Data from selective harvests underestimate temporal trends in quantitative traits

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Human harvests can select against phenotypes favoured by natural selection, and natural resource managers should evaluate possible artificial selection on wild populations. Because the required genetic data are extremely difficult to gather, however, managers typically rely on harvested animals to document temporal trends. It is usually unknown whether these data are unbiased. We explore our ability to detect a decline in horn size of bighorn sheep (Ovis canadensis) by comparing harvested males with all males in a population where evolutionary changes owing to trophy hunting were previously reported. Hunting records underestimated the temporal decline, partly because of an increasing proportion of rams that could not be harvested because their horns were smaller than the threshold set by hunting regulations. If harvests are selective, temporal trends measured from harvest records will underestimate the magnitude of changes in wild populations.

Keywords: artificial selection; sport hunting; time series; ungulates

1. INTRODUCTION

Recently, it has become evident that exploitation can lead to artificial selection [1–4]. As humans often prefer sex-age classes or morphological traits associated with high natural survival, harvest mortality differs from natural mortality [5]. Thus, harvests may lead to evolutionary responses in life histories and morphology [6], outpacing other selective agents [7,8]. There have been calls to consider potentially undesirable artificial selection in management and conservation [9,10].

A first step to avoid artificial selection is evaluating which practices have undesired consequences. As detailed, individual monitoring is rarely available, attempts to quantify artificial selection in wild populations usually rely on morphological, life history and demographic data collected from harvested animals [6,11]. Harvest data, however, will not reflect population values if harvest is selective and varies in intensity over time, as may occur with trophy hunting and size-selective fisheries. For example, the age distribution of shot red grouse (Lagopus lagopus scoticus) was biased by harvest intensity [12]. Similar biases may affect temporal trends in morphological traits estimated from harvest data. If harvest probability is affected by regulations for minimum size, gear selectivity [13] or by cultural preferences, the average size of harvested animals should be greater than the population average. These biases have been acknowledged [14], but it remains unknown how they affect our ability to detect temporal trends in phenotypic traits.

To test whether data from selective harvests can be used to detect temporal trends in phenotype, we analysed nearly four decades of detailed individual monitoring of bighorn sheep (Ovis canadensis) in a population where unlimited trophy hunting favoured rams with slow-growing horns [2,15]. We compared harvested animals with the whole population. In most of the province of Alberta, harvest of bighorn rams is based on minimum horn curl (figure 1). This management strategy protects sub-adults but leads to the harvest of rams with rapidly growing horns aged 4–6 years [5,16], before they obtain the high reproductive success associated with large horns at ages 7–11 [17,18]. Similar regulations for both bighorn and thin-horn (Ovis dalli) sheep, combining curl restrictions and unlimited resident permits, exist in most of Canada and in Alaska. The ‘legal’ definition of a harvestable ram is thus comparable to antler point restrictions often used for cervids [19].

2. MATERIAL AND METHODS

From 1975, 95 per cent of resident bighorn sheep at Ram Mountain, Alberta, Canada, have been individually marked and repeatedly measured [20,21]. We used data on horn size for males aged 4–7 years from 1975 to 2004, when rams from elsewhere were introduced to rescue the population from demographic and genetic decline. Each year, we determined whether or not each ram fitted the legal definition of 4–5-curl, similarly to how a hunter would evaluate a potential target (figure 1). Rams in this population are never legal before age 4, and only nine of 59 (15%) harvested in 1975–1996 were aged 8 years or older. Because hunters selectively harvest rams with fast-growing horns at younger ages [22,23], horn size of surviving rams is increasingly biased by sport harvest as they age. This population was subject to unlimited harvest of 4–5-curl rams until 1995. From 1996, only ‘full-curl’ rams could be harvested. Average horn size, however, began to decline about 1983, so that only 13.7 per cent of rams aged 4 years and older were legal in 1996–2004 under the revised definition.

To simulate a continuing hunting season under 4–5ths curl, we randomly assigned 37.5 per cent of ‘4–5-curl’ rams to the ‘harvested’ group from 1996 onward, based on harvest rate in 1975–1995. The simulation harvested only two rams aged 4–7 over these 11 years, as most were not ‘4–5-curl’.

Analyses involved two steps. We first explored temporal trends in the relationship between horn size and year using broken stick regression models (see Crawley et al. [24] and electronic supplementary material) without any covariates. Once the threshold year was identified, we compared temporal trends in horn length and basal circumference during the decline between harvested rams and all males aged 4–7 years. Horn size was adjusted on June 5 (see Festa-Bianchet et al. [22]). All models included age as a covariate. Linear-mixed effects models for all rams were fitted with restricted maximum likelihood including ram identity as a random effect to account for repeated measurements over time [23]. For harvest data, however, each ram contributed only one datum, in the year of death. All analyses were implemented in R v. 2.12.0 [26], using the nlme library.

3. RESULTS

Horn size began to decline in the 1980s, but Akaike information criterion (AIC) values for successive years were similar. The decline in length began in the early 1980s (thresholds between 1980 and 1983 were...
equivalent), while that in base circumference was
delayed by approximately 5 years (electronic sup-
plementary material, table S1). We quantified the
decline in horn size from 1982, when horn length
began a linear decline (electronic supplementary
material, table S1). All models indicate a decline in
horn size through time (electronic supplementary
material, table S2), but trends were underestimated
by analyses of harvested rams (figure 2). Using differ-
ent 'threshold' years provide similar results (results not
shown). The complete dataset revealed a decrease in
horn length of 0.82 cm yr\(^{-1}\), while data from harvested
rams suggested a decline of 0.45 cm yr\(^{-1}\). Hunting
data predicted a decline of 7.7 cm over 17 years, half
the actual decline of almost 14 cm. Horn base circum-
ference showed a similar trend, although confidence
intervals of the slopes for all rams and harvested
rams overlapped over most of the period (figure 2).
The complete dataset suggested a decrease of 5.6 cm
in circumference while the harvest dataset detected a
decline of only 3 cm. As horn size declined, fewer
rams were at risk of being harvested, because small
horns cannot form 4/5 of a curl. Of 100 rams born
in 1969–1985 that survived to age 4, only 29 died
without their horns reaching 4/5 curl (\(\chi^2 = 26.6, p < 0.001\)).

4. DISCUSSION
Our results suggest that trophy harvest records under-
estimate temporal trends in horn size of bighorn rams.
Average horn length declined by approximately 20 per
cent, but harvest data suggested a decline of only 11 per cent. Despite the overlap in confidence interval
of temporal trends in horn circumference, this trait
showed a similar pattern of steeper decline (15%) for
the population than for the subset of harvested rams
(8%). In several years after horn size declined, there
were no legal rams in the population, so it would

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Figure 1. (a) Legal definition of a ‘4/5-curl’ bighorn sheep ram in Alberta, Canada: a straight line drawn from the front of the base of the horn to the tip of the horn passes in front of the eye when viewed in profile. Image: Groupe PVP. (b) Harvested 4-year-old ram that just meets the definition. Photo: Alberta Fish and Wildlife.

Figure 2. Predicted temporal trends in horn size of 5-year-old bighorn rams at Ram Mountain from 1982 to 2004 for (a) horn length and (b) horn base circumference. Black circles and red line represent data from shot rams. This regression line stops in 1998 because no rams were harvested thereafter. Empty grey circles and black line are horn measurements of all rams in the population. Dotted lines are the 95% confidence intervals, whose divergence on (a) suggests that the slope estimate from shot rams differs significantly from the estimate for the entire population.
have been impossible for harvest statistics to monitor horn size. These results are likely representative of those sport-hunted ungulates where hunters typically harvest the largest available animals [19]. The extent of hunter selectivity is rarely known [27]. Size-selective harvests are particularly likely for gregarious species such as wild sheep, where hunters can choose the largest individual in a group. In our study, this situation was exacerbated by regulations making it illegal to harvest small males. Similar preferences for harvesting larger individuals are well known in fisheries [6,13]. For example, size-selectivity of fisheries for cod (Gadus morhua) in the Gulf of St Lawrence resulted in fast-growing fish being more likely to be caught than slow-growing fish. Consequently, data from declining commercial fisheries might underestimate the decline in age-specific mass for the population [6].

Base circumference began to decline about 5 years later than horn length, and the difference in temporal decline between all rams and harvested rams was not as evident as for horn length. Hunting regulations specify a minimum degree of horn curl, and short horns cannot achieve that minimum degree of curl. Horn base circumference, on the other hand, is not a direct target of artificial selection. Therefore, selective hunting could lead to changes in horn shape, as reported in European mouflon (Ovis aries) [28].

A combination of legal requirements and hunter preferences makes information from harvested animals a biased estimator of changes in trait values. These legal and cultural factors produce an ‘invisible fraction’ of animals whose size may vary according to artificial selection [16], population density and environmental effects [22], all drivers of horn and antler size. Similar considerations would apply to other species, such as fish harvested with size-selective gear [13] or birds where harvest is age-biased [12]. Thus, evolutionary ecology studies of wild populations based on data from selectively harvested animals will erroneously estimate temporal changes in phenotypic traits unless they can account for the effects of non-random harvest and temporal changes in harvest intensity.

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