Methods

Meteorology

A network of 14 meteorological stations was installed across the Annapurna range before the 1999 monsoon season, and expanded to 19 stations encompassing 28 rain gauges in 2000. Rainfall is totalled every 30 min. 'Look-down' distance rangers and γ-ray loggers measure snow depth and total water content, respectively, once a day at high elevations ($>$2,500 m in the Greater Himalaya). Only liquid precipitation is measured in the Tibetan zone, such that the annual (but not the monsoon) total is underestimated here. The data presented here (Fig. 2b) represent monsoon averages based on the longest record available from each station.

Apatite fission-track dating

Following mineral separation, apatites were polished, etched and irradiated. Standard and induced track densities were determined on Brazil ruby muscovite external detectors (geometry factor 0.5), and fossil track densities were determined on internal mineral surfaces. Ages were calculated using $\zeta = 359 \pm 20$ for dosimeter glass CN-5. All ages are central ages and are reported with 1σ errors. Long-term erosion rates are conservatively estimated on the basis of the fission-track age, and assuming a geothermal gradient of $100\,^{\circ}\mathrm{C\,km^{-1}}$ and an annealing temperature of 140 °C.

Topographic analysis

A 3-arcsec ($\sim$90 m) digital elevation model (DEM) is the basis of all topographic analyses. Hillslope angles are calculated at every pixel in the DEM based on a 3 × 3 pixel ($\sim$180 × 180 m) grid. Mean hillslope angles were extracted from a moving, 5-km-radius window centred on the Marsyandi River. Maximum, minimum and mean elevation (Fig. 2) were calculated along a 50-km-wide swath oriented perpendicular to the strike of the range and centred on the Marsyandi River (or the Nar-Phu River above its confluence with the Marsyandi).

Equilibrium-line altitude

Glacial areas were calculated from present and reconstructed ice margins mapped on aerial photographs, and transferred first to 1:50,000 scale topographic maps and then to the digital topography. Based on glacial hypsometry, equilibrium-line altitudes were estimated with an assumed accumulation-area ratio of 0.65. To avoid uncertainty introduced by avalanches on to glaciers from adjacent high peaks, 29 small glaciers (95% are $<2.5\,\mathrm{km}^2$), lacking high headwalls, were analysed. The regional equilibrium-line altitude gradient shows little sensitivity to accumulation-area ratios ranging from 0.4 to 0.8.

Specific stream power

Analysis was focused on catchments ranging from 3 to $7\,\mathrm{km}^2$ within the non-glaciated part ($<$4,200 m elevation) of the study area. These basins drain approximately half of the landscape and are sufficiently large to be fluvial, as opposed to colluvial/debris flow, channels. Monsoon rainfall was smoothed across the meteorological network to define an average precipitation gradient perpendicular to the strike of the topography. This gradient was then extrapolated parallel to strike across the study area. For each river segment $\geq$500 m long, channel gradients (S) were extracted from the DEM, and discharge (Q) was calculated as the product of upstream area and rainfall. Discharge is overestimated because all rainfall is assumed to enter channels. Channel width (W) is calculated as $10^{-2}\,Q^{0.4}$. Specific stream power (in $\mathrm{GJ\,m^{-2}\,yr^{-1}}$) is calculated as $\rho_w QS/W$, where ρ_w is the density of water and g is gravitational acceleration. Channel gradients and specific stream power are binned every 5 km.

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Undesirable evolutionary consequences of trophy hunting

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Phenotype-based selective harvests, including trophy hunting, can have important implications for sustainable wildlife management if they target heritable traits[1–3]. Here we show that in an evolutionary response to sport hunting of bighorn trophy rams (*Ovis canadensis*) body weight and horn size have declined significantly over time. We used quantitative genetic analyses, based on a partly genetically reconstructed pedigree from a 30-year study of a wild population in which trophy hunting targeted rams with rapidly growing horns[4], to explore the evolutionary response to hunter selection on ram weight and horn size. Both traits were highly heritable, and trophy-harvested rams were of significantly higher genetic 'breeding value' for weight and horn size than rams that were not harvested. Rams of

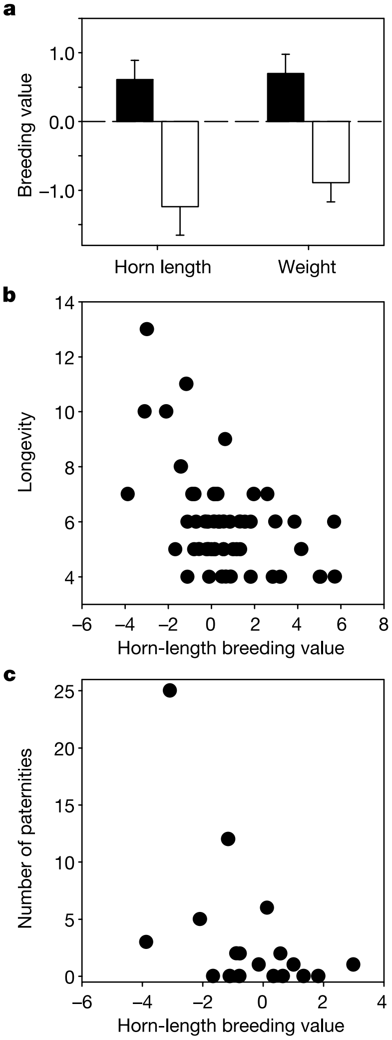

Figure 1 Selection against high-breeding-value rams imposed by trophy hunting. **a**, Breeding values (means ± s.e.m.) for horn length and weight of trophy-harvested rams (filled bars) and non-trophy-harvested rams (open bars). **b**, Relationship between the age at harvest for trophy-harvested rams and their breeding value. **c**, Relationship between the number of paternities assigned to trophy-harvested rams in their lifetime and their breeding value.

high breeding value were also shot at an early age, and thus did not achieve high reproductive success[5]. Declines in mean breeding values for weight and horn size therefore occurred in response to unrestricted trophy hunting, resulting in the production of smaller-horned, lighter rams, and fewer trophies.

Sport harvesting is one of the most pervasive and potentially intrusive human activities that affect game mammal populations globally[6]. Hunters are willing to pay large sums to hunt trophy mountain ungulates in various parts of the world, and many mountain sheep (*Ovis canadensis* and *O. dalli*) populations in North America are managed primarily to produce large-horned trophy rams for sport hunters. A world-class trophy ram is an extremely valuable commodity, and hunting permits have been auctioned for hundreds of thousands of dollars[7]. One sport hunter paid over Can$1 million in 1998 and 1999 for special permits to hunt trophy rams in Alberta, Canada[7]. In many parts of North America, sport harvest of mountain sheep is often restricted only by the availability of rams whose horns reach a minimum size prescribed by regulations. Although the use of income generated from sport hunting towards enhancing and conserving mountain ungulate habitat can be seen in a positive light[7], so far little attention has been paid to the potential evolutionary consequences, and hence the sustainability, of harvest regimes[2,3].

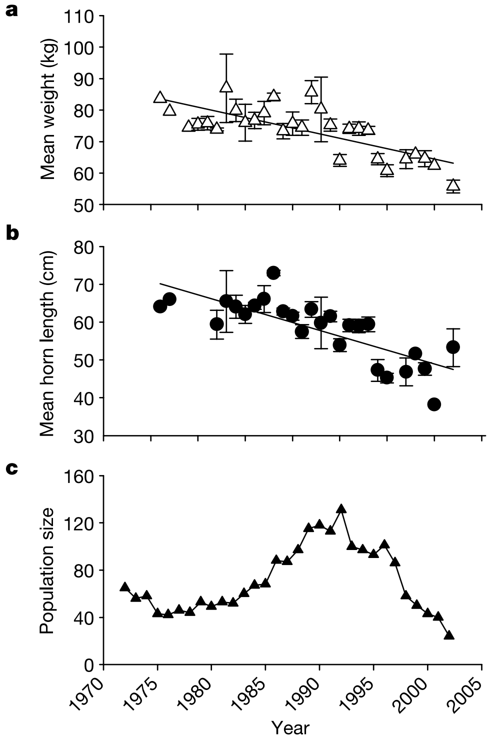

Figure 2 Observed changes in mean weight and horn length and in the population size from 1972 to 2002. **a**, Relationship between weight (mean ± s.e.m.) of 4-year-old rams and year ($N = 133$ rams). **b**, Relationship between horn length (mean ± s.e.m.) of 4-year-old rams and year ($N = 119$ rams). **c**, Changes in population size (taken as the number of ewes aged at least 2 years plus yearlings[17]) over time.

Wildlife management has traditionally focused on demographic and ecological factors that affect numbers and growth rates in harvested populations[8–11]. However, the life-history changes experienced by species subject to commercial fisheries strongly suggest that intensive harvesting practices can elicit an evolutionary response in wild stocks[12–15]. Experimental size-selective harvesting treatments on an exploited fish demonstrated evolutionary effects on somatic growth and population productivity in the opposite direction of the size bias of the harvest[13]. Recent reviews have called attention to the potential selective effects of sport hunting on wild ungulates, in which large-horned or large-antlered males are selectively targeted[2,3]. The increased frequency of tuskless elephants in many African populations has also been suggested to have occurred in response to selective ivory poaching[16]. Here we use data from the long-term study of a harvested bighorn sheep population at Ram Mountain, Alberta, Canada, to investigate the evolutionary consequences of more than 30 years of selective hunting of trophy rams.

Fifty-seven rams have been shot at Ram Mountain since 1975, or about 40% of the rams legally available for harvest in each year (see Methods), for a yearly harvest of between zero and six rams[17]. Most trophy-harvested rams were shot before reaching 8 years of age (45 of 57 rams), and nine were shot as early as the age of 4 years. In bighorn sheep, much of the total horn length is added from the ages of 2 to 4 years, and at Ram Mountain the probability of a ram being shot before the age of 6 years is positively correlated with cumulative horn growth over this interval[4]. 'Animal model'[18] quantitative genetic analysis of 395 horn-length and 447 weight measurements taken from 192 rams at ages 2, 3 and 4 years from 1971 to 2002 revealed narrow-sense heritabilities of 0.69 ± 0.10 and 0.41 ± 0.11

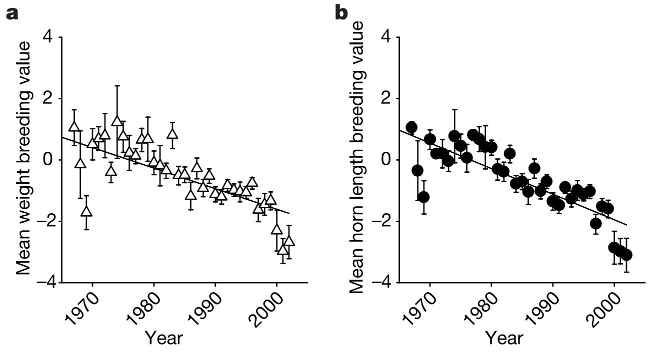

Figure 3 Changes in the mean breeding value of cohorts born between 1967 and 2002. **a**, Relationship between breeding value (mean ± s.e.m.) for weight and year of birth ($N = 783$ individuals). **b**, Relationship between breeding value (mean ± s.e.m.) for horn length and year of birth ($N = 783$ individuals).

(means ± s.e.m.), respectively (see Methods), and a strong positive additive genetic correlation between the two ($+0.84 \pm 0.10$). Comparison of expected genetic 'breeding values' (twice the expected deviation of an individual's offspring phenotype from the population mean owing to the additive effect of the offspring's inherited genes[18]) extracted from this model (Fig. 1a) indicates that hunters selectively harvest rams with high breeding values for horn length (trophy-harvested mean, $+ 0.61 \pm 0.28$; non-harvested mean, -1.24 ± 0.48; *t*-test: $t_{148} = -4.16$, $P < 0.001$) and weight (trophy-harvested mean, $+0.70 \pm 0.28$; non-harvested mean, -0.89 ± 0.48; *t*-test: $t_{148} = -3.26$, $P = 0.0014$).

Within seasons, mating success in bighorn sheep increases with dominance rank[19], age and horn length[5]. The positive effect of large horns on mating success increases from about 6 years of age[5], when rams are capable of defending oestrous ewes during the rut. The age at which a high-breeding-value ram is harvested is therefore likely to have an important impact on the number of offspring he can sire. We found a negative relationship between the age at which a trophy-harvested ram was shot and his breeding value for horn length (generalized linear model (GLM) with Poisson errors: $\chi^2_{(1)} = 4.64$, $P = 0.031$; Fig. 1b) but not for weight (GLM: $\chi^2_{(1)} = 1.80$, $P = 0.18$; data not shown). Trophy-harvested rams with high breeding values for body and horn size were therefore less likely to reach the ages at which they achieve high rates of paternity in this population[5]. As a consequence, there was a negative relationship between breeding value for horn length and lifetime mating success, measured as the number of paternities assigned over their lifetime, among trophy-harvested rams (GLM with negative binomial error: $\chi^2_{(1)} = 8.56$, $P = 0.0034$; Fig. 1c). The mean sire breeding value of individuals fathered by trophy-harvested rams was therefore significantly less than zero for both weight (one-sample *t*-test: mean $= -2.41$, s.e.m. $= 0.37$, $t_{59} = -6.50$, $P < 0.001$) and horn length (mean $= -1.84$, s.e.m. $= 0.19$, $t_{59} = -9.68$, $P < 0.001$). The mean sire breeding value of individuals fathered by rams that died a natural death was also significantly less than zero for both weight (one-sample *t*-test: mean $= -1.24$, s.e.m. $= 0.17$, $t_{182} = -7.14$, $P < 0.001$) and horn length (mean $= -2.10$, s.e.m. $= 0.16$, $t_{182} = -20.43$, $P < 0.001$). The low breeding values of rams not harvested (Fig. 1a) and the reduced longevity and potential reproductive output of the higher-quality trophy-harvested rams (Fig. 1b, c) combine to suggest that the selection imposed by trophy hunting had a negative impact on the evolutionary trajectory of horn length and body weight in this population during our study.

Is there evidence of a response to selective harvesting at the population level? Significant declines in both ram weight (linear mixed-effect model including year of birth and individual as a random effects, and age, time and resource index as fixed effects: $\beta_{\text{time}} = -0.30$, s.e.m. $= 0.09$, $t_{25} = -3.42$, $P = 0.0021$) and horn length (linear mixed-effect model including year of birth and individual as a random effects, and age, time and resource index as fixed effects: $\beta_{\text{time}} = -0.35$, s.e.m. $= 0.12$, $t_{23} = -2.97$, $P = 0.0068$) were observed over the course of the study (Fig. 2a, b) after controlling for environmental effects such as population density (Fig. 2c) using an index of resource availability (see Methods; weight: $\beta_{\text{resources}} = 0.81$, s.e.m. $= 0.17$, $t_{25} = 4.72$, $P < 0.001$; horn length: $\beta_{\text{resources}} = 0.72$, s.e.m. $= 0.22$, $t_{23} = 3.32$, $P = 0.0030$). These are very rapid rates of phenotypic change[20], corresponding to $-0.30/12.9 = -0.023$ and $-0.35/13.6 = -0.026$ standard deviations per year, or -0.14 and -0.15 haldanes (ref. 20) assuming a generation time of 6 years. Analyses of breeding values are consistent with genetically based responses (Fig. 3). Declines in breeding value (see Methods) were observed for both ram weight (linear mixed-effect model including year of birth as a random effect, and time and resource index as fixed effects: $\beta_{\text{resources}} = 0.037$, s.e.m. $= 0.025$, $t_{33} = 1.49$, $P = 0.15$; $\beta_{\text{time}} = -0.071$, s.e.m. $= 0.012$, $t_{33} = -6.02$, $P < 0.001$) and horn length (linear mixed-effect model including year of birth as a random effect, and time and resource index as fixed effects: $\beta_{\text{resources}} = 0.050$, s.e.m. $= 0.024$, $t_{33} = 2.08$, $P = 0.045$; $\beta_{\text{time}} = -0.075$, s.e.m. $= 0.011$, $t_{33=} - 6.76$, $P < 0.001$). Such declines in breeding value over time are indicative of a microevolutionary response to selection[21] in the Ram Mountain population.

Unrestricted harvesting of trophy rams has thus contributed to a decline in the very traits that determine trophy quality. Hunters have selectively targeted rams of high genetic quality before their reproductive peak, depleting the genes that confer rapid early body and horn growth. Wildlife harvesting that is selective and sufficiently severe might elicit an undesired evolutionary response when the target trait is heritable. There might also be unexpected effects on genetically correlated traits, such as female body weight or disease resistance[22], that could result in further genetic deterioration of harvested populations as anthropogenic selection pushes traits away from their naturally selected optima. Because such changes will be extremely difficult to reverse, wildlife managers must consider the genetic effects and the evolutionary implications of alternative harvest strategies[2,3]. The move to adopt a 'full curl' restriction in parts of Alberta in 1996, which limits harvest to rams with horns whose tip extends beyond the tip of the nose, is one strategy to minimize further deterioration of the genetic quality of bighorn sheep. ☐

Methods

Population and study site

The bighorn sheep population on Ram Mountain, Alberta, Canada (52° N, 115° W, elevation 1,080–2,170 m) has been monitored closely since 1971 (refs 17, 23). Immigration to Ram Mountain from the main species range has not been documented, and is probably rare because of isolation of the population by about 30 km of coniferous forest. Each year, sheep were captured in a corral trap baited with salt from late May to early October, and marked with coloured plastic ear tags or canvas collars for individual identification. Adult rams were captured once or twice in most summers from early June to mid-July. At each capture, sheep were weighed to the nearest 250 g with a Detecto spring scale. Horn length along the outside curvature was measured with tape. The longer of the left and right horn measurements was used, because rams can have a varying amount of horn removed by wear. For further details on field methods see refs 17, 23 and 24.

Bighorn males on Ram Mountain can be legally harvested by Alberta resident hunters from late August to the end of October. Until 1996, rams with horns describing at least four-fifths of a curl ('trophy' rams) could be harvested by any hunter holding a trophy sheep licence[17]. As any resident could purchase a licence, the harvest was limited only by the availability of trophy rams. A change in regulations in 1996 limited harvest to 'full-curl' rams. Consequently, only three rams have been shot since 1996. Individual weight and horn length measurements from rams captured between 1971 and 2002 were adjusted to 5 June (ref. 24). Because the youngest age at which rams were shot by hunters was 4 years, we used weight and horn length data from ages 2, 3 and 4 years to avoid bias due to hunter selection.

Pedigree reconstruction

Maternity was known from field observations for 709 of the 894 (79.3%) marked sheep whose fates have been followed since 1971. Tissue sampling for DNA analyses started in 1988. Blood samples were taken from all captured sheep until 1993 and stored in preservative at −20 °C. Sampling resumed in 1997, when hair samples were taken from all captured sheep by plucking 50–100 hairs including roots from the back or flank. Hairs were kept either in paper envelopes or plastic bags containing about 5 g of silica at room temperature. From 1998 to 2002, a tissue sample from each captured sheep was taken from the ear with an 8-mm punch. Ear tissue was kept at −20 °C in a solution of 20% dimethylsulphoxide saturated with NaCl. We sampled 433 marked individuals over the course of the study.

DNA was extracted from blood with a standard phenol–chloroform method, and from either 20–30 hairs including follicles or about 5 mg of ear tissue, using the QIAamp tissue extraction kit (Qiagen Inc., Mississauga, Ontario). Polymerase chain reaction amplification at 20 ungulate-derived microsatellite loci, 15 as described previously[5] plus MCM527, BM4025, MAF64, OarFCB193 and MAF92 (refs 25, 26), and fragment analysis were performed as described elsewhere[5]. After correction for multiple comparisons, we found no evidence for allelic or genotypic disequilibria at or among these 20 loci.

Paternity of 241 individuals was assigned by using the likelihood-based approach described in CERVUS[27] at a confidence level of more than 95% with input parameters given in ref. 5. After paternity analysis, we used KINSHIP[28] to identify 31 clusters of 104 paternal half-sibs among the unassigned offspring. A paternal half-sibship consisted of all pairs of individuals of unassigned paternity that were identified in the KINSHIP analysis as having a likelihood ratio of the probability of a paternal half-sib relationship versus unrelated with an associated $P < 0.05$ (ref. 28). Members of reconstructed paternal half-sibships were assigned a common unknown paternal identity for the animal model analyses. Paternal identity links in the pedigree were therefore defined for 345 individuals.

Animal model analyses

Breeding values, genetic variance components and heritabilities were estimated by using a multiple trait restricted-estimate maximum-likelihood (REML) model implemented by the programs PEST[29] and VCE[30]. An animal model was fitted in which the phenotype of each animal was broken down into components of additive genetic value and other random and fixed effects: $\mathbf{y} = X\mathbf{b} + Z\mathbf{a} + P\mathbf{c} + \mathbf{e}$, where $\mathbf{y}$ was a vector of phenotypic values, $\mathbf{b}$ was a vector of fixed effects, $\mathbf{a}$ and $\mathbf{c}$ were vectors of additive genetic and permanent environmental, $\mathbf{e}$ was a vector of residual values, and X, Z and P were the corresponding design matrices relating records to the appropriate fixed or random effects[18]. Fixed effects included age (factor) and the average weight of yearling ewes in the year of measurement (covariate), which is a better index of resource availability than population size because it accounts for time-lagged effects[4]. The permanent environmental effect grouped repeated observations on the same individual to quantify any remaining between-individual variance over and above that due to additive genetic effects, which would be due to maternal or other long-term environmental and non-additive genetic effects.

The total phenotypic variance (V_p) was therefore partitioned into three components: the additive genetic variance (V_a), the permanent environmental variance (V_e) and the residual variance (V_r), thus: $V_p = V_a + V_e + V_r$. Heritability was calculated as $h^2 = V_a/V_p$. The VCE[30] program returns standard errors on all variance components and ratios. Best linear unbiased predictors of individual breeding values were quantified by using REML estimates of the variance components obtained with PEST[29]. All statistical tests were conducted in SPLUS 6.1.

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The role of evolution in the emergence of infectious diseases

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It is unclear when, where and how novel pathogens such as human immunodeficiency virus (HIV), monkeypox and severe acute respiratory syndrome (SARS) will cross the barriers that separate their natural reservoirs from human populations and ignite the epidemic spread of novel infectious diseases. New pathogens are believed to emerge from animal reservoirs when ecological changes increase the pathogen's opportunities to enter the human population[1] and to generate subsequent human-to-human transmission[2]. Effective human-to-human transmission requires that the pathogen's basic reproductive number, R_0, should exceed one, where R_0 is the average number of secondary infections arising from one infected individual in a completely susceptible population[3]. However, an increase in R_0, even when insufficient to generate an epidemic, nonetheless increases the number of subsequently infected individuals. Here we show that,