

Rapid Decrease in Horn Size of Bighorn Sheep: Environmental Decline, Inbreeding Depression, or Evolutionary Response to Trophy Hunting?

PHILIP W. HEDRICK

From the School of Life Sciences, Arizona State University, Tempe, AZ 95287-4501.

Address correspondence to Philip W. Hedrick at the address above, or e-mail: philip.hedrick@asu.edu.

There are numerous examples demonstrating that selection has greatly influenced phenotypes in wild-harvested species. Here, a significant reduction in horn size in trophy desert bighorn sheep rams over 30 years in a reintroduced population in Aravaipa Canyon, Arizona is documented. After examining the potential effects of a detrimental change in the environment, inbreeding depression, and hunter-caused evolutionary change, it appears that environmental deterioration, apparently from the effects of drought, may be a major cause of the decline in horn size. In particular, the reduction in ram horn size is positively associated with reduced winter lifetime rainfall over the 3 decades. Over the same period, the demographic indicator lamb-to-ewe ratio has also declined in the Aravaipa population. On the other hand, lamb-to-ewe ratio has not declined statewide in Arizona, and the population size in Aravaipa appears to be increasing, suggesting local- and trait-specific effects. Using a theoretical context, neither inbreeding depression nor hunter selection by themselves appear to be the sole causes of the lower horn size. However, some combination of environmental factors, inbreeding depression, and hunter selection may have caused the decrease in observed horn size. It is not clear what management actions might be successful in countering the environmental effects on horn size, but supplemental feeding and cattle removal are suggested while translocation is suggested to counter the effects of inbreeding depression and reduced hunting and translocation are suggested to counter the effects of hunter selection.

Key words: bighorn sheep, drought, effective population size, gene flow, heritability, inbreeding depression

In the western United States and Canada, trophy hunting for male bighorn sheep, elk, and other ungulates is a major source of revenue for state and province departments of fish and game. For example, in Arizona, trophy hunters have paid more than \$300 000 for a single permit to hunt a desert

bighorn ram and Arizona raised more than \$5 700 000 from desert bighorn sheep special tag hunting permits between 1984 and 2006.

The annual number of permits (harvest) for trophy bighorn sheep in a population has been generally decided by determining the level at which negative demographic effects are not large. That is, where trophy hunting is not thought to result in the decline of population size or population growth rate and a continuing viable population is supported (Lee 1990). However, as Coltman (2008) states “removing 1 or 2 prime rams per year from a population of 60 or 70 sheep is likely sustainable from a demographic viewpoint, especially if the population is genetically linked to a wider network through ram-breeding migrations (Hogg 2000). However, if the ram with the biggest horns was removed every year from an isolated population, the cumulative selective effect on horn growth could be very strong.”

In recent years, high hunting and harvesting pressure has been shown to have significant evolutionary consequences in a number of different species, including bighorn sheep (Coltman et al. 2003; Allendorf and Hard 2009). For example, high harvesting rates of larger fish have resulted in significant decreases in body size and earlier age of maturation in a number of species (Allendorf et al. 2008). As a result, it appears that evolutionary impacts, as well as the ecological and demographic effects, should be considered in the determination of hunting and fishing levels.

Here, I examine and discuss the horn size of trophy bighorn sheep rams in the reintroduced population of desert bighorn sheep (*Ovis canadensis mexicana*) in Aravaipa Canyon, Arizona. I document a significant reduction in horn size over the last 30 years in this isolated population. After examining the potential effects of environmental deterioration, inbreeding depression, and evolutionary response to hunting, environmental change appears to be an important contributor to this decline. Although neither inbreeding depression nor trophy hunting appear to be strong enough

by themselves to cause the decline in horn size, they may have exacerbated the environmental effects.

Methods

Study Population, Population Survey Data, and Horn Size Score

Much of Aravaipa Canyon, Arizona (about 100 km north of Tucson) and some of the neighboring tablelands, where the contemporary desert bighorn sheep population lives, are now protected as the Aravaipa Canyon Wilderness (the bighorn sheep population in Aravaipa Canyon and adjacent areas is referred to as the Aravaipa population here). Although there are no specific numbers recorded of desert bighorn sheep in Aravaipa in the 19th century, it is assumed that there were significant numbers of bighorn sheep in the Aravaipa area and the neighboring Galiuro Mountains to the south before extensive human settlement in the late 19th century (Hadley et al. 1991).

A number of factors probably contributed to extirpation of bighorn sheep from Aravaipa in a period of only a few decades during the late 19th and early 20th centuries (Hadley et al. 1991). First, the introduction of many tens of thousands of domestic angora goats in the 1890s to the area was probably the first real threat to Aravaipa bighorns because these goats used much of the same forage, bedding areas, and terrain as bighorns. Second, the great expansion of cattle grazing in Aravaipa Canyon, its tributaries, and the surrounding tablelands during the same period probably displaced sheep from grazing areas where summer grasses were important for bighorns. Third, access to water was probably reduced by settlement during the 1890s by large numbers of goat herders, ranchers, miners, and their livestock. Fourth, an extreme drought in late 19th and early 20th centuries greatly reduced forage and water. Finally, unregulated hunting and poaching with improved rifles and disease introduced by free-ranging livestock, particularly goats and sheep, are thought to have contributed to the demise of bighorn sheep in other areas (Brown 1990) and perhaps in Aravaipa. By 1910, the Aravaipa bighorn sheep population had experienced a severe collapse, no herds were reported, and only stragglers were seen. The last bighorn from this period appears to have been shot on Brandenberg Mountain, just north of Aravaipa Creek, in the 1930s (Hadley et al. 1991).

After World War II, goats (as well as feral burros and horses) had been absent from Aravaipa for nearly a decade and cattle numbers were greatly reduced. The first attempt to reintroduce desert bighorn sheep into their historic range and habitat was in Aravaipa by the Arizona Game and Fish Department (AZGFD) in the late 1950s. The plan was to capture 25 sheep in what is now the Kofa National Wildlife Refuge in western Arizona and release them into a 45.3-hectare (112 acre) enclosure next to Horse Camp Canyon, a north side tributary near the middle of Aravaipa Canyon. The first 8 sheep were initially captured in 1958 and 1960 and moved to the enclosure. After some initial difficulties, more sheep were translocated to the enclosure in the early

1970s. In 1973, the enclosure was opened and the 22 sheep released from it formed the basis for the reintroduced population (Weaver 1973; Hernbrode 1975).

Since bighorn sheep were released into Aravaipa from the enclosure in 1973, there have been no further translocations into Aravaipa. There is a smaller separately reintroduced population of bighorn sheep in the Galiuro Mountains to the south of Aravaipa Canyon (survey numbers average less than 1/3 that of the Aravaipa population). AZGFD suggests that the Aravaipa and Galiuro groups are connected and hunts these sheep as one population, although there has been no documented gene flow between them. In any case, only 3 trophy rams have been shot from the Galiuro group in the years 1994, 2008, and 2009 (inclusion of these 3 rams has no impact on the data analysis below). The Aravaipa population is quite isolated from any other large bighorn sheep source populations, and exchange from other large source populations has never been suggested or observed, indicating that there is no effective gene flow into the Aravaipa population.

The population survey estimates used below for years 1973–1976 are from Cunningham et al. (1990), and all other numbers are from AZGFD databases. These data are mainly from intensive 1-day helicopter surveys conducted by AZGFD in the fall, generally October. Data from these helicopter surveys can be variable due to extensive variation in detection rates from such factors as windy conditions, warm weather making animals less active, mechanical issues with the helicopter, etc. Because these survey counts generally do not find all sheep, historically, AZGFD has suggested that only about 75% of the sheep are counted and have based the number of hunting permits on $1/0.75 = 133\%$ of the survey number. However, it has been estimated in western Arizona (Hervert et al. 1998) that the undercount is even greater and that about only 46% of the sheep are counted. Using the 75% and 46% detection rates, the estimated counts would be either 133% or 217% of the number counted for the surveys.

The Boone and Crockett Club scoring system is widely used to measure the size of horns in bighorn sheep rams in the United States and is recognized by desert bighorn sheep hunters and hunting groups, such as the Wild Sheep Foundation, as the best index to determine horn size. The Boone and Crockett scoring system is similar to that used by International Council for Game and Wildlife Conservation (1977). The Boone and Crockett bighorn sheep score is the sum of the lengths (in inches) of the 2 horns plus the circumference (in inches) of the horns at the base, first quarter, second quarter, and third quarter minus the difference between horns in the sum of the 4 circumference measurements. For example, for the largest hunter-harvested desert bighorn ram ever, which came from Aravaipa in 1988, the lengths of the 2 horns were 42.625 and 42.0 inches (108.3 and 106.7 cm), and the sums of the 4 circumference measurements were 57.0 and 57.625 inches (144.8 and 146.4 cm), making the score 198.625 points (504.5 cm). In addition to the Boone and Crockett score for the 47 rams harvested in Aravaipa, the age was also estimated by AZGFD for 44 rams by examination of their horn segments and annual horn rings (Monson and Sumner 1980).

Environmental Data

It is possible that drought in recent years could have reduced forage for bighorn sheep and that this could have influenced life-history characteristics and decreased horn size. To examine this, the most complete set of monthly precipitation data in the Aravaipa area from 1975 to 2010 was utilized (Schnell J, The Nature Conservancy, personal communication).

Rainfall is bimodal in Aravaipa with most rain either in the summer monsoons from July through September or the winter rains from December through March. The level of winter rains is an important determinant of the amount of forage in the late winter and spring. During the rut in the fall, horn growth subsides for several months but resumes again usually in January (Monson and Sumner 1980). As a result, for each trophy ram for which age was estimated, the association of average winter rainfall over the years of his total lifetime was calculated. For example, for a 9-year-old ram shot in 1999, this would be the mean rainfall for the 9 winters from December 1989–March 1990 to December 1998–March 1999. In addition, a measure of reproductive success, lambda-to-ewe ratio, as obtained from the surveys conducted by AZDGF, was examined over time.

Inbreeding Depression

For populations such as Aravaipa with no detailed genetic data, the effect of inbreeding depression can be estimated from the following theoretical approach. From survey data of population numbers, it is possible to estimate in a general way the effective population size, which can in turn give an estimate of the potential effects of genetic drift and inbreeding in the population. For example, the effective population size can be estimated as:

$$N_e = \frac{4N_1L}{V + 2}, \quad (1)$$

where N_1 is the number of newborns recruited to the population per year, L is the generation length, and V is the sex-averaged variance in reproductive success ($V = fV_f + mV_m$, where f and m are the fractions of female and male offspring and V_f and V_m are variances in reproductive success for females and males (Hill 1972, 1979). An estimate of the cumulative inbreeding coefficient f over t generations using this estimate of N_e is then

$$f = 1 - \left(1 - \frac{1}{2N_e}\right)^t = 1 - e^{-t/(2N_e)}. \quad (2a)$$

(for example, Hedrick 2007). We can determine likely values for these different parameters and then estimate both the effective population size and its potential impact on inbreeding depression through inbreeding from accumulated genetic drift. Or, given estimates of the effective population size in different generations, we can use the following equation:

$$f = 1 - \prod_i^t \left(1 - \frac{1}{2N_{e,i}}\right), \quad (2b)$$

where $N_{e,i}$ is the effective population size in generation i .

Evolutionary Response to Hunting

Trophy hunting results in increased mortality in the hunted population and reduced fitness of individuals with desirable phenotypes (Allendorf et al. 2008) and may therefore result in an evolutionary response to this selection pressure. As a result, based on quantitative genetics, trophy hunting is expected to produce the paradoxical situation of selection against the traits that are preferred by trophy hunters (Festa-Bianchet 2003; Allendorf and Hard 2009). Because bighorn sheep rams can fertilize multiple ewes, a reduction in the number of rams probably does not result in a great reduction in the population growth rate unless it results in behavioral interactions that reduce mating success. However, the quantitative genetic expectation is that the surviving breeding rams would be of lower value for the phenotypes desired by hunters than those rams harvested by hunters.

Without detailed genetic data for the population as in Aravaipa, the impact of hunter selection can be estimated in the following general quantitative genetics framework. The response R per generation to selection for a quantitative trait can be estimated as:

$$R = b^2S, \quad (3a)$$

where b^2 is the narrow-sense heritability, based on the additive genetic variance of a trait that can provide a directional evolutionary response, and S is the selection differential or the difference in the phenotypic mean of the selected parents and that for the whole population (Falconer and McKay 1996). Note that this “breeder’s equation” predicts the change in the mean phenotypic value from selection. Here, we are using data on the largest phenotypic values (assuming that the hunters shot the largest animals) and therefore are assuming that changes in the largest phenotypic values are reflective of changes in the mean phenotypic value. In this case, selection from hunting is only occurring in males. Therefore, the selection differential S_m for small horns is only in males (the surviving or selected rams have smaller horns), so that the response is halved or

$$R = \frac{1}{2} b^2 S_m. \quad (3b)$$

Note that here both response and the selection differential are negative because hunter harvest is reducing horn size. Further, in a finite population, the amount of response is reduced because of the loss of genetic variation due to genetic drift, an amount that is proportional to $1 - 1/(2N_e)$ (James 1971). Therefore, combining this effect with the effect of male only selection in Equation 3b gives a predicted response in generation 1 of

$$R_1 = \frac{1}{2} b^2 S_m \left(1 - \frac{1}{2N_e}\right).$$

After 2 generations, the response is expected to be

$$R_2 = R_1 + \frac{1}{2} b^2 S_m \left(1 - \frac{1}{2N_e}\right)^2 = \frac{1}{2} b^2 S_m \left(1 - \frac{1}{2N_e}\right) \left(2 - \frac{1}{2N_e}\right),$$

and after t generations, this becomes

$$R_t = \frac{1}{2} b^2 S_m \left(1 - \frac{1}{2N_e}\right) \sum_{i=0}^{t-1} \left(1 - \frac{1}{2N_e}\right)^i. \quad (3c)$$

To obtain the estimated selection differential when R , b^2 , and N_e are known, this equation can be rewritten as:

$$S_m = \frac{R_t}{\frac{1}{2} b^2 \left(1 - \frac{1}{2N_e}\right) \sum_{i=0}^{t-1} \left(1 - \frac{1}{2N_e}\right)^i}. \quad (3d)$$

Is such a level of selection possible in the Aravaipa population, given the rate of harvest? Let us define the selection differential in males as the difference in the mean in the selected males \bar{x}_{Sel} (remember the selected males are the surviving, nonharvested males, not the hunter-harvested ones) minus the mean in the population of all adult males \bar{x}_{Pop} or

$$S_m = \bar{x}_{Sel} - \bar{x}_{Pop}. \quad (4a)$$

The mean in the population of males before harvesting is

$$\bar{x}_{Pop} = (1 - p_H)\bar{x}_{Sel} + p_H\bar{x}_H, \quad (4b)$$

where p_H is the proportion of rams that are harvested and \bar{x}_H is the mean phenotypic value of the harvested rams. Substituting this in Equation 4a and solving, we get an estimate of the mean of the rams that were not harvested (surviving or selected rams) necessary for the estimated level of response or

$$\bar{x}_{Sel} = \frac{p_H\bar{x}_H + S_m}{p_H}. \quad (4c)$$

Results

Bighorn Sheep Numbers in Aravaipa

From the initial 22 animals released into Aravaipa, the population grew until reaching a maximum survey of 121 animals in 1988 (Figure 1). However, the survey in the fall of 1989 found a 59% decline in sheep numbers compared with 1988. A number of carcasses were found, and mortality was thought to have occurred between 1 August 1989 and 15 September 1989 (Mouton et al. 1991). This period is the end of the summer rainy season in Aravaipa, but there was severe drought during this period in 1989. Sheep in Aravaipa that have been serologically tested have indicated exposure to both the bluetongue virus and epizootic hemorrhagic disease (EHD)(deVos 1990). Until 11 September 1989, there was extensive cattle grazing near the sheep, suggesting that the opportunity for transmission of bluetongue and/or EHD from cattle was high. Although the exact cause of mortality of this decline was not determined, Mouton et al. (1991) concluded that it was “probably the result of livestock related viral disease compounded by nutritional distress” caused by the drought.

After this episode, the population remained at this lower level for the next decade. Beginning around 1999, the population numbers have increased for each survey

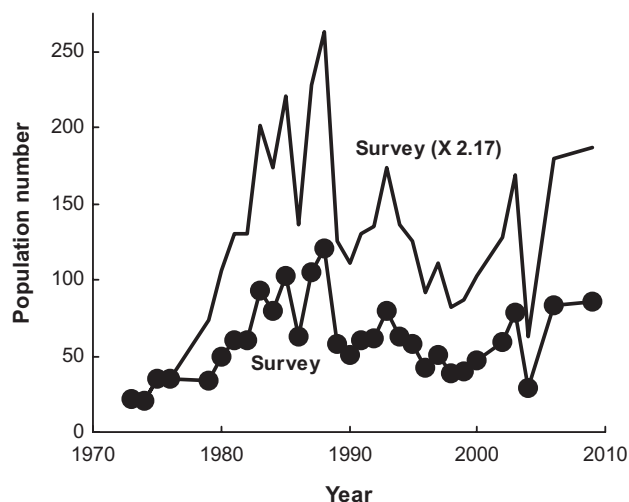


Figure 1. The survey population number (solid circles) and the survey population number ($\times 2.17$) of the Aravaipa desert bighorn sheep population (data from Cunningham et al. 1990; AZGFD files).

count, except for the survey in 2004, which showed large incongruities with the next survey in 2006, and have been close to 100 in recent years. In all but the first few years given in Figure 1 in which there was thought to be a complete count; the survey number $\times 2.17$ is also given. It is not clear what adjustment is appropriate for Aravaipa where bighorn sheep are primarily in a more linear habitat along Brandenberg Mountain and the north side of Aravaipa Canyon and are often in larger groups than in western Arizona. To be conservative, the greater adjustment (217%) will generally be used in the following analysis and discussion.

Number of Adult Rams and Trophy Ram Harvest in Aravaipa

Hunting for trophy rams in the reintroduced Aravaipa population was first allowed in 1980 when 49 sheep were detected in the survey. The amount of legal harvest in Aravaipa for each year is given in Figure 2 by closed circles. For the first 10 years, 2 permits were issued annually, and hunter success was 100% (except for 1 hunter in 1981). After the decline in 1989, there was a hunting moratorium from 1990 to 1992. In 1993, there was 1 permit; from 1994 to 1999, 2 permits were issued annually; from 2000 to 2006, 1 permit was issued annually; from 2007 to 2009, there were 2 permits; and in 2010, there were 3 permits (single permits were used in the Galurios in 1994, 2008, and 2009). Of the 40 total rams hunter harvested in Aravaipa since 1984 when the special permit program was started, 10 were taken on auction permits (the 2 auction permits in 1996 and 1997 used in Aravaipa went for \$285 000 and \$295 000). Hunter success since 1981 in Aravaipa has been 100%, probably because of relatively easy access to the sheep, lack of wariness by the sheep, and scouting efforts by permittees, guides, and members of the Arizona Desert

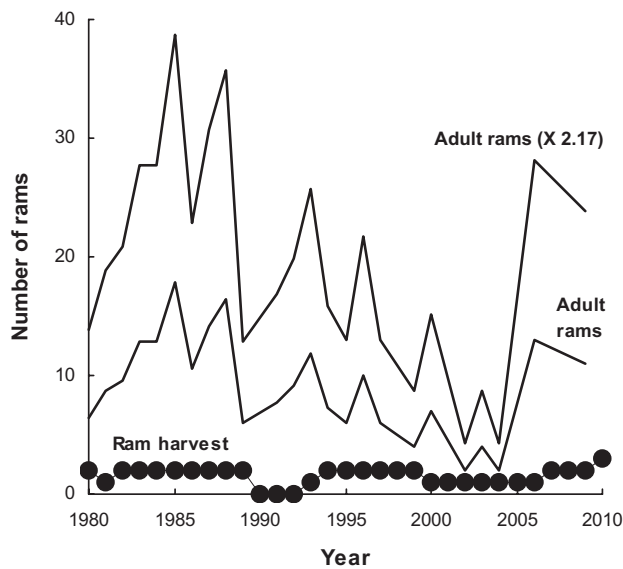


Figure 2. The annual mean number of adult rams observed and the adjusted annual mean number of adult rams ($\times 2.17$) and the number of harvested trophy rams from Aravaipa Canyon (data from AZGFD files).

Bighorn Sheep Society (ADBSS), a hunter group. Much of the total hunting time appears to be spent scouting for the largest ram to shoot, and members of the ADBSS generally help permittees find and harvest the largest trophy rams to help maintain Aravaipa's reputation as Arizona's prime desert bighorn sheep hunting area.

The number of adult rams (Class III, age 6–8 and Class IV, age 9 or older) for the years when there was a survey is also given in Figure 2. For the 10 survey times in the years from 1995 to 2009, this was the actual number of rams observed. For the earlier years, only the total number of rams was reported so an estimate of the adult ram number was obtained by multiplying the average proportion of adult rams of all rams for the times from 1995 to 2009 (0.457) times the total number of rams for each of these earlier years. Also given is the survey number multiplied by 2.17 to compensate for the expected undercount (Hervert et al. 1998).

The estimate of the number of adult rams varied greatly. The lowest numbers were 2 adults rams observed in 2002 and 2004 and 4 observed in 1999 and 2003. The highest numbers were 10 or greater for a number of years in the 1980s, 1993, 1996, 2006, and 2009. Multiplying these observations by the undercount factor 2.17 makes the lowest estimated number of adult rams 4.34 in 2002 and 2004 and the highest estimated number 38.67 in 1985.

The AZGFD Hunt Guidelines for bighorn sheep populations state that "Harvest will be managed to allow the take of 15–25% of the estimated Class III (age 6–8) and Class IV (age 9 or older) rams." The average estimated percentage harvest in Aravaipa for the first 10 years using the actual and adjusted survey numbers was 18.5% and 9.2%, respectively, in the middle of the range suggested in the hunt guidelines for the actual

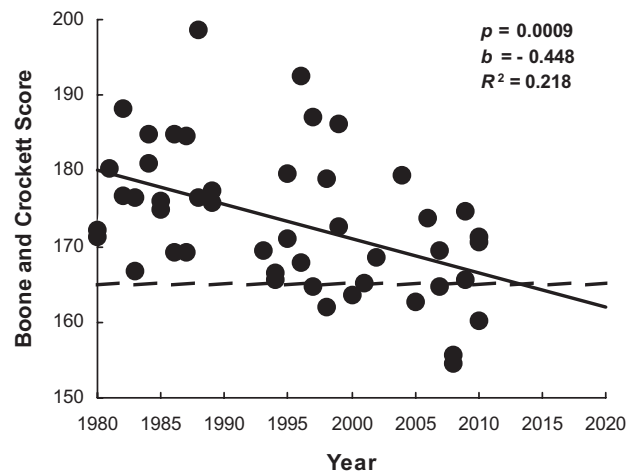


Figure 3. The Boone and Crockett score (a measurement of horn size) for 47 rams shot in Aravaipa Canyon over 30 years of hunting where the solid line is the linear regression for these data and the broken line indicates the minimum score of 165 points for inclusion of desert bighorn sheep in the Awards Program of the Boone and Crockett Club (data from AZGFD files).

observed number and well below the guideline number for the adjusted number. On the other hand, for the 12 years after the die-off in 1989 in which there was a hunt and a survey, using the actual and adjusted survey numbers, the average estimated percentage harvest was 29.1% and 14.6%, respectively, higher than that suggested by the hunt guidelines for the actual observed number and at low end of the hunt guidelines for the adjusted numbers. For the 6-year period from 1994 to 1999, the average percentages of adult ram harvest were 36.1% and 18%, respectively, with that for the actual observed numbers significantly greater than the guidelines. During this period, 4 rams were taken in Aravaipa from 1996 to 1999 with auction permits. Auction permits can be used in most hunt units but because of the reputation for rams with large horns in Aravaipa, these permittees selected Aravaipa for hunting. The level of harvest on Ram Mountain (Coltman et al. 2003) where there was a nearly 25% decline in horn size over 30 years appears to have been higher (nearly 40% of legal rams) than in Aravaipa.

Trophy Ram Horn Size in Aravaipa

The Boone and Crockett scores for the 47 rams harvested by hunters in Aravaipa from 1980 through 2010 are given in Figure 3. In the 20 years before 2000, there were 11 rams with scores of 180 points or larger, whereas in the 9 years after 2000, no rams this large were shot. The trend to smaller horn size in rams is statistically significant ($P < 0.0009$, $b = -0.448$, $R^2 = 0.218$), and the linear regression over time is given by the solid line in Figure 3, which has expected values of 180.0 in 1980 and 166.6 in 2010. (A 4-year-old ram shot in 2003 with a score of only 114.75 was excluded here; the decline would be even steeper if it was included.) The broken line indicates the minimum score of 165 points for inclusion of desert bighorn sheep in the Awards Program of the Boone and Crockett Club. If the regression line is extended to 2020,

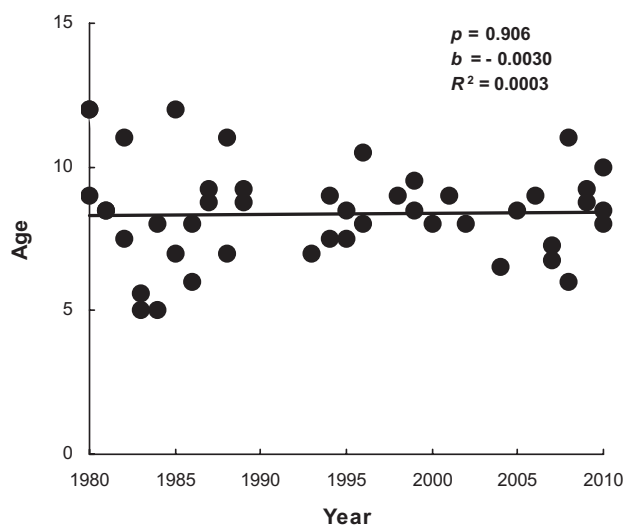


Figure 4. The ages for 44 rams shot in Aravaipa Canyon over 30 years of hunting where the solid line is the linear regression for these data (data from AZGFD files).

the predicted mean value of 162.1 points is below the minimum score for inclusion in the Awards Program.

The mean Boone and Crockett score of the 2045 desert bighorn sheep rams shot in Arizona (excluding those from Aravaipa) from 1980 to 2009 is 154.9 points. As a result, the additional expected horn size for rams from Aravaipa in 1980 from this average was $180.0 - 154.9 = 25.1$ points. However, by 2010, the additional expected horn size for Aravaipa rams had declined to only $166.6 - 154.9 = 11.7$ points. Therefore, the additional expected horn size of Aravaipa rams in 2009 is only 47.2% what it was in 1980.

Figure 4 gives the estimated age of the harvested rams over time. There is no trend of changing age over time, and the linear regression is not significantly different from zero ($P = 0.923$, $b = -0.0028$, $R^2 = 0.0002$). In other words, it appears that the rams shot in recent years are the same average age as those shot in earlier years but with smaller horn size. Interestingly, the two 5-year-old rams shot in Aravaipa in 1983 and 1984 had relatively high Boone and Crockett scores of 176.375 and 181 points, respectively. Further, the size of the horns in the harvested rams shows only a slight nonsignificant increase with age ($P = 0.0276$, $b = 0.950$, and $R^2 = 0.028$). The two 12-year-old sheep shot in 1980 and 1985 had only average size horns (actually smaller than the two 5-year old rams). One of the 11-year-old rams was the hunter harvest record of 198.625 points, and the other 11-year-old ram was only 155 points.

Environmental Change

In recent years, there have been drought conditions in parts of Arizona, and this could be an environmental factor reducing horn size compared with the early 1980s when there was more precipitation. As shown in Figure 5, the patterns of

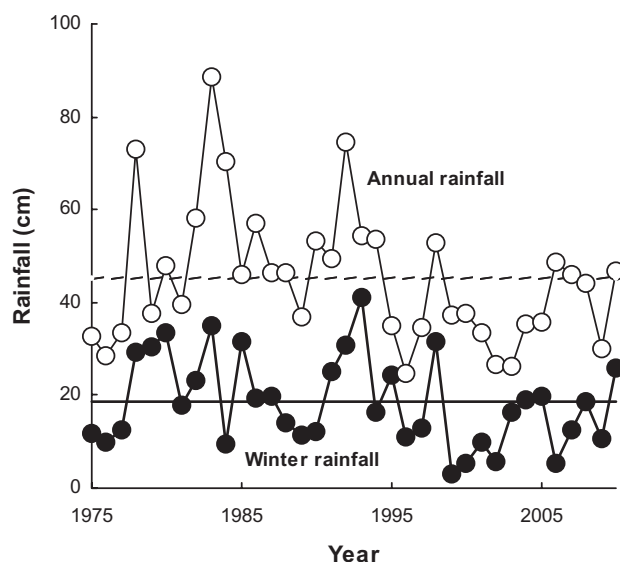


Figure 5. The annual (open circles and mean given as broken line) and winter (December through March, closed circles and mean given as solid line) rainfall for Aravaipa from 1975 to 2010 (data from J. Schnell).

annual and winter precipitation are generally similar ($r = 0.526$) and are higher before 1995 and lower in more recent years. The lowest winter rainfall period is for years 1999–2002 during which the mean winter rainfall was 5.97 cm.

For the 44 rams with estimated ages, the mean total lifetime rainfall and mean winter lifetime rainfall were calculated (only winter lifetime rainfall analysis is given here as the annual lifetime rainfall findings were similar). For this set of rams, the size of their horns is higher when the level of the winter lifetime rainfall is higher (Figure 6) ($P < 0.0018$,

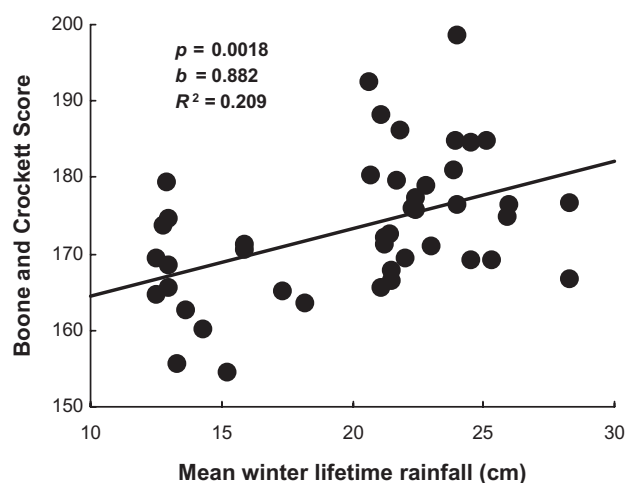


Figure 6. The Boone and Crockett score for 44 rams with estimated age for their mean winter lifetime rainfall where the solid line is the linear regression for these data (data from AZGFD and J. Schnell).

$b = 0.882$, $R^2 = 0.209$). In fact, all 9 rams with horn scores greater than 180 had mean winter lifetime rainfall values greater than 20 cm. Further, all 6 rams with horn scores of less than 165 had mean winter lifetime rainfall values of less than 20 cm. In other words, there has been a general temporal decrease in winter rainfall in Aravaipa over the past 30 years, and this lower rainfall is related to reduced ram horn size in recent years.

Although the horn size has decreased in recent years in Aravaipa, the population size has increased as we discussed above (Figure 1). In fact, based on the 2009 survey, AZGFD has increased the number of permits in Aravaipa to 3 in both 2010 and 2011, suggesting that they are confident the Aravaipa population is healthy and can withstand higher hunting pressure. On the other hand, an indicator of demographic health, the lamb-to-ewe ratio, has declined over this period (Figure 7) ($P < 0.0025$, $b = -1.45$, $R^2 = 0.322$). These data are greatly influenced by the 3 data points in 1998, 2000, and 2004 in which only 1 or 2 lambs were observed. However, these low data points may be partly the result of detection difficulty in helicopter surveys or from puma predation on lambs (Cunningham et al. 1995; Festa-Bianchet et al. 2006).

Over this same period, the statewide lamb-to-ewe ratio has not changed significantly, as indicated by the broken line in Figure 7 ($P < 0.235$, $b = -0.172$, $R^2 = 0.050$). As a result, the decline in horn size appears to be negatively correlated with changes in local population size, is positively correlated with local lamb-to-ewe ratio, but not correlated with statewide lamb-to-ewe ratio, suggesting that the decline in horn size may be correlated with local environmental factors and that these environmental factors do not reduce local population size.

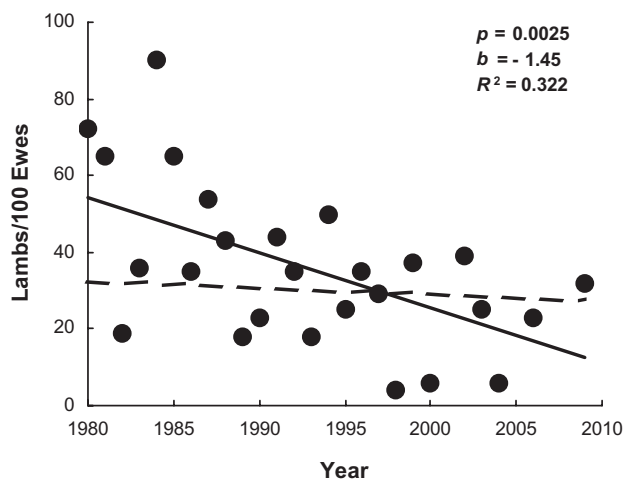


Figure 7. The observed ratio of lambs to ewes in Aravaipa Canyon where the solid line is the linear regression for these data and, for comparison, the broken line is the linear regression of the observed ratio of lambs to ewes statewide over the same period (data from AZGFD files).

Inbreeding Depression

Let us estimate values for the parameters that are necessary to calculate N_e from Equation 1, that is, L , N_1 , and V . First, L is the sex-averaged generation length, that is, the average age of parents when they have offspring. Because males are generally 6 or older when they are dominant and successful in mating and assuming that mating by subordinate males is less likely, let us assume that the mean age of paternity is approximately 7–8 years. On the other hand, females may reproduce from age 2 nearly until they die, say around age 10–12, so that the mean age of maternity is about 5, given cumulative mortality over age. Then overall, the mean age of parentage, or generation length L , is about 6 years. From demographic data, it was determined that the generation length in the Ram Mountain bighorn sheep population was also about 6 years (Coltman et al. 2003).

Second, N_1 is the number of young added annually to the population. As an estimate of this, let us use the annual mean number of lambs observed (times $1/0.75 = 1.333$ to take into account the estimated AZGFD undercount, using the adjustment of 2.17 would make N_1 and N_e larger and the likelihood of inbreeding depression even less). The average observed lamb count in Aravaipa from 1980 to 2009 is 10.9 so the estimate, taking into account the potential undercount, is 14.5.

Finally, the fractions of female (f) and male (m) offspring are probably close to 0.5. In general, both V_f and V_m may be greater than the mean number of progeny (let us assume that the population is relatively stable so that the mean number of progeny would be 2). As a general guideline, let us use $V_f = 4$ and $V_m = 8$, approximately that found by Coltman et al. (2005) so that $V = 6$. Note that an excess of females, $f > 0.5$, as often seen in bighorn surveys in Aravaipa and elsewhere, would make V smaller since $V_f < V_m$.

Therefore, with $L = 6$, $V = 6$, and $N_1 = 14.5$, then $N_e = 43.5$. Now, if we assume that there are approximately 5 generations over the 30 years, then an estimate of the cumulative inbreeding coefficient from Equation 2a is $f = 1 - e^{-5/87} = 0.056$. This is less than the level of inbreeding expected in progeny from a mating between first cousins (0.0625), although here this level has accumulated more slowly over 5 generations, not just from matings in one generation. As a result, the expected effect on lowering fitness would be less than that from one-generation inbreeding of the same level because of the opportunity for purging of detrimental variants (Hedrick 1994; Boakes et al. 2007).

To examine how this estimate is influenced by some of these parameters, let us use separate estimates of N_e for each generation, assume that the count is accurate and not adjusted for underestimation (to be conservative) and assume that the generation length is only 5 years, not 6, so that there is a total of 6 generations in the 30-year period. The average lamb counts for the six 5-year period from 1980 to 2010 are 12.8, 15.4, 9.6, 6.2, 9.0, and 12.5 so that the estimates of N_e for the 6 generations are 32.0, 38.5, 24, 15.5, 22.5, and 31.2. Therefore, the accumulated inbreeding coefficient using Equation 2b is 0.123. The level of inbreeding from a mating between half sibs is

0.125, very close to this value. Although this level of inbreeding is higher than above, it is still quite low and the accumulation slow enough that it is unlikely to have a significant detrimental phenotypic effect (Kalinowski and Hedrick 2001; Hedrick 2011). However, inbreeding depression may be greater in wild than in captive populations (Thrower and Hard 2009) so even this low level of inbreeding may have some effect.

After examining various mating systems, Nunney (1993) concluded that the ratio of the effective population size to the census number, N_e/N , within a generation should range from 0.25 to 0.75. The average survey number for the Aravaipa population size from 1980 to 2009 is 67.6, or using the AZGFD underestimation adjustment of 1.333, an estimate of 90. Assuming $N_e/N = 0.5$, then $N_e = 45$, close to the value estimated above, and results in $f = 0.054$ using Equation 2a. If $N_e/N = 0.25$, then $N_e = 22.5$, and $f = 0.105$, similar to the value when some of the parameters are relaxed above. Overall, these 2 approaches suggest that the expected decline of phenotypic traits from an inbreeding level of 0.056 (or 0.054) would be small and even if these parameters are relaxed, the 2 approaches still suggest the effect from inbreeding levels of 0.123 (or 0.105) would be small. Further, if the smaller Galiuro group of bighorns is included in the Aravaipa population or the 2.17 adjustment is used, then N_e would be slightly larger and expected inbreeding even less.

Evolutionary Response to Hunting

For horn size as measured by the Boone and Crockett score and assuming the change in horn size represents an evolutionary change, the response R between 1980 and 2010 was a reduction of 13.4 points. From family data, the narrow-sense heritability of horn size in bighorn sheep has been estimated as 0.69 (Coltman et al. 2003). Since Coltman et al. (2003) was published, “animal model” methods (see Kruuk 2004; Postma 2006; Morrissey et al. 2010) have been suggested for such multigenerational pedigree data. This approach was used on the same animals plus animals to 2006 (Poissant et al. 2008) and heritability of horn size was found to be 0.32. Further, recent research in domestic sheep has identified genes that have major effects on horn length (Johnston et al. 2010), suggesting that a few genes of large effects may be important in sheep horn size.

Assuming that $N_e = 43.5$ as above for 5 generations, then the selection differential in males per generation S_m in the Aravaipa population from Equation 3d using $b^2 = 0.69$ is approximately -10.6 points. Assuming that the generation length in bighorn sheep is approximately 6 years (Coltman et al. 2003), the estimate of the male selection differential is approximately $-10.6/6 = -1.76$ points per year. This high level of selection differential reflects both the intensity of the harvest (the proportion of individuals, adult rams, harvested) as well as the phenotypic selectivity of the harvest (Allendorf et al. 2008). In Aravaipa, intensive pre-hunting season scouting, as well as often the use of professional guides, generally assures that there is very high phenotypic selectivity increasing the selection differential so that the largest trophy rams in the population are nearly always shot.

In 4 of the 30 years between 1980 and 2010 in Aravaipa, no trophy rams were harvested, 3 years immediately after the die-off in 1989 and in 2003 when a small 4-year-old ram was harvested. Therefore, assume that the necessary selection differential for the remaining years is $-1.76 (29/25) = -2.04$ points per year. From the data given in Figure 2, p_H can be calculated, \bar{x}_H can be calculated from the data given in Figure 3, and the mean of the selected rams (surviving or nonharvested rams) \bar{x}_{Sel} can be calculated for each year from Equation 4c.

Figure 8 gives both the mean of the harvested rams and estimated mean of the selected (surviving or nonharvested) rams using both the survey numbers and the 2.17 adjustment for the number of rams for the years in which there were both trophy rams taken and a census estimate of the number of rams. Overall, the average score for the hunter-harvested rams need only be 7.0% larger than that of the surviving rams when the survey numbers are used. The hunter-harvested rams need to be from 2.5% in 1999 and 2004 to 18.0% larger in 2006, depending primarily on the proportion of rams harvested, although there could be more or less selection than these estimates in given years. On the other hand, if the 2.17 adjustment is used for the number of rams, then the hunter-harvested rams need to be 16.4% larger than of the surviving rams. Assuming this higher number of rams in the population leads to the need for selection stronger than appears to be likely. It seems possible to have a selection differential large enough to result in the response observed in this population given the survey numbers, particularly because of the strong phenotypic

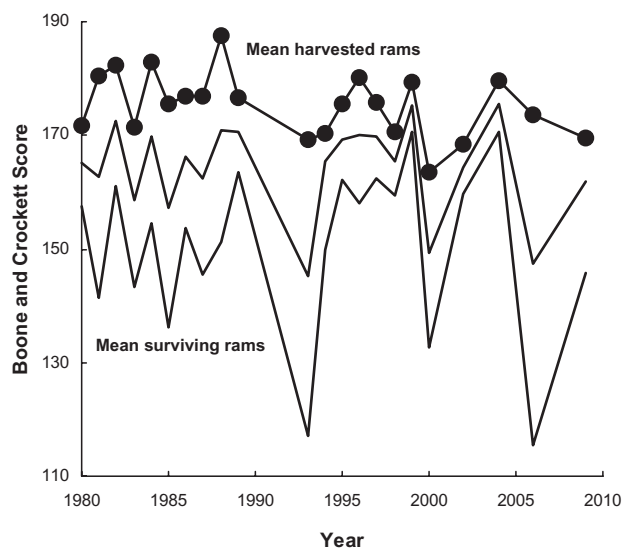


Figure 8. The Boone and Crockett score (a measurement of horn size) for the rams hunter-harvested each year in Aravaipa (solid line and closed circles) and the estimated mean of the selected (surviving or nonharvested) rams for the survey number and 2.17 times the survey number (upper and lower solid lines, respectively) necessary to result in a selection differential large enough to result in the observed response (decline) in horn size.

selectivity for large horn size in Aravaipa discussed above but unlikely if the adjusted ($\times 2.17$) survey numbers are used.

Discussion

The rapid and significant reduction in horn size observed in trophy rams over the past 30 years in Aravaipa desert bighorn sheep may potentially have several different causes. Three possible explanations have been examined above: deterioration of the environment, inbreeding depression, and an evolutionary response to hunting selection pressure, and we will discuss these results here. The implications of these explanations and the management actions that may alleviate their effects are discussed below.

As for other populations of desert bighorn sheep (and most populations of wild ungulates), there are no individual genetic data that can be used to establish a pedigree for the Aravaipa population. Such data could then be used to estimate directly inbreeding and inbreeding depression levels and to estimate the level of hunter selection. However, surveys are less frequent today than in earlier years because of budget reductions so that the quantity and quality of data may decline even further in the future. As a result, theoretical approaches are presented here that allow estimation of these factors in a population without detailed genetic information are necessary. These approaches may be useful to understand changes in other populations that also do not have intensive monitoring.

Environmental Cause of Horn Decline

Phenotypic trends, such as the reduction of horn size documented here, may be confounded with detrimental changes in environmental conditions. Quantitative genetic approaches can be used to separate genetic and environmental sources of genetic change (Lynch and Walsh 1998), but such approaches are not generally possible in most wild populations where a pedigree is not available or can be constructed from genetic data, such as the Aravaipa bighorn sheep population.

There have been 2 efforts to improve bighorn sheep habitat in Aravaipa by increasing the presence of free-standing water. In 1984 and 1989, waterers (guzzlers) were installed on Brandenberg Mountain and at the headwaters of Buzan Canyon, both on the north side of Aravaipa Creek, less than a mile from and about 400 m higher in elevation than the creek. Waterers were redeveloped in 2007 nearby both locations by AZGFD and with financial and labor support from the ADBSS. As of April 2011, cameras have documented one instance in May 2010 of one bighorn sheep ram using either of these waterers. It appears that sheep may use springs or Aravaipa Creek, which is perennial for the length inhabited by bighorn sheep, as sources of free-standing water, but they may also go for periods without accessing free-standing water as do other desert bighorn sheep populations in western Arizona (Broyles 1995; Broyles and Cutler 1999; however, see Rosenstock et al. 2001; Dolan 2006). Remember that the

original source of the reintroduced desert bighorn sheep population in Aravaipa was western Arizona, which is much drier than Aravaipa.

It is possible that low rainfall could have reduced forage for bighorn sheep and increased competition with livestock. However, Dodd and Brady (1986, 1988) showed that there was little overlap in forage between cattle and bighorn sheep in Aravaipa. Cattle have not been grazed on some of the area in Aravaipa allotments where there are bighorn sheep in the last decade (Bureau of Land Management), and the only sheep or goats presently in the area is a small, fenced, farm flock of sheep next to Aravaipa Creek. In other words, presently, there is no competition from domestic sheep or goats, and there appears to be less competition from cattle than in the past that could negatively influence bighorn sheep habitat.

Has there been a general trend for smaller horn size in harvested rams throughout Arizona during this period due to drought or other general environmental changes? One approach to test for this is to examine the statewide mean Boone and Crockett scores during this period. The statewide mean size (a total of 2182 trophy rams excluding Aravaipa) for the years during the period from 1980 to 2009 shows a slight significant downward trend in horn size during this period ($P = 0.011$), but the slope is only 28% that found in Aravaipa and results in a decline of only 3.7 Boone and Crockett points over the 29-year period. This decline is statistically significantly less ($P < 0.05$) than the slope observed for horn size in the Aravaipa population. As a result, the environmental effect on horn size in Aravaipa appears to be the result of unknown local factors.

In addition, there is no direct evidence that this decline in rainfall results in a deterioration of available forage or other factors that in turn results in ram lower horn. In fact, it is not known how much impact this environmental change would have on the desert bighorn sheep originally translocated to Aravaipa from much drier western Arizona. Therefore, we should be mindful that this effect is correlative and not known to be causative, and other factors may be involved in the decline in horn size.

Inbreeding Depression

Theoretically, an increase in inbreeding could result in a decline of phenotypic traits, including horn size. The largest study examining inbreeding depression in bighorn sheep found no effect on juvenile viability in captive animals with different levels of inbreeding (Kalinowski and Hedrick 2001). Because there is no pedigree information or molecular genetic data on the Aravaipa bighorn sheep population, it is not possible to estimate the inbreeding coefficient directly or even indirectly from the amount and pattern of molecular data. In the Ram Mountain population of bighorn sheep where there are pedigree data, the overwinter survival of inbred female lambs was significantly lower than that of noninbred female lambs (Rioux-Paquette et al. 2011).

Two other populations of desert bighorn sheep on Tiburon Island, Sonora, Mexico and at Red Rock, New Mexico, both founded by small numbers of animals, have

significantly reduced genetic variation (Gutiérrez-Espleta et al. 2000; Hedrick et al. 2001), but no studies of phenotypic effects have been carried out. There is no reported general deterioration of health or an increase in phenotypic abnormalities in the Aravaipa population that could be associated with an increase in inbreeding and inbreeding depression, but this has not been methodically evaluated.

The translocation of unrelated bighorn sheep into the Aravaipa population and monitoring their success and the success of their descendants would be one approach to determine the impact of inbreeding depression. If there was high success from these translocated individuals and their descendants indicating genetic rescue (Hedrick and Fredrickson 2010), then it would appear that inbreeding depression (genetic load) may have contributed to lower horn size. An example of genetic rescue in Rocky Mountain bighorn sheep (*O. c. canadensis*) was in an isolated population on the National Bison Range in Montana (Hogg et al. 2006). The low fitness in this population was increased by the introduction of 15 sheep from other populations.

Evolutionary Response to Hunter Selection

From the calculations above, using the 2.17 adjustment for the number of rams, then the hunter-harvested rams need to be 16.4% larger than of the surviving rams. When this higher number of rams in the population is assumed, it leads to the need for selection stronger than appears to be likely. Further, if the heritability of horn size is assumed to be only 0.32 (Poissant et al. 2008) rather than 0.69 as assumed above (Coltman et al. 2003), then selection needs to be 2.16 times higher, also making the necessary selection differential less likely. In other words, it does not appear that hunter selection is likely to be the sole contributor to the reduction in horn size.

Potential Consequences and Recommendations

Three possible explanations were examined above for the significant decrease in horn size observed in rams in Aravaipa: environmental deterioration, inbreeding depression, and hunter selection. Overall, local environmental deterioration appears to contribute to the lower horn size because of a correlation with lower local winter precipitation. Unfortunately, because of a lack of detailed information, the exact causative environmental factors are difficult to pinpoint. Further, a theoretical context for evaluating the impact of inbreeding depression and hunter selection was given above, and it appears neither inbreeding depression or hunter selection by themselves could be the sole causes of the decline in horn size. However, some combination of environmental factors, inbreeding depression, and hunter selection could have resulted in the horn size decline.

Assuming that environmental factors have been partially responsible for the observed reduction in horn size, what should be done? Studies have shown that horn size may be related to resource availability (Festa-Bianchet et al. 2004). As a result, more detailed environmental monitoring of the bighorn sheep habitat is necessary to establish the local environmental factors that may be contributing to the decline

in horn size. Of course, if environmental factors have caused the lower horn size, a return to good environmental conditions hypothesized for the early 1980s should result in a return to the horn size seen in these earlier times within 1 or 2 generations (assuming that maternal effects are significant). A detailed examination of the present environmental conditions when the horn size is low could provide a baseline for comparison with the conditions when there is a change back to good environmental conditions. Finally, any changes in present phenotypes, such as for body size, age of maturity, male mating patterns, etc. from past phenotypic values expected to be caused by the environmental factors causing the low horn size may be expected to return to earlier levels, given environmental improvement.

However, even if inbreeding depression or hunter selection contributed to lower horn size, a return to a better environment may also increase horn size due to genotype–environment interaction. For example, the effects of inbreeding depression may be greater in poorer environments so that a return to a better environment may increase horn size in inbred individuals more than in noninbred individuals. Similarly, even if hunter selection had reduced horn size, a better environment could result in larger horn size in individuals with lower horn size because of past hunter selection.

To determine what impact hunting had on the reduction in horn size in the Aravaipa population, it should be compared with a similar unharvested population. However, such a “control” population is not possible in Arizona because the only data available on horn size are from hunter-killed rams. Assuming that hunter selection has had some effect on the reduction in horn size, what impacts might this have beyond reducing horn size? From life-history theory (Stearns 1992; Myserud and Bischof 2010), it is predicted that selectively removing larger animals should result in smaller body size and maturation at an earlier age if there was a genetic correlation of body size and age. In Aravaipa, there is a potential response to hunting producing animals with smaller horns, but there does not appear to have been a change in the age of animals harvested. This lack of response of age may be because of a low genetic correlation of horn size and age of maturity or because there has been deterioration in the environment. Trophy hunting may also impact other correlated traits. For example, selection reducing horn size may result in reduction in body size, which is in turn correlated with lower disease resistance and fecundity (Coltman et al. 2005; Coltman 2008). In addition, it has been suggested that hunter selection may result in changes in sexual selection. Because there are fewer large rams to mate after trophy hunting, the likelihood of smaller males with smaller horns, and younger males, being successful in mating could increase. In general, hunting selection could have a considerable effect on the evolution of adult characteristics; particular those in prime-aged adults under sexual selection because hunting mortality may be higher than natural mortality for adult males (Festa-Bianchet 2003; Allendorf and Hard 2009).

One impact of hunter-induced selection resulting in smaller horn size is that even if hunting is greatly reduced or eliminated, time to recovery to pre-hunting levels of horn

size is likely to be slower than the time for reduction. This asymmetry occurs because hunter harvest can create large selection differentials, whereas relaxation of this selective pressure will generally result in smaller selection differentials in the opposing direction to increase horn size back to the level before the start of hunter selection (Allendorf and Hard 2009). As a result, the time expected for sexual selection to increase horn size back to pre-hunting levels may be longer than the 30 years it took trophy hunting to reduce horn size to present levels. Assuming that the goal of the management of desert bighorn sheep is to maintain a sustainable harvest of large trophy rams, it is obviously better to manage with evolutionary, as well as ecological, sustainability in mind (Coltman 2008). For example, despite a change in hunting practices on Ram Mountain in 1996 restricting trophy hunting, there has been no, or only very slow, recovery in horn size (Coltman D, personal communication).

Assuming that environmental factors were an important factor in the decline in horn size in Aravaipa trophy rams, then an obvious recommendation would be to find out what these environmental factors are and remedy them. At this point, one possible environmental factor is the drought conditions in recent years, which may in turn result in poor availability of water and/or forage. However, the 2 waterers that have already been placed in bighorn sheep habitat in Aravaipa to provide continuous free-standing water have been used only once, suggesting that free-standing water is not generally limiting. It is not clear what management actions might be taken to counter the potential effects of drought on horn size, but if bighorn sheep were observed to be starving, or even in poor nutritional condition, perhaps some type of supplemental feeding or removal of cattle from the allotments in bighorn sheep habitat could be considered as a remedy. Of course, supplemental feeding would be expensive and potentially controversial and removal of cattle contentious. If the low horn size is the result of environmental conditions, then continued hunting would probably not result in further decline in horn size or influence the potential rapid return to pre-hunting horn size once the environment returns to better conditions.

An obvious recommendation to reduce the evolutionary impact of hunter selection on horn size and related traits is to eliminate or reduce hunting in the Aravaipa population. This would be controversial and met with strong resistance by bighorn sheep hunters and AZGFD officials. However, if the potential impact that hunting may have had is understood, appropriate action may be recommended to remediate this impact. Even if a hunting moratorium was instituted immediately, the time for the population to recover to the pre-hunting levels of horn size may be a number of years, or even decades, as discussed above. Of course if a hunting moratorium was not instituted, the impact of hunting on horn size would continue to increase and the time to recover would even be longer. Reducing hunting impact would not be expected to alleviate the reduction in horn size if the cause was either environmental decline or inbreeding depression. In other species, to avoid the impact of hunting, there are hunting mandates to harvest only

certain individuals that would not result in the detrimental selection caused by trophy hunting.

Another possibility to reduce the time of recovery of horn size when hunting or inbreeding depression is a factor is to institute some artificial gene flow through translocations from other populations. For such isolated populations, translocations of animals from populations not influenced by hunting may provide a remedy for low horn size. However, if the decrease in horn size was environmentally caused and the environment was still causing the effect, translocations should have little impact.

Some have suggested that translocations should be only considered as a last resort and not as a general management strategy because translocations run the risk of introducing pathogens or maladapted genotypes (Coltman 2008). As discussed earlier, presently, there is no gene flow into Aravaipa to increase response as suggested by Allendorf et al. (2008). Genetic rescue, introduction of animals from unrelated populations (Hedrick and Fredrickson 2010), is recommended only for low-fitness populations (there is some evidence of lower lamb-to-ewe ratio in recent years, but this may be environmentally caused), not necessarily for a population with a reduction in horn size. Therefore, the risks involved with genetic rescue to increase trophy ram horn size may not be worth the potential costs.

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References

- Allendorf FW, England PR, Luikart G, Ritchie PA, Ryman N. 2008. Genetic effects of harvest on wild animal populations. *Trends Ecol Evol.* 23:327–337.
- Allendorf FW, Hard JJ. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proc Natl Acad Sci U S A.* 106:9987–9994.
- Boakes EH, Wang J, Amos W. 2007. An investigation of inbreeding depression and purging in captive pedigreed populations. *Heredity.* 98:172–182.
- Brown DE. 1990. Early history. In: Lee RM, editor. *The desert bighorn sheep in Arizona.* Phoenix (AZ): Arizona Game and Fish Department. p. 1–11.
- Broyles B. 1995. Desert wildlife water developments: questioning use in the Southwest. *Wildl Soc Bull.* 23:663–675.
- Broyles B, Cutler TL. 1999. Effect of surface water on desert bighorn sheep in the Cabeza Prieta National Wildlife Refuge, southwestern Arizona. *Wildl Soc Bull.* 27:1082–1088.
- Coltman DW. 2008. Molecular ecological approaches to studying the evolutionary impact of selective harvesting in wildlife. *Mol Ecol.* 17:221–235.
- Coltman DW, O'Donoghue P, Hogg JT, Festa-Bianchet M. 2005. Selection and genetic (co)variance in bighorn sheep. *Evolution.* 59:1372–1382.

- Coltman DW, O'Donoghue P, Jorgenson JT, Hogg JT, Strobeck C, Festa-Bianchet M. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature*. 426:655–658.
- Cunningham S, Dodd N, Olding R. 1990. Arizona's bighorn sheep reintroduction program. In: Lee RM, editor. *The desert bighorn sheep in Arizona*. Phoenix (AZ): Arizona Game and Fish Department. p. 203–239.
- Cunningham SC, Haynes LA, Gustavson C, Haywood DD. 1995. Evaluation of the interaction between mountain lions and cattle in the Aravaipa-Klondyke area of southeast Arizona. Phoenix (AZ): Arizona Game and Fish Department Research. Branch Technical Report Number 17.
- deVos J. 1990. The role of disease in Arizona's bighorn sheep. In: Lee RM, editor. *The desert bighorn sheep in Arizona*. Phoenix (AZ): Arizona Game and Fish Department. p. 30–62.
- Dodd NL, Brady WW. 1986. Cattle grazing influences on vegetation of a sympatric desert bighorn range in Arizona. *Desert Bighorn Council Trans.* 30:8–13.
- Dodd NL, Brady WW. 1988. Dietary relationships of sympatric desert bighorn sheep and cattle. *Desert Bighorn Council Trans.* 32:1–6.
- Dolan BF. 2006. Water developments and desert bighorn sheep: implications for conservation. *Wildl Soc Bull.* 34:642–646.
- Falconer DS, McKay TFC. 1996. *Introduction to quantitative genetics*. 4th ed. Harrow (UK): Longman.
- Festa-Bianchet M. 2003. Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. In: Festa-Bianchet M, Apollonio M, editors. *Animal behavior and wildlife conservation*. Washington (DC): Island Press. p. 191–207.
- Festa-Bianchet M, Coltman DW, Turelli L, Jorgenson JT. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. *Behav Ecol.* 15:305–312.
- Festa-Bianchet M, Coulson T, Gaillard J-M, Hogg JT, Pelletier F. 2006. Stochastic predation events and population persistence in bighorn sheep. *Proc R Soc B Biol Sci.* 273:1537–1543.
- Gutiérrez-Espleta GA, Kalinowski ST, Boyce WM, Hedrick PW. 2000. Genetic variation and population structure in desert bighorn sheep: implications for conservation. *Conserv Genet.* 1:3–15.
- Hadley D, Warshall P, Bufkin D. 1991. *Environmental change in Aravaipa, 1870–1970. An ethnoecological survey*. Phoenix (AZ): Bureau of Land Management. Cultural Resource Series No. 7. Available from: http://www.blm.gov/heritage/adventures/research/StatePages/PDFs/Arizona/arizona_7.pdf.
- Hedrick PW. 1994. Purging inbreeding depression and the probability of extinction: full-sib mating. *Heredity.* 73:363–372.
- Hedrick PW. 2009. Conservation genetics and North American bison (*Bison bison*). *J Hered.* 100:411–420.
- Hedrick PW. 2011. *Genetics of populations*. 4th ed. Boston: Jones and Bartlett.
- Hedrick PW, Fredrickson RJ. 2010. Genetic rescue: guidelines and examples from Mexican wolves and Florida panthers. *Conserv Genet.* 11:615–626.
- Hedrick PW, Gutierrez-Espeleta G, Lee R. 2001. Founder effect in an island population of desert bighorn sheep. *Mol Ecol.* 10:851–857.
- Hembrode RD. 1975. Aravaipa bighorn update—1975. *Desert Bighorn Council Trans.* 19:42.
- Hervert JJ, Henry RS, Brown MT, Kearns RL. 1998. Sighting rates of bighorn sheep during helicopter surveys on the Kofa National Wildlife Refuge, Arizona. *Desert Bighorn Council Transactions.* 42:11–26.
- Hill WG. 1972. Effective size of populations with overlapping generations. *Theor Popul Biol.* 3:278–289.
- Hill WG. 1979. A note on effective population size with overlapping generations. *Genetics.* 92:317–322.
- Hogg JT. 2000. Mating systems and conservation at large spatial scales. In: Apollonio M, Festa-Bianchet M, Mainardi D, editors. *Vertebrate mating systems*. Singapore (Singapore): World Scientific Publishing. p. 332.
- Hogg JT, Forbes SH, Steele BM, Luikart G. 2006. Genetic rescue of an insular population of large mammals. *Proc R Soc B Biol Sci.* 273:1491–1499.
- International Council for Game and Wildlife Conservation. 1977. *The game trophies of the world*. Budakesi (Hungary): International Council for Game and Wildlife Conservation.
- James JW. 1971. The founder effect and response to artificial selection. *Genet Res.* 16:241–250.
- Johnston SE, Beraldi D, McRae AF, Pemberton JM, Slate J. 2010. Horn type and horn length genes map to the same chromosomal region in Soay sheep. *Heredity.* 104:196–205.
- Kalinowski S, Hedrick PW. 2001. Inbreeding depression in captive bighorn sheep. *Anim Conserv.* 4:319–324.
- Kruuk LEB. 2004. Estimating genetic parameter in natural populations using the 'animal model'. *Philos Trans R Soc Lond B Biol Sci.* 359:873–890.
- Lee RM. 1990. Bighorn sheep hunting. In: Lee RM, editor. *The desert bighorn sheep in Arizona*. Phoenix (AZ): Arizona Game and Fish Department. p. 240–256.
- Lynch M, Walsh B. 1998. *The genetics and analysis of quantitative traits*. Sunderland (MA): Sinauer Publishing.
- Monson G, Sumner L. 1980. *The desert bighorn: its life history, ecology, and management*. Tucson (AZ): University of Arizona Press.
- Morrissey MB, Kruuk LEB, Wilson AJ. 2010. The danger of applying the breeder's equation in observational studies of natural populations. *J Evol Biol.* 23:2277–2288.
- Mouton RJ, Lee RM, Olding RJ. 1991. A desert bighorn sheep decline in Aravaipa Canyon, Arizona. *Desert Bighorn Council Trans.* 35:18–19.
- Mysterud A, Bischof R. 2010. Can compensatory culling offset undesirable evolutionary consequences of trophy hunting? *J Anim Ecol.* 79:148–160.
- Nunney L. 1993. The influence of mating system and overlapping generations on effective population size. *Evolution.* 47:1329–1341.
- Poissant J, Wilson AJ, Festa-Bianchet M, Hogg JT, Coltman DW. 2008. Quantitative genetics and sex-specific selection of sexually dimorphic traits in bighorn sheep. *Proc R Soc B Biol Sci.* 275:623–628.
- Postma E. 2006. Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. *J Evol Biol.* 19:309–320.
- Rioux-Paquette E, Festa-Bianchet M, Coltman DW. 2011. Sex-differential effects of inbreeding on overwinter survival, birth date and mass of bighorn lambs. *J Evol Biol.* 24:121–131.
- Rosenstock SS, Hervert JJ, Bleich VC, Krausman PR. 2001. Muddying the water with poor science: a reply to Broyles and Cutler. *Wildl Soc Bull.* 29:734–743.
- Stearns SC. 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- Thrower FP, Hard JJ. 2009. Effects of a single event of close inbreeding on growth and survival in steelhead. *Conserv Genet.* 10:1299–1307.
- Weaver RK. 1973. Progress at Aravaipa. *Desert Bighorn Council Trans.* 17:117–122.

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Corresponding Editor: Gordon Luikart