \( y \), we first summed each age class over the entire 20 year harvest dataset, and regressed \( y_i \) (proportion of females in the harvest) against \( i \) (age). We weighted the regression by total bears harvested at each age to account for smaller sample sizes at older ages. We solved the regression equation for 50% females in the harvest to estimate \( y \) and used \( y \) to estimate harvest rate.

We used qualitative comparisons of the structure of the harvest data to determine whether the assumption of constant relative vulnerability between sexes was violated. We also assessed the potential bias in differences in natural mortality by calculating male and female harvest rates using the Montana estimate of \( y \) and varying the ratio of male mortality to female mortality, \( \frac{1-s_m}{1-s_f} \), from 1 to 1.1. We were specifically interested in the case where male mortality was higher than female mortality, the most likely situation for black bears, and quantified the bias separately for male and female harvest rates.

To assess possible trends in Montana’s harvest rate, we estimated annual harvest rates using the age and sex structure of each year’s harvest. We also estimated harvest rates using non-overlapping 5-year sets to increase precision of estimates. We used the estimated harvest rates through time to estimate population size. Finally, we examined the total population size estimates and the total harvest to determine whether the population appeared to be decreasing.

Results

Analysis of assumption violations

Simulations in which adult females were harvested at half the rate of subadult females produced a noticeable break in both the proportion of females harvested and in the number of females harvested at each age (Fig. 1). If the relative vulnerability of females decreased at age of primiparity, the proportion of females in the harvest at that age dropped, and if total vulnerability decreased, the total number harvested dropped. In this scenario, the average estimated female harvest rate (2.72%) underestimated the actual simulated harvest rate of adult females (3.05%) by about 10%. Other simulations were explored with varying violations of this assumption, with the same general result.

The sex and age structure of the harvest when male natural mortality was greater than female natural mortality was not distinguishable from a scenario with a greater harvest rate and equal adult survival for both sexes. Increased male mortality resulted in an overestimation of both male and female harvest rates (Fig. 2).

An increase in the number of years incorporated in the estimation yielded more precise estimates of the harvest rate. Given the levels of variance seen in black bear vital rates across the western half of their range, much improvement was gained in the first 5 years of data gathering (Fig. 3). The
inter-percentile ranges in the estimate of harvest rate leveled out after about 15 years. Populations experiencing lower levels of variance would require fewer years to gain similar precision in harvest rate estimates.

Simulations indicated that estimates of harvest rate lagged as much as 10 years behind actual changes in rates (Fig. 4). The age structure of the harvest data, however, did not change over time as harvest rate changed, and was therefore not helpful in indicating a violation of this assumption. The sex ratio of the harvest at young ages (1–4 yrs) did not change over the 20-year timeline, but the proportion of females in the harvest at older ages, especially 10–20 years, changed by about 1%/year. This change was much smaller than the variation among the
simulated populations and was therefore also not helpful in indicating a violation of this assumption.

**Using harvest to detect declines**

Given the estimated harvest rate and variation in Montana (described below) and the population growth rate and variance for western North America, a decline in the population was observed in the harvest in 80–86% of simulations after 15 years of harvest data collection (Fig. 5). Only 44–80% of the population estimate series showed statistically significant declines after 15 years of harvest data collection (Fig. 5). Larger population sizes produced larger harvests, better estimates of total population size, and greater power to detect declines.

As the population growth rate approached 1, the number of years required to reach 90% power in detecting declines using only the harvest numbers increased dramatically (Fig. 5B). Populations decreasing at 1–5% a year were reliably identified with 10–20 years of harvest data; annual decreases of less than 1% a year took considerably longer to detect. After 5 years, only 20% of the most rapidly declining populations, $\lambda = 0.95$, displayed statistically significant declines in the harvest numbers.

**Montana black bear data**

The $R^2$ of the regression of proportion females in Montana’s harvest from 1985–2005 against age was 0.94, and the estimated value of $y$, the age at which males and females are equally represented in the harvest, was 14.2 years (Fig. 6). The high $R^2$ value implies either that the basic tenets of this model were borne out by Montana’s data, or that biases created by assumption violations were in opposite directions and canceled each other out. The estimated annual harvest rates for male and female black bears in Montana were 10.6% and 4.3%, respectively, given

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**Fig. 4.** Estimates of annual American black bear harvest rates in 2,500 simulated western populations as the harvest rates increased linearly from 4–14% for males and from 2–7% for females over a 20-year time horizon.

**Fig. 5.** Estimate of the proportion of simulated American black bear populations in which a statistically significant negative trend was identified in the estimated population size or the total number of bears harvested through time (A) and the time it took to achieve 90% power to detect decline using total harvest numbers of simulated unstructured populations (B).
an initial sex ratio of 1, constant relative vulnerability of the sexes, equal natural mortality rates for males and females, and constant harvest rate through time. These estimated rates are an average across the state and most representative of the harvest rates in western Montana, where the largest harvests occur, rather than the harvest rates in the sparser populations in central Montana.

Montana’s proportion of females in the harvest was not consistent with expectations based on reduced relative vulnerability at primiparity (Fig. 6). At the age when vulnerability changed in the simulations, a break was noticeable in both the proportion of females harvested and in the number of females harvested at each age (Fig. 1).

Annual estimates of harvest rate and estimates using 5-year periods suggested a declining trend in Montana’s harvest rate, with some autocorrelation evident in the annual estimates (Fig. 7). Estimates of population size calculated from annual harvest rates and pooled 5-year harvest rates and the reported total number of bears harvested each year
depicted a population that had risen from approximately 12,000 bears in 1985 to between 20,000 and 40,000 bears in 2005 (Fig. 7B), for an average annual population growth rate of approximately $\lambda = 1.05$.

**Discussion**

Though estimation of harvest rate from the sex and age of harvested individuals has several limitations, the method we applied can produce usable harvest rate estimates and information on population status or trend that can be applied in decision making. The confidence in these estimates is higher given more years of harvest data and lower temporal stochasticity. Our results supported the hypothesis that at least some assumption violations of Fraser's (1984) and Paloheimo and Fraser's (1981) methods can be identified by the harvest data themselves. Additionally, biases due to violations of assumptions in our simulations were generally less dramatic than those found by Harris and Metzgar (1987), likely due to much larger harvest samples. Furthermore, the expectations that Montana's black bear population was declining and that the relative vulnerability of females compared to males changed as bears reach adulthood due to the protection of mothers with cubs were not borne out by the data.

Examination of harvest data can reveal whether some of the assumptions needed for this method are violated. If the relative vulnerability of the sexes changes with age, a discontinuity will be present in the proportion of females in the harvest at the transition ages. If the absolute vulnerability of either sex changes with age, a discontinuity will be present in the total harvest of that sex at the transition ages. It is important that this violation is identified because it can lead to non-conservative underestimation of harvest rate if the relative vulnerability of females decreases at primiparity (our results, also Harris and Metzgar 1987).

We were unable to identify whether the assumption of equal natural mortality for both sexes was violated using harvest data. However, harvest rate estimates based on this assumption will be conservative when male mortality is higher than female mortality, which is likely true in a variety of mammalian and avian species (Promislow 1992, Promislow et al. 1992), because they will overestimate harvest rate. If these harvest rates are used to estimate population size, they will underestimate population size.

Changing harvest rates will be apparent if annual sex and age structures are used to estimate yearly harvest rates, although the estimates will lag behind the actual value of harvest rate until it stabilizes. This generally agrees with the results of Harris and Metzgar (1987), which were based on scenarios where harvest rates changed between 2 seasons then remained constant rather than changing across all seasons in the time horizon. It is important to note that the age structure of the harvest data did not show an obvious trend, and the sex structure changed slowly in the adult age classes and not at all in the young age classes. It has been shown that age and sex composition of the harvest reflected relative vulnerability rather than population size or structure (Harris and Metzgar 1987, Garshelis 1990). Likewise, monitoring harvest via mean age or sex ratio alone is inappropriate. Despite this, Miller et al. (2011) point out that these sex and age ratios are still used inappropriately by managers to monitor populations.

It appeared unlikely that the vulnerability of female black bears to harvest in Montana changed dramatically at the presumed age of primiparity, and this contradicted our expectation that protection of females accompanied by cubs reduces the vulnerability of adult females (McLoughlin et al. 2005). Estimates based on reproductive tracts suggest adult females spend half their time accompanied by cubs (Mace and Chilton-Radandt 2011), which implies that vulnerability of adult females should be half that of subadults because females with young are illegal to take. Females are more likely to be accompanied by young in the spring than in the fall because family break-up occurs over the summer; thus, it is possible that the vulnerability to the spring harvest changes but the unchanged vulnerability and larger total harvest during the fall obscure that change. Alternatively, a greater proportion of young female bears could be producing their own cubs or accompanying their mothers or siblings than we expect, giving them as much protection as adults, or hunters could be taking females with cubs more often than previously assumed. If cubs are in trees or hiding as a hunter approaches, it may not be obvious to the hunter that the mother has young. Because bears are not baited or hunted with dogs, hunters may have less opportunity to observe young nearby than in jurisdictions where these methods are...
allowed. Hristienko et al. (2004) estimated only a 2% orphanning rate for black bear cubs during spring hunts in Manitoba, but Montana’s may be near 4% if protection of mothers with young is completely ineffective.

In Montana, harvest data show annual negative autocorrelation in harvest rate as well as a declining trend in the harvest rate, and this trend remained when 5-year periods were pooled to increase precision. Autocorrelation can be induced even by weak responses by managers to change quotas each year and can make populations more variable and susceptible to decline (Fryxell et al. 2010). Unless new information is available about the population status, it may be unwise to tinker with harvest quotas based solely on the number of individuals harvested the previous year. Because Montana’s estimated harvest rate leveled out from 1997 onward, more recent estimates are probably more accurate.

The total number of individuals harvested may reflect changes in population size more accurately than estimates of total population produced by dividing the total harvest by the estimated harvest rate. This is likely due to the amplification of error that occurs when going from an estimated rate to an estimated population size. In either case, identification of declines lagged well behind changes in simulated population size, even when the population was declining relatively rapidly. Annual changes in environmental conditions, such as natural food availability, can affect the vulnerability of individuals to hunters (Fieberg et al. 2010), and the ability to detect changes in population size will depend on how variable that vulnerability is and how consistent harvest effort and methods are. Hristienko and McDonald (2007) suggested that occasional over-harvest of black bears will not be a problem because managers will respond rapidly to reduce harvest in subsequent years. The time lags apparent in both the decline of harvest numbers and the estimates of harvest rate indicate that managers may not be able to respond rapidly because they cannot discover the problem quickly enough.

It is encouraging that with more than 20 years of harvest data for Montana, we do not have evidence of a negative trend, let alone a statistically significant one. Indeed, annual estimates of harvest show that harvest rates have declined while the total harvest has been fairly stable. Because the same number of bears harvested represents a smaller proportion of the population (the harvest rate), these results suggest the population has increased. This is consistent with the fact that our estimated rates (4.3% for females and 10.6% for males) are well below reported estimates of sustainable harvest rates for black bears (14.2% [Miller 1990], 15% [McLaughlin 1998], 21% [Klenzendorf 2002], 12.6% [Dobey et al. 2005]).

On its face, this contradicts our hypothesis, based on the meta-analysis of demography (Beston 2011), that black bears have been decreasing in western North America. The average population growth rate based on the demographic work was less than 1, but our present harvest analyses indicate that, if anything, the population was increasing. The actual growth rate may be in the right tail of the distribution (at or above 1), the demographic work could be biased, or there may be other processes occurring for which we have not accounted. Although demographic studies are often considered the gold standard, they are more limited in space and time and therefore may not be representative of the true population status across large geographic areas. Demographic studies included in the meta-analysis had a median sample size of about 30 bear-years (Beston 2011), and because adult female survival rates are close to 1 (0.88 in the west; Beston 2011), researchers might only observe 3 or 4 deaths over the course of such a study. The small sample sizes typical of bear demographic work reduce precision of resulting estimates and make added information from harvests even more valuable. Harvest data can provide another means of estimating population trends at large scales to check against intensive demographic studies at smaller scales. If the demographic work is concurrent with harvest data collection, it can be used as auxiliary information in a statistical catch-at-age analysis that uses the age structure of harvest and prior knowledge about demography to estimate harvest rate and population size (Gove et al. 2002).

Another possibility is that spatial structuring and source–sink dynamics allow growing populations to support those that would otherwise decline. Some regions rely on wildlife refuges and sanctuaries to boost populations subjected to harvest in surrounding habitats (Powell et al. 1996). The meta-analysis suggested about 34% of western populations were growing (Beston 2011), and these could serve as sources that allow bears to persist despite low population growth rates elsewhere. In Montana,
Glacier National Park provides protection from harvest, and black bears living deep in the Bob Marshall and other wilderness areas may be essentially inaccessible to most hunters. Further work needs to be done to determine the effect of these and other potential source habitats on surrounding populations.

In theory, the harvest rate estimation method we used can be applied to any game species with differential selectivity in the harvest for which we can collect sex and age data. Male-biased harvesting occurs in mammals with multi-annual parental care, such as bears and elephants (*Loxodonta africana*), when females with young are protected and when adult males are targeted as trophies (McLoughlin et al. 2005). It is also intentionally applied in some ungulate systems because females are considered the limiting component of the population (Ginsberg and Milner-Gulland 1994). In reality, harvests need to be large enough to overwhelm demographic stochasticity, and the nature and degree of assumption violations need to be explored. The largest biases and sensitivities to assumption violations for the method we used occur when harvests are small (Harris and Metzgar 1987). This method could also be extended to incorporate differing harvest rates and relative vulnerabilities for spring and fall harvest seasons and geographic structuring to analyze different regions or management units. Because we analyzed the state as a whole, our estimated harvest rates are probably most representative of the western part of Montana, where most black bears live and are harvested. Extensions would require harvest sample sizes in each season or geographic area to be large. Although this method can be applied in principle to many game species, other methods may be more appropriate in some situations. For example, if it is possible to couple field studies with harvest data in approaches such as statistical catch-at-age analysis, researchers can obtain more accurate information in fewer years (Gove et al. 2002). When management is consistent across years, the target species has a short life-span and simple age structure, or the harvests are relatively large (in the hundreds), the method we employed could be a valuable way to garner information about the target population.

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**Literature cited**


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