

Hunter selection and long-term trend (1881–2008) of red deer trophy sizes in Hungary

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Summary

1. Human harvesting has a large impact on natural populations and may cause undesirable life-history changes. In wild ungulate populations, unrestricted trophy hunting may cause strong selection pressures resulting in evolutionary change towards smaller trophies. It has rarely been tested how harvesting selection varies in space and time, and whether directional hunter selection is sufficiently strong to induce long-term decreases in trophy size in century-scale data.

2. We analysed two unique data sets of harvesting records spanning decade (1973–2008) and century scales (1881–2008) to identify changes in trophy size and how harvesting selection varies in space and time in red deer *Cervus elaphus*. We contrasted predictions from the trophy-hunting depletion, the restricted trophy hunting and the hunting pressure hypotheses.

3. Foreign hunters selected older and larger males than local hunters, but selection patterns for age-specific trophy size between counties and over time were dynamic. Patterns of red deer trophy size development from exhibitions (representing the ‘upper tail’ of antler sizes) were remarkably similar across Hungary from 1881 to 2008. A weak decline in trophy size between 1881 and 1958 was followed by a strong increase in trophy size between 1958 and 1974, culminating in a period of stable antler tine numbers and a weak decline in beam length until 2008.

4. We rejected the trophy hunting depletion hypothesis due to the increase in trophy size after a period of decline; patterns were most consistent with the hunting pressure hypothesis. Large increases in trophy size during 1958–1974 were likely due to a relief in hunting pressure due to implementation of strict management regulations allowing stags to grow old after the massive overharvesting during World War II, but we cannot exclude impacts from environmental factors, and that data from trophy exhibitions may underestimate trends.

5. *Synthesis and applications.* Trophy hunting does not necessarily lead to a non-reversible decline in trophy size, even over century-long time-scales. To ensure sustainable trophy hunting management, we need to consider factors such as spatial and temporal refuges, compensatory culling, saving stags until prime-age culmination and higher prices for larger trophies.

Key-words: antlers, *Cervus elaphus*, evolution, game management, life history, selective harvesting, sustainability

Introduction

Human harvesting can impose strong selection pressures on natural populations and may cause undesirable

life-history changes over shorter periods of time than expected from natural selection (Coltman *et al.* 2003; Carroll *et al.* 2007; Garel *et al.* 2007). Evidence is accumulating that harvesting may affect maturation trends and growth rates. Harvesting is often a non-random process, and humans tend to be selective of certain

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qualities or morphological traits exhibited by animals (Festa-Bianchet 2003; Johnson *et al.* 2010; Mysterud 2011). This is particularly obvious in unrestricted trophy-hunting cultures. When removing the largest trophies, hunters target the traits they actually desire. This may cause an evolutionary response generating decreased trophy size (and altered shape) of prime-aged males (Coltman *et al.* 2003; Garel *et al.* 2007).

Trait changes under directional harvesting are predicted (Thelen 1991), and the reports on mountain sheep populations clearly give cause for concern (Coltman *et al.* 2003; Garel *et al.* 2007). However, the wider occurrence of reduction in trait sizes under trophy hunting remains uncertain, as current studies only provide data over fairly short time-spans (32 years; Coltman *et al.* 2003; 28 years; Garel *et al.* 2007), have low sample sizes and are not replicated time series. Further, these are isolated alpine populations, and one might expect stronger effects of selection under such conditions, as found in husbandry (Hill & Kirkpatrick 2010). Indeed, on isolated game farms in Africa, strong declines in trophy sizes have also been reported (von Brandis & Reilly 2007), although these declines may also be due to factors other than selective harvesting, such as mismanagement in the sense of not allowing males to age or density dependence. Theoretical work suggests that refuges may buffer the effect of selective harvesting (Tenhumberg *et al.* 2004), indicating that the effect might be reduced by gene flow.

Key to evolutionary changes in trophy size are hunter selectivity for specific phenotypic traits, that the targeted trait is heritable, and adequate genetic variance underlying the trait. As life-history data from long-term monitoring are rare and hard to obtain in harvested populations, patterns of harvesting selection in ungulates have been studied by comparing hunting methods (Martinez *et al.* 2005; Torres-Porras, Carranza & Perez-Gonzalez 2009) or categories of hunters (local hunters vs. foreign trophy hunters; Mysterud, Tryjanowski & Panek 2006). All hunters hunt the same population of animals regardless of method or category, but are expected to differ in their efficiency or motivation for hunting. Thus, any variation in average trait size between hunter groups or methods is expected to be a result of differential selection. These studies have revealed that hunter selection is age-specific for traits such as body and antler size (Martinez *et al.* 2005; Mysterud, Tryjanowski & Panek 2006; Torres-Porras, Carranza & Perez-Gonzalez 2009), but there has been limited focus on how variable such patterns might be in space and time. Series of hunting records spanning century-long time-scales rather than decade scales have not yet been analysed. Here, we analyse two unique data sets of harvesting records spanning decade (1973–2008) and century scales (1881–2008) to answer questions about hunter selectivity and long-term trophy size development in red deer *Cervus elaphus*, one of the most desired game species in Europe.

To investigate whether age-specific hunter selection for red deer antler size varies between regions and years, we used a complete data set of the total annual male harvest in Hungary comprising 126 017 male red deer harvested in 14 counties and 24 unique years from 1973 to 2008. Trophy hunters are expected to show preference for individuals with large trophies, and we therefore predict a consistent targeting of the largest prime-aged stags, the trophy hunter selection hypothesis (H₁; Table 1). The hunting culture in countries such as Hungary, Germany and Poland is known to enforce counteracting selection pressures by harvesting young males of apparent low quality, the compensatory culling hypothesis (H₂; Csik 1902; Széchenyi 1948; Mysterud & Bischof 2010), and by harvesting trophy stags late in life, allowing them to reproduce (Apollonio, Andersen & Putman 2010; Csányi & Lehoczki 2010). H₂ also predicts foreign trophy stalkers to target older males and males with larger age-specific trophy size, but also that local hunters harvest a substantial amount of younger and smaller males (Table 1).

To identify potential phenotypic changes in trophy size, we analysed trophy exhibition records from 2926 male red deer harvested in 14 counties over more than a century, from 112 unique years between 1881 and 2008. Such data are biased, representing the 'upper tail' of the antler sizes relative to the average. The trophy-hunting depletion hypothesis suggests that unrestricted trophy hunting (as for bighorn sheep *Ovis canadensis*) induces long-term declines in both trait mean (Coltman *et al.* 2003) and variance (Shnol & Kondrashov 1993), assuming evolutionary responses to directional selection are the main drivers of long-term trait development in antler size (H₃; Table 1). If genes are depleted from the pool during declines, natural selection and environmental variability may not be strong enough for the population to reach the pre-harvesting state (Heino 1998; Hutchings 2000; Swain, Sinclair & Hanson 2007; Darimont *et al.* 2009). H₃ predicts no recovery in trait size after periods of decline. The restricted trophy hunting hypothesis states that countermeasures of management, such as compensatory culling (Mysterud & Bischof 2010), are sufficient to lead to long-term stable trophy sizes (H₄; Table 1). Alternatively, the hunting pressure hypothesis suggests that variations in trait sizes are primarily driven by the management regulations determining hunting pressure, and in turn the number of males allowed to grow old. Thus, if declines in trophy size are due to high hunting pressure leading to a younger male age structure, genes may not be depleted, and recovery is possible when hunting pressure is relieved, and stags are allowed to age again (H₅; Table 1). We would particularly expect changes sparked by periods of wartime (World War I and II), with delays arising from age-structure changes. Other environmental drivers, like climate, land use or population density, may also be important for antler development (Pélabon & van Breukelen 1998; Mysterud *et al.*

Table 1. An overview of hypotheses, predictions and conclusions regarding selection and long-term trait development of red deer antlers in Hungary

Hypotheses	Rationale	Prediction	Observation	Conclusion	Reference
<i>Selection (1973–2008)</i>					
H ₁ . The trophy hunter selection hypothesis	Trophy hunters have a preference for large individuals	P ₁ . Trophy hunters will consistently target the largest prime-aged stags	Proportion of stags shot by foreign hunters: Age 1: 19.22% Age 3: 45.46% Age 9: 76.36%	Supported, trophy hunters shoot larger males, but with considerable variation	Coltman <i>et al.</i> (2003)
H ₂ . The compensatory culling hypothesis	Foreign hunters, paying more money to hunt, consistently select for larger trophies than local hunters, who are responsible for compensatory culling of smaller stags	P _{2A} . Foreign hunters will target older stags, while local hunters will target younger males P _{2B} . Foreign hunters will target stags with larger age-specific antler size than local hunters	Size difference foreign to local hunter: Age 1: 13.07% [9.58, 16.79] Age 3: 8.56% [5.83, 11.43] Age 9: 2.99% [1.87, 4.12]	Supported	Mysterud & Bischof (2010)
<i>Long-term trait development (1881–2008)</i>					
H ₃ . The trophy hunting depletion hypothesis	Directional selection for large size will lead to evolution towards smaller trait sizes and a depletion of the potential to recover after declines	P ₃ . Size of trophies decreases over years, with no recovery after periods of decline	Time number: 1881–1958: $\beta = -0.030$ [−0.038, −0.020] 1958–1974: $\beta = 0.245$ [0.208, 0.281] 1974–2008: $\beta = 0.006$ [−0.010, 0.023]	Not supported, because recovery after decline	Coltman <i>et al.</i> (2003)
H ₄ . The restricted trophy hunting hypothesis	Management regulations is sufficient to counter potential negative effect of trophy hunting	P ₄ . Size of trophies is stable over years	Beam length: 1881–1961: $\beta = -0.025$ [−0.048, −0.002] 1961–1976: $\beta = 0.414$ [0.237, 0.591] 1976–2008: $\beta = -0.121$ [−0.169, −0.072]	Partly supported, but periods of decline suggest this was not always the case	Mysterud & Bischof (2010)
H ₅ . The hunting pressure hypothesis	Heavy hunting pressure will lead to smaller trait sizes due to age-structure changes, but recovery is possible as there is no depletion of gene pool	P ₅ . Size of trophies decreases over years if high pressure, such as during wartime, with recovery after periods of decline if hunting pressure is relieved, but only if not correcting for age	Age-corrected antler weight prime stags: 1973–2008: $\beta = 0.004$ [0.003, 0.006]	Supported, but age-structure data lack to test this in depth	Vanpé <i>et al.</i> (2007)

2005), but data to test this for the current data set are not available.

Materials and methods

STUDY AREA AND RED DEER DATA

Decade-scale data

Since 1970, it is compulsory in Hungary to present antlers of harvested cervids to Trophy Scoring Committees authorized by the state authorities for a trophy evaluation (scoring) according to the International Council for Game and Wildlife Conservation (CIC) rules of trophy measurements (CIC 2010; Csányi & Lehoczki 2010). Data on antler size used in this study came from the annual trophy scoring data base on red deer in Hungary. Antler mass from 183 610 individuals was available for 26 unique years (1973–1974, 1981, 1984 and 1987–2008) and from all 19 counties in Hungary (Fig. 1). According to the CIC trophy evaluation, antler mass was measured in kilograms (kg), and 0.5–0.7 kg of the gross weight could be subtracted when measuring the trophy, depending on the cut and on the size of the skull (CIC 2010). To compare age classes, we only considered individuals of age 1–4 (yearlings and non-trophy stags) and 7–12 (prime-aged trophy stags) years. Individuals shot outside the hunting season (prime stags: September 1st–October 15th, all other stags: September 1st–January 31st; Csányi & Lehoczki 2010) were excluded. We also excluded counties 4, 6, 9, 15 and 16 (Fig. 1) and the years 1987 and 1988 from both data sets, and also 1989 from the prime stag data set because of low harvesting numbers, leaving a total of 126 017 individuals available for analyses. Age was estimated by tooth wear (Szidnai 1978), a method known to show some variation for older individuals (Myerud & Østbye 2006) but also variation between (Veiberg *et al.* 2007) and within populations (Nussey *et al.* 2007). As the same method was utilized over the full data set, it is unlikely that over- or underestimation of age plays a role for the observed patterns, but we are aware that the ageing method probably adds some noise to the data, particularly for older individuals. The county and date of harvesting and information on whether the hunter was local or a foreign trophy stalker was available for all individuals (Csányi, Lehoczki & Sonkoly 2010).

Century-scale data

Data on century-scale trophy size came from records of the 3264 best red deer antlers presented at trophy exhibitions and record books in Hungary from 112 years between 1881 and 2008. Antler size can be measured by several variables such as number of tines (pointed branches), beam length (the average length of the two central stalks of the antlers) or antler mass (weight). Only number of tines was consistently reported. Although correlated, we aimed to assure that the chosen measure of antler size was reliable. As antler mass was recorded in different ways over the times series (e.g. with and without a cut skull, and without corrections), this could not safely be used in the analysis. We therefore used the number of antler tines and the average beam length as measures of antler size, as these are known to be good measures of trophy and body size (Fierro *et al.* 2002; Myerud *et al.* 2005). We removed data that could not be assigned to a particular county and data from counties with low amounts of data (counties 4, 6, 9, 15 and 16). For tine number, two observations were removed as outliers after visual inspection of the data. The final data set consisted of 2926 records of male red deer trophy size recorded over 112 years between 1881 and 2008, in 14 counties in Hungary. After tine number, average beam length was the most consistently reported measure. The average beam length was available for 107 years between 1885 and 2008. Five outliers were removed after a visual inspection, and a subset of 2683 records was used in the analyses.

STATISTICAL ANALYSES

Analyses of decade-scale data

To investigate how trophy size [antler weight (kg)] and hunter selection (hunter types) varied over time (years) and between regions (counties), we used a Bayesian approach (Andrew *et al.* 1995) combined with integrated nested Laplace approximations (INLAs; Rue, Martino & Chopin 2009). The INLA approach is a considerably faster and more accurate numerical procedure compared to the more standard Markov chain Monte Carlo methods usually applied to such Bayesian models (Rue, Martino & Chopin 2009). The variables (see below) were included as independent random noise models fitted in the statistical software R (R Development Core Team 2012) using the ‘iid’-model argument

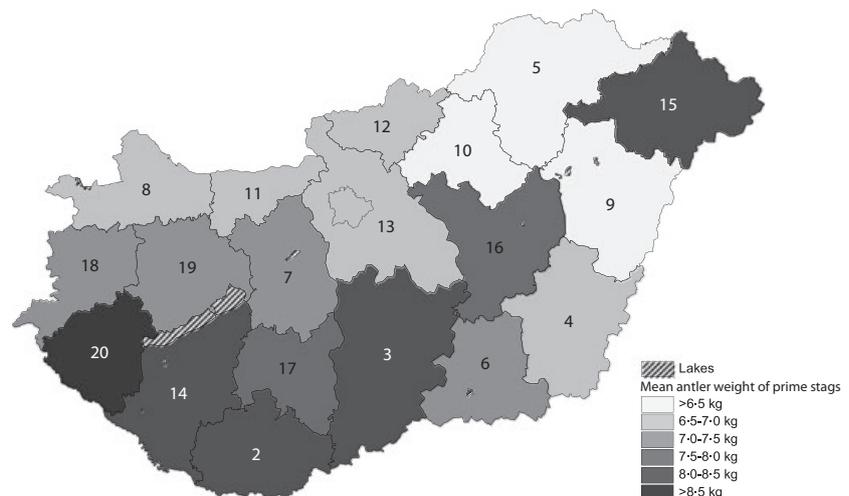


Fig. 1. Map of Hungary divided into 19 counties with corresponding mean antler weight in kilograms (kg) for 7- to 12-year-old red deer stags (prime-aged) from 1973 to 2008. Darker areas show higher mean antler weight. Diagonal striped areas represent lakes.

in the 'inla'-function, implemented in the library 'INLA' (Rue, Martino & Lindgren 2009). To mimic fixed and random effects in a Bayesian framework, we altered the precision matrix in the prior model (Clayton 1996), using default non-informative priors on all variance parameters involved in the random effects and default non-restricted priors directly on the fixed effects.

The response variable was antler weight, measured in kg and log-transformed to assure normality of the error terms. The predictor variables age and hunter type (foreign or local) were fitted as categorical effects using fixed-effect priors, together with the interaction between the two variables. Year was fitted as a continuous variable using fixed-effect priors to check for any linear trends in trophy size over time, but as year showed strong nonlinear trends with trophy size in initial plots, we also fitted it as a categorical effect using random-effect priors. Further, county (categorical) and all two-way interactions including hunter, age, year (categorical) and county (excluding hunter \times age), as well as all three-way interactions including hunter, were fitted using random-effect priors to explore variation in hunter selectivity over time and in space. Model selection was performed through Bayes factors given in log marginal likelihoods (Kass & Raftery 1995). According to Kass & Raftery (1995), the following recommendations regarding differences in log marginal likelihoods are given: 1–3, not worth more than a bare mention; 3–20, positive; 20–150, strong; >150, very strong.

To compare younger animals and prime-aged stags, having differing duration of the hunting season (see above for dates), we ran separate models for the age classes 1- to 4-year-olds and 7- to 12-year-olds (prime-aged stags). The number of observations used in the models was 79 280 for 1- to 4-year-olds and 46 737 for prime-aged stags (see Supporting Information, Tables S1 and S2 for a distribution of the data over counties and years). Compensatory culling and trophy hunting lead to differing motivation for the hunter types, and age groups are expected to experience different hunting pressures due to antler growth. To compare between age groups, we present predicted values for 1-year-olds (yearlings), 3-year-olds and 9-year-olds (prime-aged stags). Finally, chi-square tests were used to check for differences in age distribution between foreign and local hunters.

Analyses of century-scale data

Initial plots of the century-scale trophy size data indicated a nonlinear development of trophy size over time. This was confirmed by fitting generalized additive models (GAMs; Wood 2006) to the data using the number of antler tines as response and the year shot as predictor fitted as an isotropic thin plate regression spline ($F_{8,8} = 113.5$, $P < 0.001$), with the degree of smoothing chosen through the generalized cross validation criterion (library 'mgcv' in the statistical software R). We therefore used segmented linear regression to identify break points and quantify changes in the nonlinear relationship between trophy size and time (library 'segmented' in the statistical software R; Muggeo 2008). Segmented linear regression estimates more than one linear relationship (if present) between the dependent and the independent variable, by partitioning the data into segments separated by clear break points. From the individual segments, we can quantify potential periodic increases or decreases in trophy size and identify when these occur. We used the number of antler tines as response variable, and predictors included the year shot (continuous) and place shot (county), and the interac-

tion between these. The predictor for which the segmented relationship was estimated was year shot. Model selection was by comparison of increasingly complex models starting with only year shot as predictor and adding county and the interaction between the two predictors. Models were compared using the Akaike Information Criterion (AIC) corrected for finite sample size (AICc) to identify the most parsimonious model. The procedure was repeated using the average beam length as response for comparison.

Results

PATTERNS OF HUNTER SELECTION IN SPACE AND TIME

Figure 2 shows how the red deer shot are distributed between foreign and local hunters. Chi-square tests confirmed a significant difference in red deer age distribution between the hunter types (1–4 years: $\chi^2_3 = 3182.5$, $P < 0.001$; prime-aged stags: $\chi^2_5 = 671.7$, $P < 0.001$). Foreign trophy stalkers in general shot a lower proportion of younger animals and a much higher proportion of older and prime-aged stags, as predicted by the compensatory culling hypothesis.

Model selection based on the Bayes factor found positive evidence (log marginal-likelihood >16.9) for the model including all terms to be the most parsimonious model for 1- to 4-year-olds (Table S3). For prime-aged stags, the model excluding the interaction between year (as factor), hunter type and age (as factor) was preferred (log marginal-likelihood >4.8, positive; Table S4).

Foreign trophy stalkers consistently targeted significantly larger individuals than local hunters, as predicted by both the trophy hunter selection and the compensatory culling hypotheses. However, the magnitude of the trait difference of antler weight varied with age. The difference was largest when targeting yearlings [1-year-olds; 9.85% larger when shot by foreign trophy stalkers (95% credibility interval, CI = 7.96–11.77%)] and intermediate for intermediate ages [3-year-olds; 6.99% larger (95% CI = 6.30–7.68%)], while the smallest difference between hunter types was found for prime-aged stags [(9-year-olds; 2.70% larger (95% CI = 1.60–3.81%)].

We found evidence of large spatio-temporal variation in age-specific hunter selectivity over regions and years, that is, the trait difference of antler weight of deer shot by local and foreign trophy stalkers varied largely among years and between counties (Figs 3 and 4). The spatial pattern showed variation for all three ages, but yearlings and 3-year-olds shot by foreign trophy stalkers were always larger than when shot by local hunters (Fig. 3). The difference between hunter types was smallest for yearlings and 3-year-olds in county 2 [yearlings shot by foreign trophy stalkers were 6.36% larger (95% CI = 3.28–9.53%); 3-year-olds 2.63% larger (95% CI = 0.93–4.33%)] and largest in county 20 [yearlings 15.90% larger (95% CI = 12.52–19.58%); 3-year-olds 12.09% larger

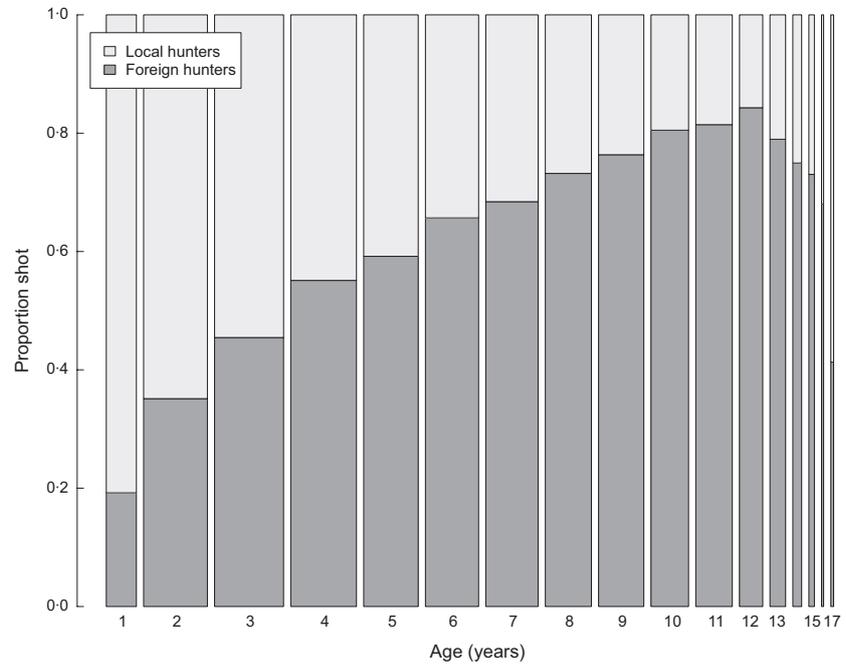


Fig. 2. Barplot showing the proportion of red deer males shot by foreign trophy hunters (darker grey) and local hunters (lighter grey) from 1973 to 2008 (decade-scale data; $N_{\text{obs}} = 178\,450$). The width of the bars represents the relative amount of observations within each age category.

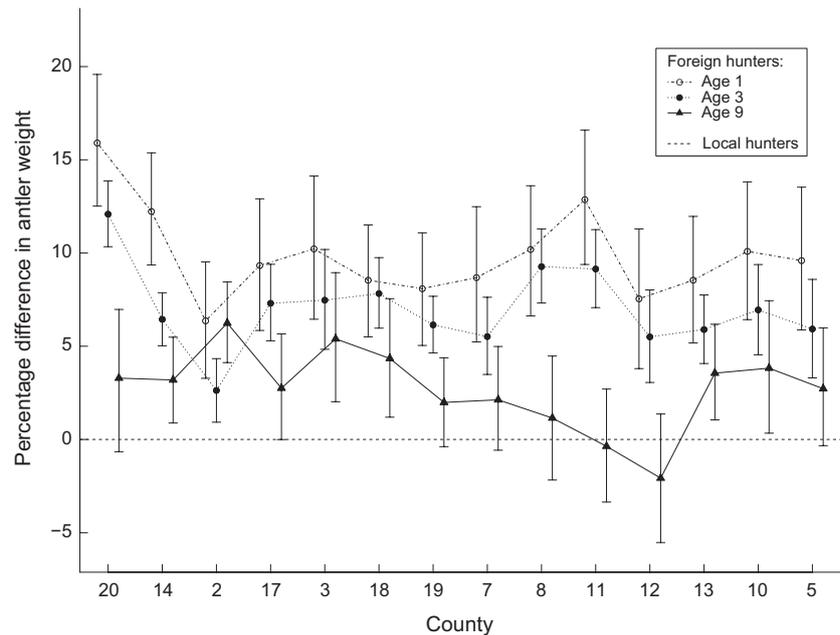


Fig. 3. Spatial variation in the percentage difference in the selection of antler size [antler weight (kg)] for foreign trophy hunters (points with corresponding 95% CIs) compared to local hunters (dashed line) based on integrated nested Laplace approximations of 126 017 red deer males from 1973 to 2008 (decade-scale data) in 14 Hungarian counties, predicted for 1 (open circles)-, 3 (closed circles)- and 9 (triangles)-year-old males. The counties are grouped after the amount of harvested red deer, starting with the ‘best’ counties from the left. N_{obs} model for 1- to 4-year-olds = 79 280, N_{obs} model for 7- to 12-year-olds = 46 737.

(95% CI = 10.34–13.87%). The pattern was less consistent for prime-aged stags (Fig. 3). Foreign trophy stalkers shot significantly larger prime-aged stags than local hunters in the majority of the counties, with the largest positive difference found in county 2 [9-year-olds 6.24% larger (95% CI = 4.12–8.45%)]. However, in some counties, antler sizes of prime-aged stags shot by different hunter types overlapped (i.e. counties 8 and 11; Fig. 3), and the pattern was nearly reversed in county 12, with foreign trophy stalkers harvesting 2.08% smaller trophies (95% CI = -5.53% to 1.37%).

Patterns of hunter selectivity also varied over time (Fig. 4). The foreign trophy stalkers harvested

significantly larger males than local hunters in the majority of the years, but for prime-aged stags in particular, the size of harvested deer shot by the different hunter types often overlapped, that is, for 8 of 9 years in the 2000s (Fig. 4). The largest difference for 9-year-olds was found in 1974, where the predicted value of trophies harvested by foreign trophy stalkers was 8.04% larger (95% CI = 5.28–10.91%), while the hunter types overlapped in 2008 [foreign hunters harvested 1.13% smaller trophies (95% CI = -3.03 to 0.80)], where the largest negative difference was found.

Finally, we added year as a continuous variable to look for linear trends in antler weight. For the 1- to 4-year-olds

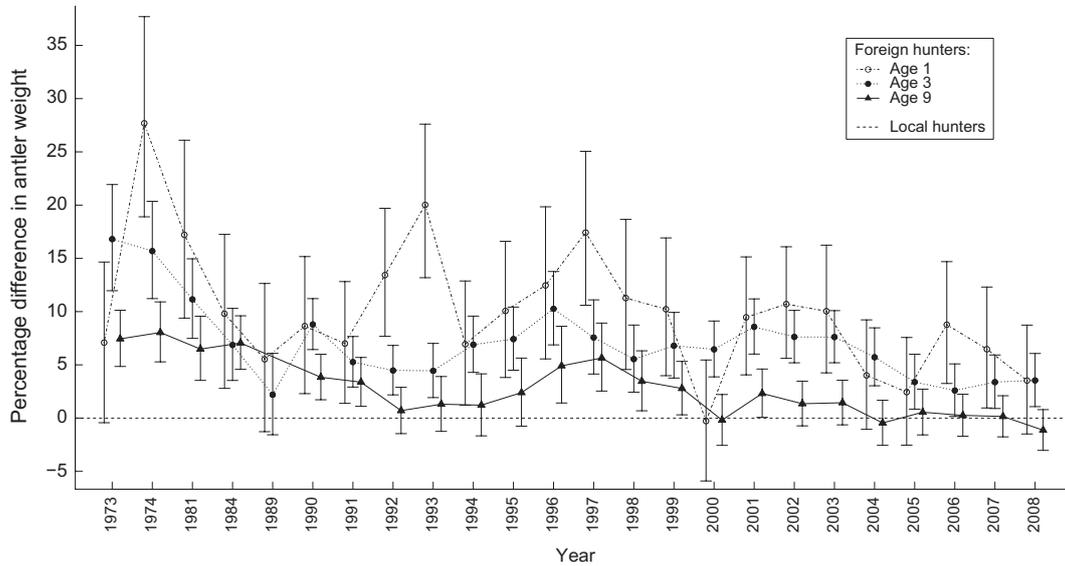


Fig. 4. Yearly variation in the percentage difference in the selection of antler size [antler weight (kg)] for foreign trophy hunters (points with corresponding 95% CIs) compared to local hunters (dashed line) based on integrated nested Laplace approximations of 126 017 red deer males from 1973 to 2008 (decade-scale data) in 14 Hungarian counties, predicted for 1 (open circles)-, 3 (closed circles)- and 9 (triangles)-year-old males. N_{obs} model for 1- to 4-year-olds = 79 280, N_{obs} model for 7- to 12-year-olds = 46 737.

we found a slight, but significant decrease in trait size [$\beta = -0.005$ (95% CI = -0.008 to -0.003)]. Seven- to 12-year-olds also showed a significant trend over time, with a slight increase in trophy size [$\beta = 0.004$ (95% CI = 0.003 – 0.006)], contradicting the hunting pressure hypothesis.

The total variance explained by the models was 74.8% and 39.7% for 1- to 4-year-olds and 7- to 12-year-olds, respectively. In the Supporting Information we show plots with predicted values for both hunter types and from all counties and years for 1-, 3- and 9-year-olds (Figs S1–S3).

TROPHY SIZE DEVELOPMENT AT CENTURY-LONG TIME-SCALES

Model selection of trophy size (tine number) recorded from trophy exhibitions from 1881 to 2008 showed that the model including the predictors year and county and the interaction between these was the most parsimonious model based on the AICc (Table 2). The segmented regression identified two clear break points in the data with narrow confidence intervals (CIs) [years 1958 (95% CI = 1957–1960) and 1974 (95% CI = 1971–1976); Table 3], suggesting three main periods of trophy size trends (1881–1958, 1958–1974 and 1974–2008). All models tested identified similar break points with overlapping CIs, and the trophy size trends (the slope of the segments) were consistent between models (Table 3). As models were so similar, and to be able to show trophy size trends for all of Hungary and not just a specific county, the following plots and predictions are taken from the model only including year as a predictor.

The first period from 1881 to 1958 showed a significant decline in trophy size [$\beta = -0.030$ (95% CI = -0.038 to -0.020); Table 3], predicting a decrease from 15.9 antler tines in 1881 to 13.5 antler tines in 1958 (15.1%), with the lowest point following World War II (Fig. 5a), in support of the trophy-hunting depletion hypothesis. Contradicting this hypothesis, the model predicted a large increase [$\beta = 0.245$ (95% CI = 0.208 – 0.281); Table 3] of 28.9% in trophy size (from 13.5 to 17.4 antler tines) from 1958 to 1974 (the second period). The third period from 1974 to 2008 showed no change in trophy size, with a slope not different from 0 [$\beta = 0.006$ (95% CI = -0.010 to 0.023); Table 3] and predicted values ranging from 17.2 to 17.4. This means that overall, the pattern showed increase in trophy size over the century, towards a stabilization during the last three decades (Fig. 5a). The lack of an overall decline at least partly supports the restricted trophy hunting hypothesis, while only the hunting pressure hypothesis could predict the post-World War II increase.

For average beam length, the model including year and county as predictors was the preferred model based on AICc (Table 2). For the same reasons as stated above for models investigating tine numbers, we present results from the model only including year as a predictor, but all model outputs can be found in Table 3. Comparing the models using the number of tines with the models using average beam length of antlers as a response, we found an overall similar pattern (Fig. 5b), with the 95% CI of the break points [years 1961 (95% CI = 1957–1966) and 1976 (95% CI = 1972–1980)] overlapping between the models (Table 3). However, when comparing the slopes of the individual segments, the third segment showed a slight

Table 2. Model selection on segmented regression for trophy size of red deer males shown in trophy exhibitions in Hungary between 1881 and 2008 (century-scale data)

Formula	AIC	<i>K</i>	AICc	Δ AICc	AICc weights
Response: number of antler tines					
Year + county + year \times county	13795.75	32	13796.47	0.000	0.874
Year + county	13800.20	19	13800.46	3.991	0.119
Year	13806.19	6	13806.22	9.748	0.007
Response: beam length					
Year + county	17512.61	19	17512.89	0.000	0.999
Year + county + year \times county	17527.03	32	17527.81	14.912	0.001
Year	17557.23	6	17557.26	44.363	0.000

The response variables in the models are number of tines ($N_{\text{obs}} = 2926$) and average beam length ($N_{\text{obs}} = 2683$).

Model selection is based on the corrected Akaike Information Criterion (AICc). The columns show AIC, the Akaike Information Criterion; *K*, the number of parameters; AICc, AIC corrected for sample size; Δ AICc, the AICc of the model relative to the best model; AICc weights, the relative likelihood of the model.

decrease for average beam length [$\beta = -0.121$ (95% CI = -0.169 to -0.072); Table 3]. Overall, the average beam length showed a 1.7% decrease between 1885 and 1961 (from 109.12 to 107.26 cm), an increase of 7.6% between 1961 and 1976 (from 107.26 to 115.45 cm) and finally a 3.3% decrease between 1976 and 2008 (from 115.45 to 111.59 cm). Thus, the trends in average beam length were similar to that for number of antler tines, except in the last period.

Discussion

There is currently much concern for potential deleterious consequences of unrestricted harvesting on the development of trait sizes, even in the short term (Allendorf *et al.* 2008; Allendorf & Hard 2009). In contrast to such a view, there was no clear evidence of a long-term negative trend over more than a century of the largest red deer antlers recorded at trophy exhibitions in Hungary. Instead, we found three distinct time periods with different trophy size trends: a small decrease (1881–1958) followed by a rapid and quite large increase (1958–1974) until a new fairly stable level was reached (1974–2008). This suggests that even though trophy size was temporarily declining, there was no genetic depletion preventing recovery, as predicted by the trophy hunting depletion hypothesis (Table 1). We thus present evidence that under restricted trophy harvesting in Hungary, it is possible to have a sustainable system in the sense that trophy sizes are not declining steadily over longer time-scales. More likely, the development of trophy sizes reflects underlying changes in the political and management system driving hunting pressure. This provides important insight for management of trophy hunting world-wide, as it can spark a search for conditions under which trophy hunting can be sustainable.

TROPHY SIZE DEVELOPMENT DURING A CENTURY OF POLITICAL CHANGES

Europe has been through dramatic changes in the political system during 1881–2008, and this has markedly affected game management in Hungary (Csányi 1997). During most of this period, Hungary has implemented what can be termed restricted trophy hunting management, where young and promising stags are allowed to reach older ages and develop large antlers before they are shot (Csik 1902; Széchenyi 1948; Mysterud & Bischof 2010). However, the strength in implementation of these rules has varied considerably. The two break points in the century-scale analyses identified three time periods with different trophy size trends, corresponding to changes in political regimes and management systems affecting hunting pressure with some years' delay resulting from age-structure changes. Short-term effects like changes in age and sex structure and viability selection due to harvesting are known to cause spatial and temporal variation in trophy size (Vaupel & Yashin 1985).

After World War I, Hungary lost 2/3 of the land area, and big game populations reached the lowest levels in 50 years (Csányi 1997). Between the world wars, big game management was less important, restricted to aristocrats and large forest estates, with no firm rules set by any legislation and more driven by individual ethics of sportsmanship. This corresponds to the period of decline in trophy sizes until World War II. After World War II, populations of red deer were historically low due to wartime overharvesting. Very strict management rules were established in 1945 with the aim to increase the income from hunting partly as part of the compensations paid to the Soviet Union (Tóth 2007). The availability of rifles was very low, resulting in low hunting pressure and an increase in population size and age of stags. Thus, stags

Table 3. Model summaries of the break points and slopes with 95% confidence intervals (CI) of the different segments in segmented regression models for trophy size of red deer males shown in trophy exhibitions in Hungary between 1881 and 2008 (century-scale data)

Model	Parameter	Estimate	SE	95% CI
Response variable: number of antler tines				
Year + county + year × county	$\beta_1^{(1)}$	-0.027	0.007	(-0.040, -0.014)
	$\beta_1^{(2)}$	0.234	0.022	(0.191, 0.277)
	$\beta_1^{(3)}$	0.013	0.009	(-0.005, 0.031)
	r_1	1958	-	(1957, 1960)
	r_2	1974	-	(1971, 1976)
Year + county	$\beta_1^{(1)}$	-0.031	0.004	(-0.039, -0.022)
	$\beta_1^{(2)}$	0.226	0.021	(0.185, 0.268)
	$\beta_1^{(3)}$	0.006	0.008	(-0.010, 0.022)
	r_1	1958	-	(1956, 1960)
	r_2	1974	-	(1971, 1976)
Year	$\beta_1^{(1)}$	-0.029	0.005	(-0.038, -0.020)
	$\beta_1^{(2)}$	0.245	0.019	(0.208, 0.281)
	$\beta_1^{(3)}$	0.006	0.008	(-0.010, 0.023)
	r_1	1958	-	(1956, 1959)
	r_2	1974	-	(1972, 1976)
Response variable: average beam length				
Year + county + year × county	$\beta_1^{(1)}$	-0.010	0.019	(-0.048, 0.028)
	$\beta_1^{(2)}$	0.515	0.062	(0.393, 0.638)
	$\beta_1^{(3)}$	-0.111	0.028	(-0.166, -0.055)
	r_1	1960	-	(1957, 1962)
	r_2	1977	-	(1974, 1979)
Year + county	$\beta_1^{(1)}$	-0.027	0.012	(-0.051, -0.003)
	$\beta_1^{(2)}$	0.417	0.082	(0.256, 0.577)
	$\beta_1^{(3)}$	-0.121	0.025	(-0.170, -0.072)
	r_1	1961	-	(1957, 1964)
	r_2	1976	-	(1972, 1980)
Year	$\beta_1^{(1)}$	-0.025	0.012	(-0.048, -0.002)
	$\beta_1^{(2)}$	0.414	0.090	(0.237, 0.591)
	$\beta_1^{(3)}$	-0.121	0.025	(-0.169, -0.072)
	r_1	1961	-	(1957, 1966)
	r_2	1976	-	(1972, 1980)

The response variables in the models are number of tines ($N_{\text{obs}} = 2926$) and average beam length ($N_{\text{obs}} = 2683$)

SE, standard error.

$\beta_1^{(1-3)}$ = the slopes of segment 1-3; r_{1-2} = the break points of the segmented regression.

born after 1945 were allowed to reproduce and reach their prime, and by 1955, foreign hunters were allowed into Hungary because of the demand for foreign currency. This is termed the second Golden Age in game management, the first one before World War I (Tóth 2005).

Spring population size of red deer increased from around 10 000 in 1960 to over 50 000 in 1985 (Csányi 1994). From the onset of the third period identified by our century-scale analyses (*c.* 1974), the management gradually changed as increased population densities caused damage to agriculture and forestry leading to demand for higher hunting pressure. Implementation of

the rules to save stags became weaker and more difficult with increasing hunting pressure and may explain the weak decline in antler beam lengths during this period, although low sample size in the mid-period (1958–1974) may add to this (Fig. 5b). In 1991, the Iron Curtain fell, and in 1996, a new act on game management was introduced. Until this point, the shooting of prime stags had been the privilege of paying foreigners and the Hungarian political elite. We see clearly that from around 2000 onwards, foreign and local hunters shoot approximately equally sized prime-aged stags because of this change in management policy (Fig. 4).

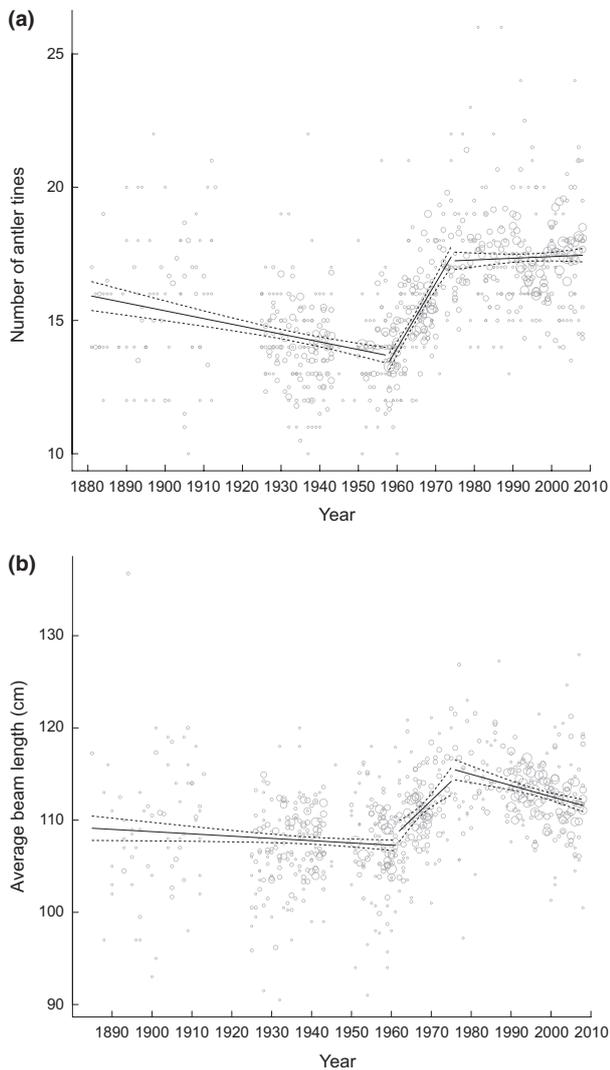


Fig. 5. The predicted pattern of (a) number of antler tines and (b) average beam length over time based on a segmented regression of 2926 red deer males shown on trophy exhibitions during 1881–2008 (century-scale data) in Hungary. Points represent the mean trophy size for each county and year, and the size of the points represents the relative amount of observations used to calculate each mean. (b) is based on slightly reduced sample size ($n = 2683$ from 1885 to 2008).

Thus, the patterns observed are consistent with expectations from the hunting pressure hypothesis. Unfortunately, data on age structure or more detailed accounts of population sizes to test this more firmly at century scales are lacking. At least, the patterns observed beg the important question of why there is no steady decline in antler size consistent with an evolutionary response.

PATTERNS OF HUNTER SELECTION IN SPACE AND TIME

A common view is that hunter selection in trophy hunting cultures always is sufficiently strong to yield directional

selection towards smaller body and trophy sizes (Allendorf & Hard 2009). If hunters show large variation for given traits when selecting their trophies, directional selection will be weaker, and the process towards evolutionary change will be slower and more likely to be less important than other environmental drivers. Actual population estimates on large herbivores are expensive and time-consuming to obtain and are therefore rarely available, providing a limitation in most hunter selection studies (review in Myrnerud 2011). One approach is to compare patterns of selection between hunter types differing in their motivation for hunting. Both foreign and local hunters hunt the same population of red deer, and we therefore expect patterns to be a result of differential selection arising from different motives of hunting. In the total annual harvest of 1973–2008, we found that foreign trophy stalkers generally selected for larger trophies than local hunters, as previously shown for roe deer *Capreolus capreolus* in Poland (Myrnerud, Tryjanowski & Panek 2006). For red deer, we found strong evidence for a marked difference between hunter types with respect to age of the animals harvested (Fig. 2). In general, foreign trophy stalkers selected for the biggest trophies, as expected. However, comparing counties, there was large variation in the difference between hunter types, sometimes even with the expected pattern reversed. This provides evidence that harvesting selection is more variable than previously assumed. It would also be interesting for future research to determine how differences in selectivity between local hunters and foreign trophy stalkers arise. Trophy hunters typically use guides, and in Hungary, the guides determine when foreign trophy hunters are allowed to shoot prime stags. Increased selection for large bull moose was found in Alaska as an effect of guides knowing low-density areas where trait sizes were larger (Schmidt, Hoef & Bowyer 2007).

TROPHY SIZE DEVELOPMENT AND TROPHY HUNTING

Overall, there is no doubt that trophy hunters, if not restricted, would select for larger males. If there is directional selection on a particular trait in a population and this trait is heritable, evolutionary theory predicts depletion of genetic variance and possible evolutionary change (Fisher 1930). Antler size in free-living red deer has earlier been shown to be heritable, with a narrow-sense heritability of 0.327 ± 0.12 (Kruuk *et al.* 2002). Thus, one can expect sufficiently strong directional selection to have an impact on the genetic composition in the population. From the domestic literature on related species (Hill & Kirkpatrick 2010), there is no doubt regarding the potential for evolutionary change. Several studies investigating selection pressures from human harvesting in wild animal populations have also found support for these predictions (Coltman *et al.* 2003; Garel *et al.* 2007). This implies that selection pressures in these populations were sufficiently strong to cause a decline in trait size. In some periods (1881–1958), we found evidence for a decline in antler

size, but the rapid increase in the following period (1958–1974) suggests no depletion of the gene pool for large antler size. Thus, the trophy hunting depletion hypothesis failed to predict the variation in trait size over a century in Hungary. Note that the century-scale data stem from trophy exhibition records and are therefore a biased sample representing the upper end of the size scale. Trophy harvest data may thus underestimate the temporal trend in trophy size. However, when comparing horn size of bighorn sheep in hunting records with those from proper monitoring data during a period of decline, Pelletier, Festa-Bianchet & Jorgenson (2012) identified the decline also in the hunting data although the slope estimates differed. Also, directional selection is expected to decrease variance (Shnol & Kondrashov 1993), so these upper-end data from trophy exhibitions should be expected to decline if directional selection from trophy hunting was the primary driver of antler size development.

OTHER POTENTIAL DRIVERS NOT ACCOUNTED FOR

Distinguishing evolutionary responses in phenotypic traits from plasticity or environmental effects is indeed challenging (Allendorf & Hard 2009). Antler development is well known to be dependent on environmental factors and nutritional quality. Environmental factors like climate change and land-use change may therefore have a large influence on traits like trophy size in ungulates (Frank & Slatkin 1992; Kruuk *et al.* 2002). We were able to obtain data on mean annual temperature only from Budapest from 1901 to 2008, but this may not be representative for the whole of Hungary. However, including these data in the segmented regressions did not alter the observed patterns (results not shown). Kruuk *et al.* (2002) found evidence for natural selection in red deer antler size on the Isle of Rum, Scotland, but because environmental factors affected antler development, the selection found did not result in an evolutionary change in the trait. The population sizes of red deer have increased dramatically over the last 50 years. This can affect antler development and may also impact how the different hunter types select. In some areas and periods, there has also been artificial feeding that might affect antler size, but the extent of this is not known. Other processes like immigration and emigration, natural selection and random drift may also cause genetic changes in the population. Unfortunately, there are no available data to estimate the relative contribution of this wide range of potential drivers in this system.

TOWARDS EVOLUTIONARILY ENLIGHTENED MANAGEMENT OF TROPHY HUNTING

We cannot with certainty identify the management regime as a primary driver for the observed trends in trophy size due to lack of data on age structure, but the hunting culture is likely to at least contribute to the overall pattern

of antler size reported here. Other factors that potentially change the phenotypic expression of desired traits must also be taken into account when managing populations. The insight that trophy hunting is not always causing long-term declines in trait sizes is important, as it can aid the search towards a set of factors forming the basis for a theory of evolutionarily enlightened management (*sensu* Ashley *et al.* 2003) of trophy hunting. For such a framework, we identify spatial refuges (Tenhumberg *et al.* 2004), temporal refuges both between years and within the year (this study), compensatory culling (Mysterud & Bischof 2010), saving stags until prime-age culmination allowing most trophy stags to breed (Csik 1902; Széchenyi 1948; Apollonio, Andersen & Putman 2010) and likely also redirecting hunter preferences, issuing fines or penalties for what can be termed mismanagement (shooting the wrong size of prime stags – a former practice in Hungary) or with higher prices for larger trophies. Further, prices for shooting red deer stags in Hungary increase progressively with trophy size, from €850 for trophies weighing less than 4 kg, to more than €9000 when trophy weight exceeds 11 kg. This contrasts with the bighorn sheep system, which operates with only one legal size category, referred to as ‘4/5-curl’ (Coltman *et al.* 2003). The price differentiation found in Hungary may contribute to a weaker directional selection against large trophy size, as hunters are likely to differ in the amount of money they are willing to pay for their trophies. Also, the prime stag season in Hungary is short and has been so for a century, spanning over only 45 days (1 September to 15 October). The short season gives hunters less time to be selective and allows the stags to develop further, providing yearly temporal refuges. Our study highlights how trophy hunting under certain management restrictions and given environmental conditions can be sustainable from a trait size perspective even in the long-term.

Acknowledgements

We are grateful to the Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, for funding of Inger Maren Rivrud. The National Game Management Database is financed by the Ministry of Rural Development of Hungary and maintained by the Szent István University, Institute for Wildlife Conservation. We are grateful to Marco Festa-Bianchet, Loeske Kruuk and Anne Loison for very constructive comments to previous drafts.

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Received 3 July 2012; accepted 26 September 2012
Handling Editor: Johan du Toit

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1–S3. Hunter selection patterns based on INLAs per county and year for 1-, 3- and 9-year-olds.

Table S1–S2. The number of observations per county and year used in INLAs for 1-4- and 7-12-year-olds.

Table S3–S4. INLA model selection for 1–4- and 7–12-year-olds.

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