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Pozo et al. • Hunting Effects on Red Deer Antler Size

Modeling the Impact of Selective Harvesting on Red Deer Antlers

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ABSTRACT Hunting is a common component in the management of ungulate species.

Despite its widespread use, the influence of selective harvesting on phenotypic trait change is
still ambiguous, and represents a critical gap in our understanding of the responses of wild
populations under harvest. Using the long-term red deer (*Cervus elaphus*) dataset (1972-

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2012) from the Isle of Rum National Nature Reserve, Scotland, we assessed the relationship between antler length and key demographic processes (i.e., survival, recruitment, antler growth, parent-offspring trait correlation) for the male component of the population. We then constructed the first integral projection model for this species to examine the effects of simulated trophy hunting on 2 population-level parameters: the stable antler size distribution and the relative reproductive value of males. When male mortality rates due to hunting were <20% the effect on antler size distribution and the reproductive value function were relatively small. However, as mortality due to hunting increased to 50% in large individuals, the direct effects of hunting on mean antler size and reproductive value became evident. Our model acts as a useful starting point to investigate the ecological and evolutionary consequences of hunting in red deer.

KEY WORDS antler size, integral projection model, Isle of Rum, red deer, Scotland, sexual selection.

Wild ungulates have been hunted for centuries, however the consequences of their exploitation remain unclear. In particular, the influence of selective harvesting on phenotypic change is not well understood, and represents a critical gap in our knowledge of the responses of wild populations to harvest. Trophy hunting represents one form of selective harvesting that has been traditionally implemented in wild cervids. This harvesting regime is a non-random process whereby humans select individuals to be removed from a population based on 1 or several phenotypic traits (Festa-Bianchet 2003, Mysterud 2011). Typically, males with the largest trophies (e.g., antlers or horns) are sought and removed from the population, imposing an unnatural mortality rate on prime-age males (i.e., those that have attained asymptotic body mass prior to senescence) or young adults (Gaillard et al. 1998, Monteith et al. 2013). This harvesting regime can result in negative demographic consequences including changes in population structure (Traill et al. 2014), skewed sex-ratios (Ginsberg and Milner-

Gulland 1994, Milner-Gulland et al. 2003), and decreased antler or horn size (Milner et al. 2007, Monteith et al. 2013). Such deleterious effects have been observed in bovidae (Pérez et al. 2011, Festa-Bianchet et al. 2014) and cervidae (Monteith et al. 2013).

Antler size is often under natural and sexual selection. In wild populations of deer, males differ markedly in their fertility rates (Malo et al. 2005a) and antler size (Kruuk et al. 2002), with adult males with larger antlers attaining the highest breeding success (Clutton-Brock 1981, Andersson 1994, Kruuk et al. 2002, Malo et al. 2005b). In addition, the key role of antlers in male-male combat (Clutton-Brock 1982, Andersson 1994) suggests that individuals with larger antlers may live longer (Lemaître et al. 2014). Because sexually selected characteristics are by definition under selection, any unnatural intervention that changes mortality or reproductive schedules of individuals with specific trait values has the potential to generate evolutionary change. Harvest by humans has been reported to cause changes in phenotypic traits (Darimont et al. 2009), and to generate evolutionary responses (Palumbi 2001). Trophy hunting may impose selective impacts on wild populations. One way to investigate this is to evaluate how hunting is likely to influence fitness. We examined how hunting might affect the distribution of trophy sizes within the population and reproductive value (i.e., a quantity describing the expected representation in terms of descendants across all trait values of an individual with a specific character value in the future population; Fisher 1930).

Artificial removal of males with large trophies will likely lower the reproductive value of large individuals and mean trophy size within the population. However, trait size response to trophy hunting has not been consistent across species, and in many cases environmental factors play a much stronger role on mean values than selective removal (Schmidt et al. 2007, Mysterud 2011). However, other studies have reported that phenotypic change in hunted populations can also be due to an evolutionary response (Coltman et al.

2003), although it should be noted that this conclusion is controversial (Traill et al. 2014).

In long-term studies of individual life histories, experimental culling of individuals often conflicts with other research interests and cannot therefore be used to test harvesting hypotheses. As a result of this, the use of structured models to represent population structure has become popular (Caswell 2001, Ellner and Rees 2006, Coulson 2012). In particular, integral projection models (IPMs), a generalization of matrix models, have been developed to study and track the dynamics of continuous characters (Easterling et al. 2000, Coulson 2012). Integral projection models can be parameterized directly with observational data (Ellner and Rees 2006), and enable key population-level parameters, such as a stable phenotypic trait distribution and reproductive values, to be predicted from individual-level data (Caswell 2001). Importantly, IPMs can be perturbed to simulate harvesting regimes in wild populations and have provided reliable information on how demographic parameters change within and between age groups (Traill et al. 2014).

We used individual based data on red deer (*Cervus elaphus*) from the Isle of Rum National Nature Reserve, Scotland (Clutton-Brock et al. 1982, Pemberton et al. 1996) to assess the effects of trophy hunting on 2 population-level parameters: stable antler size distribution (i.e., the expected distribution of antler length/age-group within the population) and reproductive value (i.e., the relative contribution of an individual with a specific antler size to the future population). We investigated the relationship between antler size and key demographic processes relating to the male component of the population because we expected selective hunting to change the relative reproductive value between males with different antler sizes, and because the relative contribution of individuals with different character values to future populations elucidates the likely consequences of selective harvesting. We then constructed the first IPM for the species (exclusively for M), from which we extracted estimates of stable antler size distribution and reproductive value. Finally, we

perturbed the resulting IPM to simulate the effects of different harvesting regimes at the population and age-group levels.

STUDY AREA

The data used in this study come from the unmanaged red deer population in the North Block of the Isle of Rum National Nature Reserve (578019 N, 068179 W; NM-402996), Scotland. A detailed description of the Isle is presented by Clutton-Brock et al. (1982). The 10,600-ha island has a mild, wet and windy oceanic climate. Rainfall varies widely across the island, with April generally the driest month and November and January the wettest (Clutton-Brock et al. 1982). Rum is a mountainous island characterized by productive valleys, including extensive grassland cover closer to seashores, and fen vegetation on higher elevations (Virtanen et al. 2002, Ball 1987).

In 1972, the routine 14% red deer cull of the North Block stopped and a long-term, individual-based investigation into behavior, evolution, life history, and population dynamics was initiated (Clutton-Brock 1981, Pemberton et al. 1996). Females give birth in May and June each year, and since culling stopped, approximately 90% of calves born in the North Block have been caught, individually marked (i.e., collar, ear tags or ear punches attached as calves) and followed throughout their lives. Censuses in the study area are carried out at least 5 times a month between January and May (Coulson et al. 1997), during which all individuals are recorded as present or absent. Although all breeding attempts and deaths are recorded within the study area, animals that emigrate to other parts of the island cease to be monitored and their whereabouts are thereafter often unknown (Clutton-Brock et al. 1982).

Male red deer grow antlers annually from the age of 1 or 2 years old (Kruuk et al. 2002). Antlers are used in male-male encounters once the individual is sexually mature (at 3–4 years of age), even though they are unlikely to sire any offspring until they are ≥ 4 years old (Nussey et al. 2009, Kruuk et al. 2014). Males cast their antlers annually between March and

May (casting season), following which they grow a new set of antlers until August. These lose their velvet (i.e., cleaned) around September prior to the start of the rutting season. To fit in with antler growth, the deer year in our study ran from 1 August to 31 July of the next year. This ensured that only pairs of antlers used during the latest rutting season were assessed in relation to male calves recruited the following year.

METHODS

Antler Measurements

The Isle of Rum Red Deer Project recovered antlers in the field during the casting season (March-May) every year since the 1970s. In our study we used data collected by the project between 1972 and 2012. Members of the survey team followed each male within the study area and collected antlers immediately after they were shed. Thus, each antler was associated with a specific individual identified by observation of unique ear tags or punches. Previous genetic analysis has suggested this method is 93% accurate (J. P. Petley and J. M. Pemberton, Institute of Evolutionary Biology, University of Edinburgh unpublished data). The project collected antler length, mass, the number of tines, genetic samples, and other measurements in the field (Kruuk et al. 2002, Walling et al. 2010). They used genetic samples to construct a multigenerational pedigree, in which they estimated paternity using genetic (genotypes at ≤ 15 microsatellite loci), phenotypic, and behavioral data (Kruuk et al. 2014). We focused on the length of antlers, which we used as an indicator of antler size, because antler length is one of the main characteristics targeted during trophy hunting activities.

The Red Deer Project team measured antler length as the distance from the coronet to the furthest tip of the main beam, around the curves (Fig. 1). Where measures from both antlers (i.e., left and right) were available for the same individual for a given casting season, we used the average. For juveniles (1–3 years old), antlers are often simple spikes. Members of the project estimated spike length of living male calves by eye in the field. For any 1 male

calf, multiple observers (2–4) estimated spike size using the ear length of the same individual as a reference. The project recorded observed spike length as the consensus between observer measurements. We organized individual information in a file with equivalent structure to that used in Coulson (2012; Appendix A).

All animal measurements in this study were collected noninvasively. The data used in this study was gathered in the field under the approval of the University of Edinburgh’s Animal Welfare and Ethical Review Body.

Construction of IPM and Statistical Analysis

Because only individuals that have reached reproductive maturity are able to defend harems and reproduce, both antler size and reproductive status can be expected to vary between male life stages. Consequently, we included age class as a factor in our analyses. Considering that environmental variation imposes different selective forces on individual survival and reproduction, we grouped males into 4 reproductive and 4 survival age classes. Reproductive age classes consisted of juveniles (1–3 years old), young adults (4–6 years old), adults (7–11 years old), and seniors (≥ 12 years). Survival age classes consisted of calves (0–1 years old), juveniles (2–3 years old), adults (4–8 years old), and seniors (≥ 9 years). In both cases, age classes were based on Kruuk et al. (2002), with the exception of the adult age class, which in our case was extended to include individuals of 4 years old because these were observed to reproduce in our study population.

Integral projection models are composed of 4 fundamental functions describing the processes of survival (S), recruitment (R), growth (G), and parent-offspring trait correlation (D ; inheritance), which together predict, in this case, the distribution of antler length (l) per age-class (a) at time $t + 1$, as a function of antler length at time t (Ozgul et al. 2010, Traill et al. 2014). Together, these predict the distribution of the number of individuals (n) with antler length (l) per age-class (a) at time $t + 1$, as described by the following equations:

$$n(1, t + 1, l') = \sum_a \int dl D(l' | l) R(a, l) n(a, t, l) \quad \text{Equation 1}$$

$$n(a + 1, t + 1, l') = \int dl G(a, l' | l) S(a, l) n(a, t, l), a \geq 1 \quad \text{Equation 2}$$

Equation 1 describes the distribution of offspring antler length at time $t + 1$, which is calculated from the number of offspring produced by a male with antler length l per age class (i.e., $R(a, l)$) and the offspring distribution of a parent of age a and antler length l (i.e., $D(l' | l)$). Together these describe the probability that an individual with antler length l at time t of age a will produce a son with antler length l' at time $t + 1$. In both cases dl belongs to the integral sign and means that the integral is taken over the whole range of l . Additionally, $R(a, l)$ includes the product of fertility (R_F), which describes the probability that a male will reproduce or not, and the number of offspring produced from those individuals that do reproduce (R_N). In our model, we considered only individuals ≥ 4 years (i.e., males producing offspring) in the reproduction analysis.

Equation 2 describes the probability that an individual of age a and antler length l will survive from time step t to time step $t + 1$ (i.e., $S(a, l)$). The growth function (i.e., $G(a, l' | l)$) describes the growth of antler from l at time t to l' at time $t + 1$ of individuals from an age class a . Both functions in equation 2 describe the distribution of antler lengths from individuals that survive from one time step to the next one. Below, we describe how we parameterized and statistically analyzed each of the 4 fundamental functions.

Effects of antler length on survival.— We performed a mark-recapture (MR) analysis to test for the effect of age and antler length on male survival, while accounting for imperfect detection of individuals (Lebreton et al. 1992). We considered a Cormack–Jolly–Seber (CJS) model (Lebreton et al. 1992) with 2 states to describe the fate of an individual (1 = alive; 0 = dead), and 2 events to describe the observation process (0 = antler not found, 1 = antler detected). At each time step t (i.e., 1 year), an individual can be alive with probability S_t , and its antler can be found with probability P_t .

We first performed goodness-of-fit tests starting from a general CJS model allowing survival and detection probabilities to vary with time (Lebreton et al. 1992) using program U-CARE (Choquet et al. 2009). We detected a lack of fit due to transient (i.e., individuals in transit across the study area) and trap-happiness (i.e., individuals whose antlers are found once are usually more likely to be found again in the field) effects (Pradel et al. 1997). Once we had accounted for the presence of transient individuals, the over-dispersion coefficient relating to the trap-happiness effect was acceptable ($\hat{c} = 2.48 < 5$; Burnham and Anderson 2002). To account for the transient effect, we considered a 2 age-class structure for survival (Pradel et al. 1997), whereby we defined individuals as being either juveniles (i.e., calves and juveniles from the IPM age classes) or adults (i.e., adults and seniors from the IPM age classes). This choice is sensible because younger individuals tend to stay with their mothers (and therefore within the study area) in their first 2 years whilst older males disperse across the island. Thus, using a CJS model that included a time-varying individual covariate (Choquet and Nogue 2011), we tested for additive effects and an interaction between age class and antler length on survival. Collinearity was not an issue, even when the range of antler length varied within age classes and its relationship with survival because we used age as a group (Fig. 2). We also tested for an effect of age on detection probability. We fitted models using program E-SURGE (Choquet and Nogue 2011) and used standard maximum likelihood procedures to obtain parameter estimates (Lebreton et al. 1992). Model selection for the MR analysis and each fundamental function of the IPM were based on Akaike's Information Criterion (AIC; Akaike 1973). We retained the model with the lowest AIC value for subsequent analysis. We used R v3.0.1 for all statistical analysis (R Core Team 2014).

We used estimates for the intercept and slope from the best model to parameterize the survival function of the IPM:

$$S(a, l) = \frac{1}{1 + e^{-(\alpha_{s,a} + \beta_{s,a} l)}} , \quad \text{Equation 3}$$

where an individual from age class a and antler length l at time t has a probability of survival of $S(a, l)$. Here, $\alpha_{s,a}$ and $\beta_{s,a}$ denote the intercept and slope per age-class, respectively.

Effects of antler length on recruitment.—We used generalized linear models (GLM) to estimate male fertility (R_F ; the probability for an individual to reproduce or not in a given year) and the number of recruits produced per male (R_N) once he reproduces, each as a function of antler length and age class. We estimated R_F from a GLM with a binomial error and logit link function and it had the same structure as $S(a, l)$ but with $\alpha_{F,a}$ and $\beta_{F,a}$ representing intercept and slope for fertility, respectively.

$$R_F(a, l) = \frac{1}{1 + e^{-(\alpha_{F,a} + \beta_{F,a} l)}} \quad \text{Equation 4}$$

We modeled R_N using a Poisson error structure and a log link function because of the count nature of our data. The R_N function within the IPM takes the following form:

$$R_N(a, l) = e^{-(\alpha_{N,a} + \beta_{N,a} \times l)} \quad \text{Equation 5}$$

This function describes the number of offspring that individuals from age group a , and of antler length l , will recruit conditional on reproduction into the population at time t . In equation 5, $\alpha_{N,a}$ and $\beta_{N,a}$ are the intercept and slope of recruitment per age-class, respectively.

If R_F is the number of individuals that reproduce per age group in the population and R_N is the number of offspring that individuals that do reproduce contribute per age group, the final equation for the recruitment function corresponds to the product of both:

$$R(a, l) = R_{F,a} \times R_{N,a} \quad \text{Equation 6}$$

Effects of antler length on growth.— We combined 2 sources of information to determine the ontogenic development of antler length. First, we used a linear model to fit regression lines per age class within both age group classifications (i.e., survival and reproduction) between measures from males sampled at time step $t + 1$, in relation to the

same individual at time t . The expected (E) antler length at time $t + 1$ for a given antler length at time t had the form $E(a, l') = \alpha_{g,a} + \beta_{g,a} \times l$, where $\alpha_{g,a}$ and $\beta_{g,a}$ are the intercept and slope relating to growth for individuals of age class a ; l is antler length at time t , and l' is antler length at time $t + 1$. We then squared the residuals from this first model and regressed them against the antler length in a second linear model. We obtained the following equation, $\sigma^2(a, l') = \alpha_{gv,a} + \beta_{gv,a} \times l$, in which the growth variance (gv) intercept and slope per age group are represented by $\alpha_{gv,a}$ and $\beta_{gv,a}$ respectively. Finally, to estimate G in the IPM, we incorporated both functions in the following equation:

$$G(l' | l) = \frac{1}{\sqrt{2\pi\sigma^2(l,a)}} e^{-\frac{(l - E(l,a))^2}{2\sigma^2(l,a)}} \quad \text{Equation 7}$$

Effect of antler length on inheritance.—We compared the antler length of male offspring that survived from birth to their first census ($t + 1$), with that of their respective fathers at the time when the offspring was sired (t). We collected 1,992 repeated antler measurements from the field between 1970 and 2012, representing 869 unique males. Of these, 388 had known male offspring at time step $t + 1$, with spike length measured on 29 of the latter. We used these available data to predict the spike length at age 1 of adults for which this measurement had not been taken, but which had been observed in later life stages ($n = 143$ out of 388). Offspring that died before age 1 and were not seen in later life stages could not be included in this analysis because it was not possible to estimate their spike length.

We used 2 linear models to estimate the inheritance function: one to regress antler length of offspring at time $t + 1$ against antler length of the males that sired them at time t (i.e., the mean); and another to determine the relationship between squared residuals and average antler length in the population (i.e., the variance). The final equation for D followed a Gaussian distribution in the IPM:

$$D(l' | l) = \frac{1}{\sqrt{2\pi\sigma^2(l)}} e^{-\frac{(l' - (\alpha_d + \beta_d * l))^2}{2\sigma^2(l)}} \quad \text{Equation 8}$$

The model for D did not consider age classes because we did not find a statistical difference between age groups for this function (Table 1). We therefore did not obtain intercepts and slopes per age class as in S , R , and G . We used only 1 intercept (α_d) and 1 slope (β_d) from the first linear model, and 1 intercept (α_{dv}) and 1 slope (β_{dv}) from the variance model (i.e. $\sigma^2(l) = \alpha_{dv} + \beta_{dv} \times l$) to predict $D(l' | l, t)$ in the IPM.

Numerical implementation.— To construct the matrix approximation for the IPM, we first discretized a range of values for antler length between the minimum (0 cm) and maximum (93.8 cm). We considered values between 0 and 100 to create 200 bins separated by an interval of 0.5 cm. We used the midpoint rule (Ellner and Rees 2006) in numerical approximation of the integrals to implement the IPM. We constructed a projection kernel from the 4 fundamental functions. We then discretized the latter to obtain a matrix model from which we calculated parameters of interest by eigen analysis, which in turn provided us with eigenvectors. These demographic parameters corresponded to the stable antler size distribution and the reproductive value. Because we did not include females in our analysis, we standardized reproductive value over all males (i.e., male population reproductive values summed to 1) for the entire study period.

291 Elasticity Analysis

We performed an elasticity analysis to examine how stable antler size distribution and reproductive value responded to perturbation of parameters in the model. We independently increased each of the age class coefficients (i.e., intercepts and slopes) by 1%, meaning that we multiplied positive and negative values by 1.01 and 0.99, respectively. After each perturbation we re-ran the IPM, returning to the original coefficients before altering the next parameter. This process is a conventional way of assessing how demographic parameters of

interest are influenced by small perturbations (Easterling et al. 2000, Coulson et al. 2010). By perturbing each parameter, we aimed to understand how that specific value affected transition rates in the sub-matrices within and between age groups, and how this change ultimately altered stable antler size distribution and reproductive value. If we observed no changes in the demographic parameters of interest (i.e., stable antler size distribution and reproductive value) between perturbed and unperturbed models, we concluded there was no association between antler size and the model predictions calculated from the IPM (Coulson 2012).

Harvesting Analysis

To investigate the effects of harvesting on the male component of the red deer population, we simulated the removal of males under 2 scenarios: trophy hunting and uniform culling. For the purpose of this study, uniform culling was defined as the removal of a certain percentage of the population of males, regardless of antler length. In contrast, trophy hunting is a non-random process whereby humans select individuals to be removed based on 1 or several phenotypic traits (Festa-Bianchet 2003, Mysterud 2011). For the trophy hunting simulation, 3 proportions of males with antlers above a threshold length were removed from the population: 10%, 20%, and 50%. We focused on these 3 harvesting values because these are known to represent an unusually low hunting off-take (10%), a threshold above which male red deer population size is known to decrease (20%; Clutton-Brock and Lonergan 1994), and an over-intensive harvest quota (50%; Clutton-Brock and Lonergan 1994, Clutton-Brock et al. 2002). Because trophy-hunting stalkers generally avoid shooting calves and juveniles, we fixed trophy harvest as a decrease in survival rates of individuals >4 years (i.e., adults and seniors).

We implemented the trophy hunting approach by targeting only individuals with antler lengths that were above the mean antler length of antlered deer, which we calculated from the unharvested male population. Accordingly, we multiplied the probabilities of

survival for antler sizes above this threshold by 0.9, 0.8, and 0.5. For each of these, we re-calculated stable antler size distribution and reproductive value from the IPM. We then calculated what harvest rates would have to implemented in the uniform culling approach to obtain identical values of mean antler length and reproductive value as those obtained with trophy hunting. To do this, we obtained values of mean antler length and mean reproductive value for a range of uniform culling rates (0–50%). We then regressed harvest rate against mean antler length, and mean reproductive value and used the resulting equation to derive the required uniform harvest rate values for the whole population of males that have antlers. In addition, we also investigated potential reproductive compensatory responses of smaller antlered males once the biggest trophies were removed through trophy hunting (see Supplemental Material, available online at www.onlinelibrary.wiley.com). To simulate this, we multiplied the probabilities of recruitment of individuals with antler size below the threshold remaining in the population by 1.1, 1.2, and 1.5 respectively. For each of these, we re-calculated reproductive value from the IPM. Finally, we standardized the resulting reproductive value to better represent males' contribution per age group within the population.

RESULTS

Fundamental Functions

Antler length had a positive influence on survival and recruitment rates (Table 1; Fig. 2, rows a & b) with the exception of senior survival rates, which decreased with antler length. Survival in younger age groups (i.e., calves and juveniles) was positively correlated with antler length, although this relationship was stronger in juveniles (Fig. 2a.2). Adults with longer antlers were more likely to survive than those with shorter ones (Fig. 2a.3). For seniors, increasing antler length was associated with a decrease in survival (Fig. 2a.4).

The number of male offspring recruited per adult or senior male followed similar trends across age classes that were reproductively active (i.e., young adults, adults, seniors; Fig. 2, row b). Within reproductive age groups, the probability of recruiting offspring into the population increased with antler length.

Growth, measured as the association between antler length at years t and $t + 1$ (Table 1) showed positive trends (Fig. 2, row c). However, the regression lines crossed the zero-growth line for all age classes, indicating that antler growth rate declines with antler size (Fig. 2). In calves and juveniles, mean antler growth presented great variation around the regression line. For calves especially, mean antler size at $t + 1$ was as much as 35 times the size at t . Regression lines showed a much tighter fit in adults and seniors, reflecting a consistent growth of antlers for these age groups.

The inheritance function is understood as the correlation between father's antler length at siring to offspring antler length when recruited to the population (Table 1). As expected, the slope value for D was close to 0 (Fig. 2, row d).

IPM Demographic Parameters

The stable antler size distribution was characterized by a high proportion of males with small antlers (0–30 cm), representing the high percentage of calves and juveniles that grow small antlers during their first and second year (or do not grow them at all). Representation in the population decreased with antler size (Fig. 3a), with very few individuals possessing antlers over 90 cm. The estimated mean antler length for adult and senescent males was 56.58 cm, which is similar to the average antler size calculated from the raw data (56.08 cm).

The relative reproductive value estimated by the IPM increased in relation to antler size (Fig. 3b). However, the reproductive potential for age groups in which antler length increases rapidly (1–3 years old) showed higher slopes than older age groups at equivalent antler sizes. Thus, the relative reproductive value decreased proportionally in older

individuals (>8 years old; Fig. 3b).

Elasticity Analysis

Population mean antler length and mean reproductive value were sensitive to function parameters (Fig. 4). The upward change in the intercepts and slopes of the survival and growth functions had stronger effects on mean antler length and mean reproductive value than changes in any other function. Both were extremely elastic to changes in juvenile survival parameters (Fig. 4a.1 and b.1); this is not unexpected given that the effect of antler length on juvenile survival was significant. Perturbations to the growth function showed consistent positive effects on mean antler length. Antler length was primarily determined by changes in the adult group (Fig. 4a.2). Mean reproductive value was particularly elastic to perturbed parameters associated with calf and adult antler growth (Fig. 4b.2) and to an upward change in adult parameters for the recruitment function (Fig. 4b.3).

Harvesting Analysis

For simulated trophy hunts of 10%, 20%, and 50% of males with antler length greater than the population mean, the values for mean antler length were 55.90, 55.19, and 53.17 cm, respectively, and corresponded to uniform culling rates of 11.9, 21.5, and 49.5%, respectively. The same trophy hunting resulted in population mean reproductive values of 4.47, 4.20, and 3.42, respectively. These were equivalent to uniform culling rates of 35.3, 53.8, and 72.7%. As expected, the simulation of trophy hunting quotas of 10%, 20%, and 50% in our modified IPM skewed the stable antler size distribution towards individuals with smaller antlers (Fig. 5a). In contrast, changes in mean antler length appeared to be very small.

Under the same harvesting simulation, the relative reproductive value of individuals with antler length above the population mean experienced a rapid decrease (Fig. 5b). The removal of 10%, 20%, and 50% of males in the population also showed proportionally higher relative reproductive value for individuals with shorter antlers (Fig. 5b). Overall, after the

harvesting simulation, the mean relative reproductive value decreased with higher quotas of trophy hunting for adults and seniors (Fig. 6). In addition, we ran an IPM in which we included the compensatory responses of smaller antlered males remaining in the population after harvesting quotas were simulated (see Supplemental Material). However, we found no evidence of a significant effect of compensatory responses (Fig. S1).

DISCUSSION

The demographic consequences of selectively harvesting wild ungulates remain uncertain in spite of trophy hunting being a popular recreational activity worldwide (Milner et al. 2007, Palazy et al. 2011). The literature suggests that harvesting of males in mammals does not affect population dynamics significantly (Mysterud et al. 2002). In other words, the population dynamics of males is determined primarily by the number of females. However, the phenotypic attributes of males in future populations are determined by the reproductive value of males, and the fidelity with which antlers are passed from parents to offspring. In addition, males are typically culled by fee-paying hunters and generate more income than females (Clutton-Brock et al. 2002). Taken together, these insights have led to the suggestion that harvesting of adult male ungulates for antler trophies may represent a sustainable conservation tool. The approach we present here, despite some limitations, has shown how IPMs can be used to gain an understanding of the consequences of hunting on male reproductive value, a measure of relative fitness, and the distribution of antler sizes within the population.

Under unmanaged conditions, the fundamental functions of our IPM revealed, for some age classes, a noteworthy relationship between antler length and key demographic processes. Adults with larger antlers were more likely to survive and recruit individuals into the population, a finding that is consistent with the notion that antler size reflects the health of an individual (Hamilton and Zuk 1982, Andersson 1994, Malo et al. 2005*b*), and confers

higher reproductive success (Clutton-Brock 1988, Andersson 1994, Kruuk et al. 2002). A stag's ability to defend a harem is closely related to its ability to win fights (Clutton-Brock et al. 1979; Clutton-Brock 1981, 1988), and it can be expected that individuals with smaller antlers have a higher risk of being evicted from potential territories, and thus, a reduced probability of holding harems (Carranza et al. 1990), or being injured during rut. Although we exclusively considered demographic processes as influences of antler size, Kruuk et al. (2002) reported the same relationship between antler size and breeding success for males of the same population after accounting for environmental effects. Given these pronounced associations, trophy hunting has the opportunity to impose considerable impact on the male component of the population. However, our study revealed that this was not always the case.

Inheritance in the IPM (i.e., the correlation between the parental trait at age a and the offspring trait at age 1) was low. This function should not be confused with heritability (Coulson 2012). Previous studies have reported that antler size has a low heritability within this red deer population (Kruuk et al. 2002, 2014). It is important to stress that the inheritance function in our study was particularly susceptible to measurement error resulting from the estimation of spike length for some individuals. Additional biases may also have arisen from male calves failing to survive to later ages. However, we do not believe our results to be strongly affected by these potential biases because the responses of mean antler size and reproductive value to changes in the inheritance function parameters were relatively small.

Our results show that mean antler size is highly elastic to parameters in the growth function. This is unsurprising because to evolve a larger or smaller trait, it is necessary to alter how long an individual develops the trait for, or the speed at which the trait develops. In contrast, the reproductive value of individuals was most elastic to the survival function. In a long-lived species like deer, population growth rate, a measure for population-level fitness, is usually most sensitive to survival rather than fertility (Coulson et al. 2004). Similarly, we

report that relative reproductive value and mean antler sizes are sensitive to selective harvesting only when culling rates are as high as 50%. These results suggest that lower levels of trophy hunting are unlikely to have a large effect on key aspects (i.e., survival and reproduction) of hunted populations and are in agreement with conclusions from previous studies (Mysterud 2011, Traill et al. 2014).

We obtained results from a simple model. First, we did not include the female component of our study population. This precluded us from studying aspects of population dynamics in a system that is largely female dominant. Females do not develop antlers and no maternal effects have been found to significantly influence antler size (Kruuk et al. 2002, 2014). Therefore, we did not explicitly model this aspect of our study system. Because of the above, we do not expect our focus on males to be entirely inappropriate.

Our model did not include the effects of density dependence or environmental stochasticity, both of which are known to play important roles in shaping population dynamics (Coulson et al. 2004) and antler development. The nutritional consequences of increased population density are influential in determining antler size in red deer (Clutton-Brock and Albon, 1989, Kruuk et al. 2002, Schmidt et al. 2007). In deer species, habitat quality influences not only the absolute but also the relative size of antlers (Ramanzin and Sturaro 2014), and males are more susceptible to bad weather conditions than females (Pelletier et al. 2012). Selective culling experiments have reported that reductions in female density often lead to increases in male numbers (Clutton-Brock et al. 2002). However, for sexually dimorphic species, it remains unclear whether males are sensitive to either female or male densities, or a combination of both (Bonenfant et al. 2009). Therefore, and because the focus of our study was to investigate purely demographic effects of selective hunting on mean antler length and reproductive value, including density dependence and environmental stochasticity would have limited our ability to attribute our results to hunting exclusively.

Nevertheless, we are aware these are important variables in determining demographic parameters in wild populations and suggest that future models should include them to obtain results more illustrative of the effects of trophy hunting on wild populations of red deer.

MANAGEMENT IMPLICATIONS

Integral projection models offer a powerful tool for understanding the phenotypic and life-history consequences of harvesting (Bunnefeld and Keane 2014, Traill et al. 2014). Our study offers valuable insights into how trophy hunting may influence reproductive value and mean antler size in red deer at unusually high hunting quotas (>50%). Our findings lead us to the tentative conclusion that a trophy hunting rate between 10% and 20% is unlikely to have a substantial impact on mean antler size.

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645 Figures



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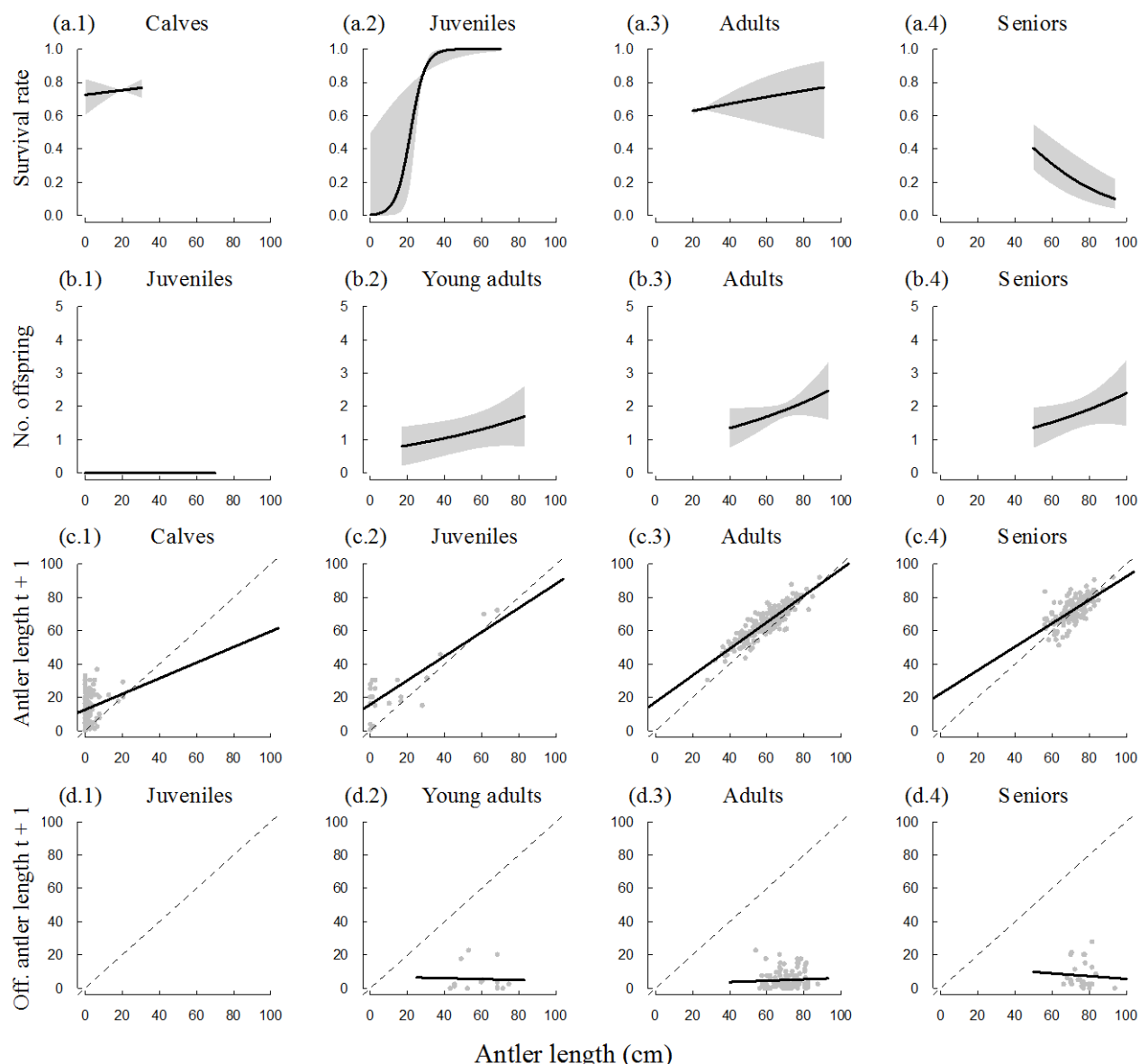
647 Figure 1. Antler length measurements taken for red deer on the Isle of Rum, Scotland, during
648 casting seasons 1972-2012. The white dashed line shows the distance between a) the antler
649 coronet and b) the highest point of the mean beam around the curves.

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655 Figure 2. Relationship between antler length (cm) of red deer on the Isle of Rum, Scotland,
656 1972–2012 and 4 fundamental demographic processes: a) survival, b) recruitment, c) antler
657 growth (antler length at t vs. antler length at $t + 1$), and d) inheritance (as a function of
658 offspring (Off. in row d) antler length at time step $t + 1$). Survival and antler growth age
659 classes consist of calves (0–1 yr), juveniles (2–3 yr), adults (4–8 yr), and seniors (>9 yr).
660 Reproductive and inheritance age groups consist of juveniles (1–3 yr), young adults (4–6 yr),
661 adults (7–11 yr), and seniors (>12 yr). In all panels shaded areas indicate the 95% confidence
662 intervals. In rows c and d, dashed lines represent the $x=y$ function and grey dots the raw data.

Antler length is positively correlated with survival and recruitment, except for senior individuals. Antler growth rate was found to decline with antler size, and no correlation was found between antler length and inheritance. Since juveniles do not reproduce, no relationship was obtained for b.1 and d.1.

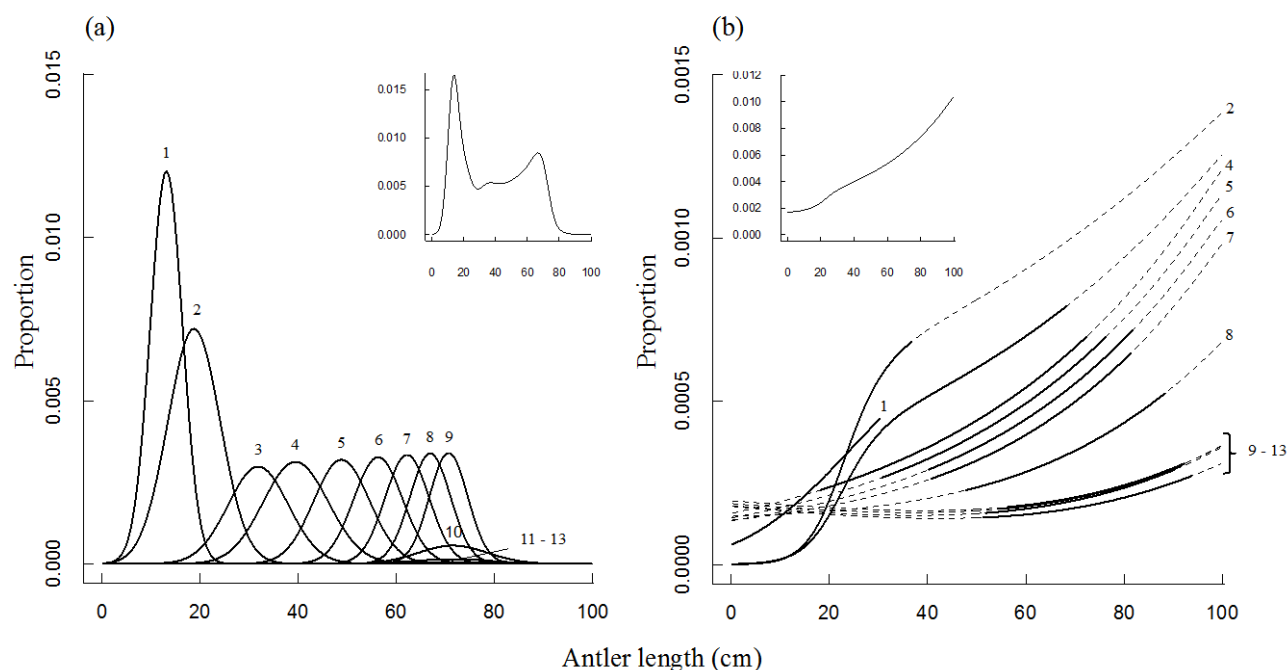


Figure 3. a) Stable antler size distribution (SAD) of antler length per age class for red deer on the Isle of Rum, Scotland, 1972–2012. Each line represents the antler size distribution associated with ages 1 to 13 (see numbered labels). The inset plot shows the additive SAD for the whole population. b) Relative reproductive value (rRV) as a function of antler length per age class. Each line represents the antler size distribution attributed to ages 1 to 13 (see numbered labels). Solid lines denote rRV distributions within age group antler length ranges, and dashed lines represent distributions predicted from the integral projection model for antler lengths out of age group ranges. The inset plot shows rRV for the whole population. The stable antler size distribution is characterised by a high proportion of males with small antlers, and few individuals with antlers over 90 cm. The estimated mean antler length was 56.58 cm. Relative reproductive value increased in relation to antler size, and decreased proportionally in older individuals (i.e. ages classes over 8 years old).

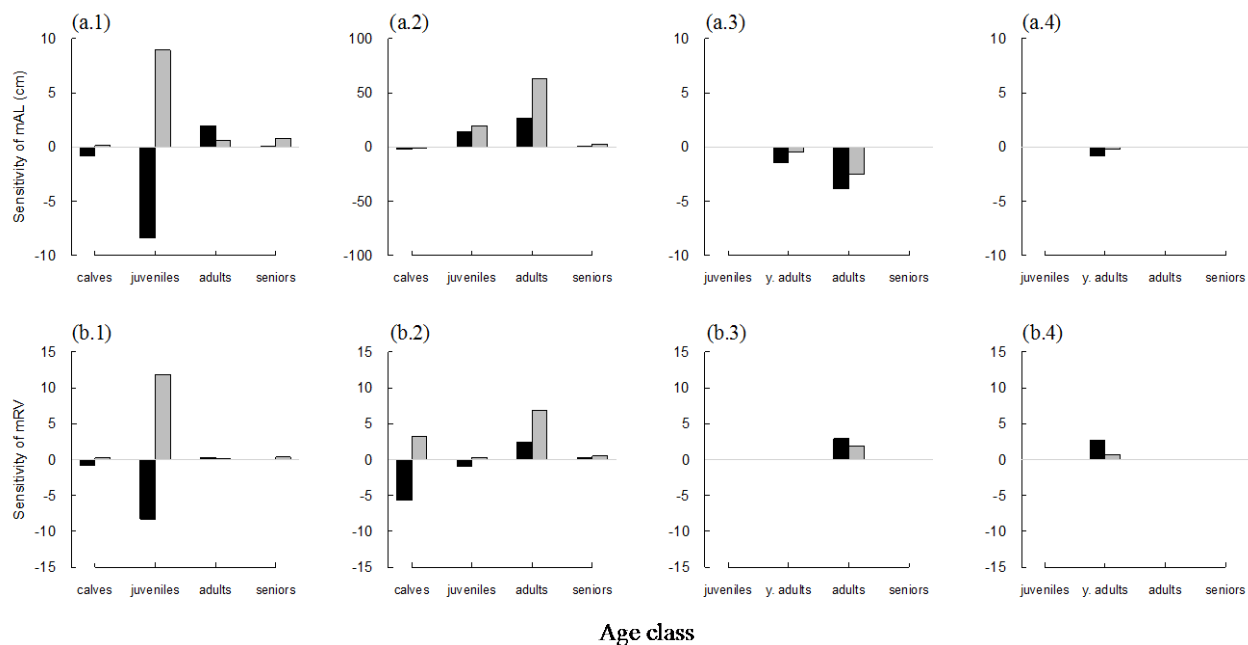
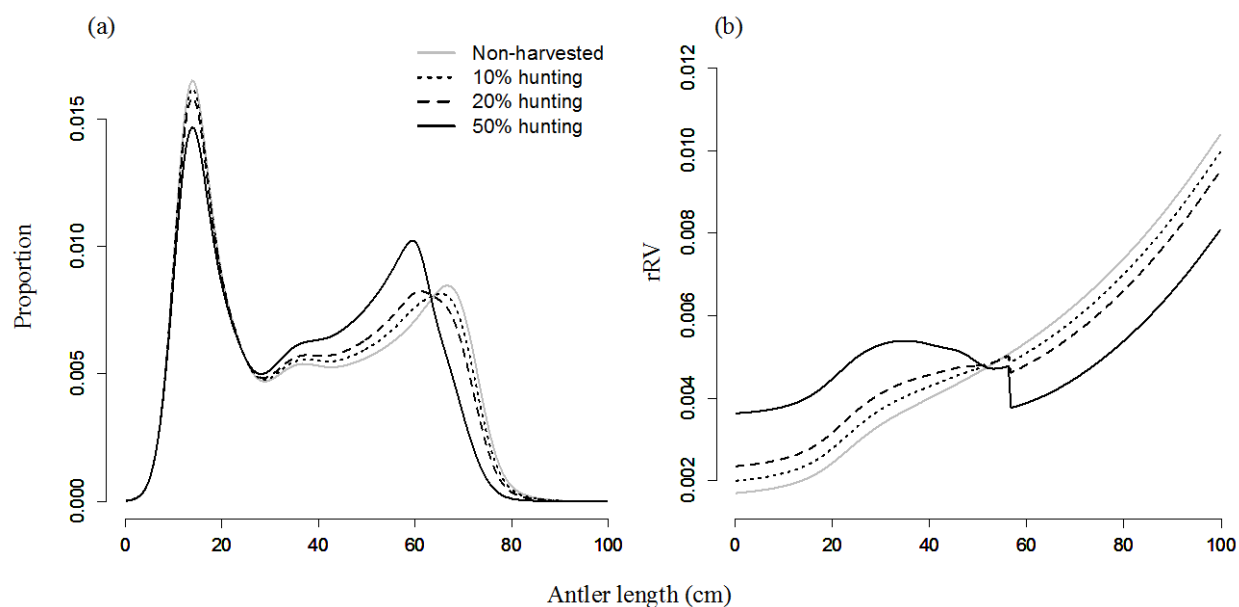


Figure 4. Elasticity of population mean antler length (mAL) and mean reproductive value (mRV) to perturbation of integral projection model function parameters for red deer on the Isle of Rum, Scotland, 1972–2012. Black and grey bars represent the change in mAL or mRV following perturbation to intercepts and slopes, respectively. Age classes for survival (a.1 and b.1) and growth (a.2 and b.2) functions are represented by calves (0–1 yr), juveniles (2–3 yr), adults (4–8 yr), and seniors (>9 yr). Age classes for the recruitment (a.3 and b.3) and inheritance (a.4 and b.4) functions are defined as juveniles (1–3 yr), young (y.) adults (4–6 yr), adults (7–11 yr), and seniors (>12 yr). Survival and growth functions had stronger effects on mAL and mRV than changes in any other function. Although mAL and mRV were elastic to changes in juvenile survival, antler length was determined mainly by changes in the adult group.



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714 Figure 5. Harvesting effects on a) the stable antler size distribution (SAD) and, b) the relative
715 reproductive value (rRV) of male red deer on the Isle of Rum, Scotland, 1972–2012. Grey
716 lines represent a non-harvested population. Dotted, dashed, and full black lines represent
717 trophy hunting regimes of 10%, 20%, and 50%, respectively. No significant change in the
718 shape of either distribution (SAD and rRV) was detected unless 50% of the male population
719 was hunted.

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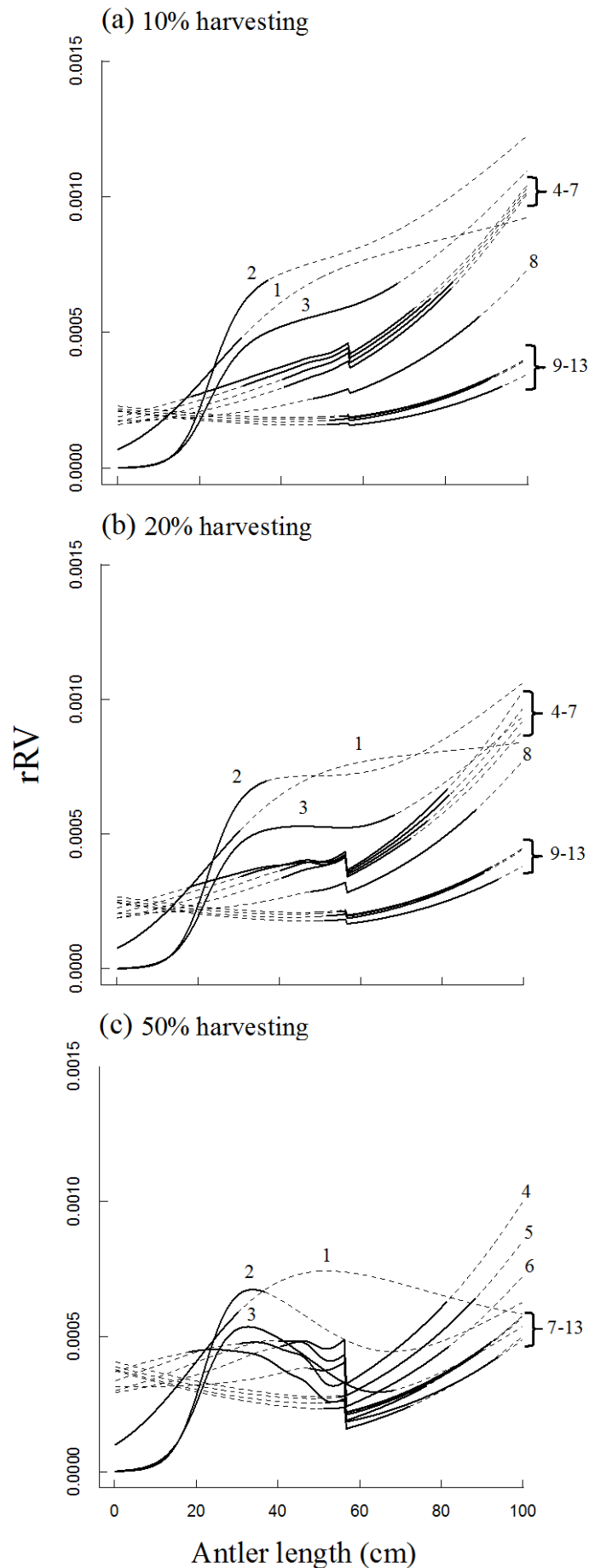


Figure 6. Change in relative reproductive value (rRV) per antler length and age class following different trophy hunting rates for red deer on the Isle of Rum, Scotland, 1972–2012. Numbered lines represent antler size distributions associated with ages 1 to 13. We ran simulations of 10% (a), 20% (b), and 50% (c) of harvesting. Simulation of trophy hunting quotas of 10%, 20% and 50% decreased the rRV for adults and seniors.

Table 1. Summary of model selection with Akaike's Information Criterion (AIC) evaluating relationships of antler length with 4 demographic processes of red deer on the Isle of Rum, Scotland, 1972–2012. The model column indicates explanatory variables included in each fundamental function. Antler length and male age classes are represented by length and age, respectively. Delta AIC (ΔAIC) shows the difference between each model and the best model selected for our analysis. K is the number of parameters considered in each model.

| Function | Model | AIC | ΔAIC | K | Model weight |
|-------------|---------------------|--------|--------------|-----|--------------|
| Survival | length \times age | 5340.1 | 0 | 8 | 0.170 |
| | length + age | 5347.4 | 7.3 | 5 | 0.004 |
| | length | 5520.9 | 180.8 | 2 | 0 |
| | null | 5525.5 | 185.4 | 1 | 0 |
| Growth | length + age | 3320.1 | 0 | 5 | 0.170 |
| | length \times age | 3321.8 | 1.7 | 8 | 0.073 |
| | length | 3338.1 | 18.0 | 2 | 0 |
| | null | 4767.9 | 1447.8 | 1 | 0 |
| Recruitment | length + age | 917.9 | 0 | 5 | 0.170 |
| | length \times age | 920.5 | 2.6 | 8 | 0.046 |
| | length | 953.9 | 36.0 | 2 | 0 |
| | null | 1310.6 | 392.7 | 1 | 0 |
| Inheritance | null | 1098.1 | 0 | 1 | 0.170 |
| | length + age | 1099.2 | 1.1 | 5 | 0.098 |
| | length | 1099.6 | 1.5 | 2 | 0.080 |
| | length \times age | 1102.8 | 4.7 | 8 | 0.016 |

Appendix A: Data Formatting

The data used in this project was individual-based information on males from the red deer population of the Isle of Rum, Scotland. Each row in the dataset corresponded to information of an individually identified male in a particular year of study between 1972 and 2012 (see Table A1 as an example). The information per individual was organized similarly to Coulson (2012).

Table A1. Example of data structure for 2 individuals of male dataset from the Isle of Rum.

| Code ^a | Cast year ^b | Age ^c | Survival ^d | Reproduce ^e | No. males ^f | Antler length (cm) ^g |
|-------------------|------------------------|------------------|-----------------------|------------------------|------------------------|---------------------------------|
| EID01 | 2000 | 9 | 1 | 1 | 5 | 80.4 |
| HRM90 | 2009 | 9 | 1 | 0 | 0 | 70.9 |

^a unique combination of names and numbers to individually identify males from the population.

^b deer year running from 1 August to 31 July that indicates time t at which an individual cast its antlers.

^c an integer representing the year of the male at time t . For instance a calf born in May 2000 (i.e., time t) would be 1 year old anytime after August 2000 (i.e., time $t + 1$). Thus, when the same male cast his antlers in April 2004 (i.e., time $t + 4$), he was considered to be 4 years old.

^d survival of an individual using 1 when a particular male was seen alive, and a 0 when the male was seen dead. This data was gathered between 1 August of year t and 31 July at year $t + 1$.

^e individual denoted with a 1 when it produced a live male offspring and with a 0 when no male offspring were identified for the male at year t .

775 ^f number of male offspring recruited by a single individual at year t that survived to recruit
776 to the population in August of year $t + 1$.

777 ^g the length of antlers (cm) collected during the casting season (Mar–May) at year t .

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