BioOne COMPLETE

Genetic implications of reduced survival of male red deer Cervus elaphus under harvest

Authors: Hard, Jeffrey J., Mills, L. Scott, and Peek, James M.

Source: Wildlife Biology, 12(4) : 427-441

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2006)12[427:GIORSO]2.0.CO;2

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Genetic implications of reduced survival of male red deer *Cervus elaphus* under harvest

Jeffrey J. Hard, L. Scott Mills & James M. Peek

Hard, J.J., Mills, L.S. & Peek, J.M. 2006: Genetic implications of reduced survival of male red deer *Cervus elaphus* under harvest. - Wildl. Biol. 12: 427-441.

We use simple, multivariate evolutionary models to evaluate the short-term potential for size-selective harvest to reduce genetic variability and alter life history in cervids. These genetic effects limit sustainable levels of harvest of the animals because they determine how changes in sex ratio, generation length and traits contributing to fitness influence population growth rate and local adaptation. Our analysis of harvest-mediated adaptive evolution employs a genetic approach that parameterizes models with empirical data obtained from European red deer *Cervus elaphus*. The analysis indicates that harvest, if sufficiently high to reduce the breeding ratio of males to females to below about 15:100, can reduce effective population size to a level that threatens adaptive potential. The reduction in effective size is realized through decreases in both sex ratio of breeders and the age of breeding males. Predicted selective effects of harvest on body size indicates a weak potential to alter most life-history traits over 10 generations under two harvest scenarios; the patterns suggest that current modes of harvest are unlikely to produce substantial life-history changes in red deer over 10 or fewer generations unless the genetic influences on red deer traits are considerably higher than those predicted here. Nevertheless, male reproductive success is expected to decline detectably if male harvest rate is sufficiently high (> 30%). Collectively, our results imply that harvest methods should permit higher post-hunt male:female ratios (18:100 or higher) and ensure that a sufficient number of larger, older males survive the breeding season. The capacity of selective harvest to alter demography and life history depends heavily on the genetic covariance structure underlying variation in these traits, information that is unknown for many red deer populations. Prudent harvest management should therefore implement and monitor approaches to hunting that aim to conserve life-history variation; meanwhile, use of less selective methods can reduce the risk to long-term adaptive potential and may permit higher sustainable harvest rates.

Key words: Cervus elaphus, effective population size, elk, fitness, harvest, quantitative genetics

Jeffrey J. Hard, Conservation Biology Division, NOAA/NMFS Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington, 98112, USA - e-mail: jeff.hard@noaa.gov
L. Scott Mills, Wildlife Biology Program, University of Montana, Missoula, Montana, 59812, USA - e-mail: scott.mills@cfc
James M. Peek, Department of Fish & Wildlife Resources, University of Idaho, Moscow, Idaho, 83844, USA - e-mail: peek@uidaho.edu

Corresponding author: Jeffrey J. Hard

Received 30 April 2005, accepted 20 October 2005

Associate Editor: Atle Mysterud

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Red deer and wapiti *Cervus elaphus* populations respond readily to changes in density and environment. Attributes that vary include differences in survival by sex (Peek et al. 1967, Flook 1970, Kruuk et al. 1999, Clutton-Brock et al. 2002), antler size (Schmidt et al. 2001, Kruuk et al. 2002), body size (Lowe 1969, Yoccoz et al. 2002), and production and survival of young (Coughenour & Singer 1996, Taper & Gogan 2002). Harvest management is a major means by which density and survival are altered in this species.

Harvest management varies extensively for red deer and wapiti. Unrestricted numbers of hunters, or limited entry seasons of varying lengths for both sexes or only for males occur in many areas in western North America (Connelly et al. 2005). Limited entry seasons with hunter participation determined by lottery are common in areas where wapiti populations are highly accessible or small enough to require restriction of hunting activity. Emphasis is given to retaining as much recreational opportunity for as many hunters as possible in most North American harvest regimes. Hunting regimes in Europe are generally more highly regulated with more emphasis given to retention of adult males and culling of females or younger males to limit population size, maintain physical condition, and trophy quality (Ueckermann 1987, Clutton-Brock et al. 2002).

Concern over harvest regimes that reduced male survival to sex ratios of < 5:100 was prompted by observed declines in calf production and survival in North America (Noyes et al. 1996). Surveys of populations where sex ratios were > 5:100 did not find correlations between calf survival and low sex ratios (White et al. 2001, Hamlin & Ross 2002). The observed changes are reversible by altering harvests to increase the proportion of males in populations and to reduce population density (Langvatn & Loison 1999).

Nevertheless, Hartl et al. (1991) reported differences in allele frequencies among red deer populations managed under different harvest regimes. Small, isolated populations may show differences in genetic structure (Kuehn et al. 2003) that may be accentuated by harvest regimes that cause differences in survival of the sexes. While there may be a demographic advantage from skewing a sex ratio toward more breeding females if no adverse physiological or behavioural changes accompany the skew (Caughley 1977, Ginsberg & Milner-Gulland 1994, Noyes et al. 1996), there are potential detrimental effects of sex-based harvest on genetic structure (Scribner et al. 1985). By reducing the proportion of males among breeding adults through harvest, the effective population size (N_e) can be reduced, thereby making a small and isolated population more susceptible to effects of genetic drift (Harris et al. 2002). For example, Briton et al. (1994) demonstrated in a model fruit fly *Drosophila melanogaster* system that a skewed sex ratio will increase inbreeding (the increase in homozygosity from matings among relatives), decrease heterozygosity and decrease relative fitness. Furthermore, Mills & Smouse (1994) reported that the reduced fitness that accompanies inbreeding depression can substantially decrease population persistence in mammals over a range of inbreeding costs, starting population sizes, and population growth rates (see also Frankham 1995b).

The evolutionary consequences of harvest include loss of genetic and genetically based phenotypic diversity and loss of fitness through changes in adaptive characteristics. Loss of genetic and phenotypic diversity may involve characters that are neutral (i.e. largely transparent to natural selection) or those that contribute to adaptation (e.g. most life-history traits; Harris et al. 2002).

The most compelling empirical evidence for genetic consequences of selective harvest comes from fisheries (reviewed in Law 2000, Essington 2001, Ashley et al. 2003, Hard in press). In many fisheries, the largest fish are most valuable, and several gears and regulatory mechanisms (e.g. net mesh size and minimum size thresholds) tend to favour capture and retention of larger fish (Law 2000, Hard in press). Thus, selection on size in such fisheries can lead to evolution of smaller mean fish size through the inheritance of size and age in progeny of smaller, younger individuals (Conover & Munch 2002, Hard 2004). Coupled with often marked demographic effects, reductions in fish size from harvest can have correlated effects on traits that affect population growth, such as earlier age at maturity (Hard 2004, Olsen et al. 2004), depressed growth rates of larvae and juveniles (which can expose immature individuals to higher predation), and decreased egg sizes (Conover & Munch 2002).

Such patterns may also result from harvests of terrestrial mammals. Hartl et al. (1991) reported that selection for large body size, large number of antler points and against yearling males with small spikes was related to differences in length and intensity of the hunter harvest. Changes in the length of main beam of antlers were also noted. Selective hunting led to changes in allele frequencies and could lead to the loss of rare alleles (see also Malo et al. 2005).

Assuming that the number of antler points in elk follows polygenic inheritance, Thelen (1991) used a simple stochastic model of harvest of antlered males to hypothesize that the yield of trophy animals would decline over time if male harvest was sufficiently high, even as overall yield increased. Selective harvest for trophy rams from an isolated mountain sheep *Ovis canaden-*

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

sis population led to selection for lighter and smaller-horned rams (Coltman et al. 2003); it is not yet known whether this selection will also yield changes in genetically correlated traits (e.g. female body weight, calving rate or disease resistance).

As in other exploited species, genetic variability and long-term adaptive potential in cervids can be affected by breeding population size, aspects of mating structure such as the proportions of males and females breeding, harem size of dominant males, generation length and adult longevity (Ryman et al. 1981, Martinez et al. 2002, Mysterud et al. 2002, Wade & Shuster 2004). Harvest will change the characteristics of the breeding population by skewing the sex ratio of breeders and reducing adult longevity. Both factors can reduce effective population size, which estimates how rapidly genetic variation is lost and inbreeding accumulates within a population. An undivided population of a given size achieves its maximum N_e when the number of males and females is equal and there is no variance among parents in number of progeny; N_e is reduced when the breeding population fluctuates in size, the adult sex ratio deviates from 1:1, or the variance in reproductive success is elevated. Differing generation lengths of males and females can contribute to each of these conditions, which are common to red deer. Overlapping generations, also the case for red deer, make predicting the consequences of these situations for adaptive potential more difficult (Lande & Barrowclough 1987).

We provide an evaluation of two simple harvest scenarios, described below, to illustrate how size-selective harvest can affect genetic and phenotypic diversity in red deer populations. We adapt models of phenotypic evolution, parameterized with genetic and phenotypic data from studies of antlered game, to address two questions: 1) How do changes in life-history characteristics of red deer induced by harvest influence effective population size? 2) Is selective harvest likely to change life-history characteristics of red deer over time frames of primary concern to managers? In addressing these questions, we hope to illuminate key factors that reduce the sustainability of harvest management strategies and to identify alternatives that can minimize adverse genetic consequences.

Material and methods

Effective population size

Simple models developed by Nunney (1993), based on Wright (1938), assess the dynamics of N_e under population changes that could be affected by harvest. These models (Appendix I) of a single, isolated population incorporate the harem polygyny breeding structure of red deer. This breeding structure is one of the most spectacular departures from a random mating model, and the consequences for sex ratio and variance in reproductive success (especially of males) reduce N_e. Nunney (1993) showed that for many organisms with overlapping generations under harem polygyny, the ratio of N_e/N (where N is the census size) is expected to be about 0.5 over a wide range of sex ratios, generation lengths, and variance in reproductive success (but see Kuehn et al. 2003 for a counter-example in red deer).

Nunney (1993) assumed that survival and fecundity are independent of age and that all animals mature at the end of their first year. We varied survival with age according to empirical data but used mean fecundity for all ages; we also allowed for older ages at first maturity in parameterizing the models. In applying these models to red deer, we assumed that the variation in sex ratio was due to a bias in survival to adulthood rather than a bias in sex ratio at birth; although Clutton-Brock & Iason (1986) suggested that significant variation in birth sex ratios can occur, Kruuk et al. (1999) and Bonenfant et al. (2003) did not detect such variation. For elk, Flook (1970) and Peek et al. (1967) reported minor differences in sex ratio at or near birth; for red deer, Clutton-Brock et al. (1982) reported no significant deviation from parity except for hinds > 12 years of age. The differences were considerably smaller than those related to survival. Nunney's (1993) equations compute changes in N_e under varying conditions of generation time, sex ratio and harem size. Assumptions are that a) all mature females mate once per season; b) the harem bull does the breeding; c) mean generation length is the sum of mean age at maturity and mean adult reproductive lifespan (computed for each sex and then averaged); d) the sex ratio can be computed from the ratio of mean male reproductive lifespan to twice the mean adult reproductive lifespan; and e) harem size is a simple function of the proportion of females breeding during the season, the proportion of males among adults, and the proportion of

Table 1. N_e model parameter values employed for red deer. Longevity refers to reproductive lifespan.

Parameter	Values
Annual adult male survival	0.87
Annual adult female survival	0.85
Mean male longevity (SD)	3.1 (1.0)
Mean female longevity (SD)	6.4 (1.0)
Male age at maturity	6.2
Female age at maturity	4.0

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

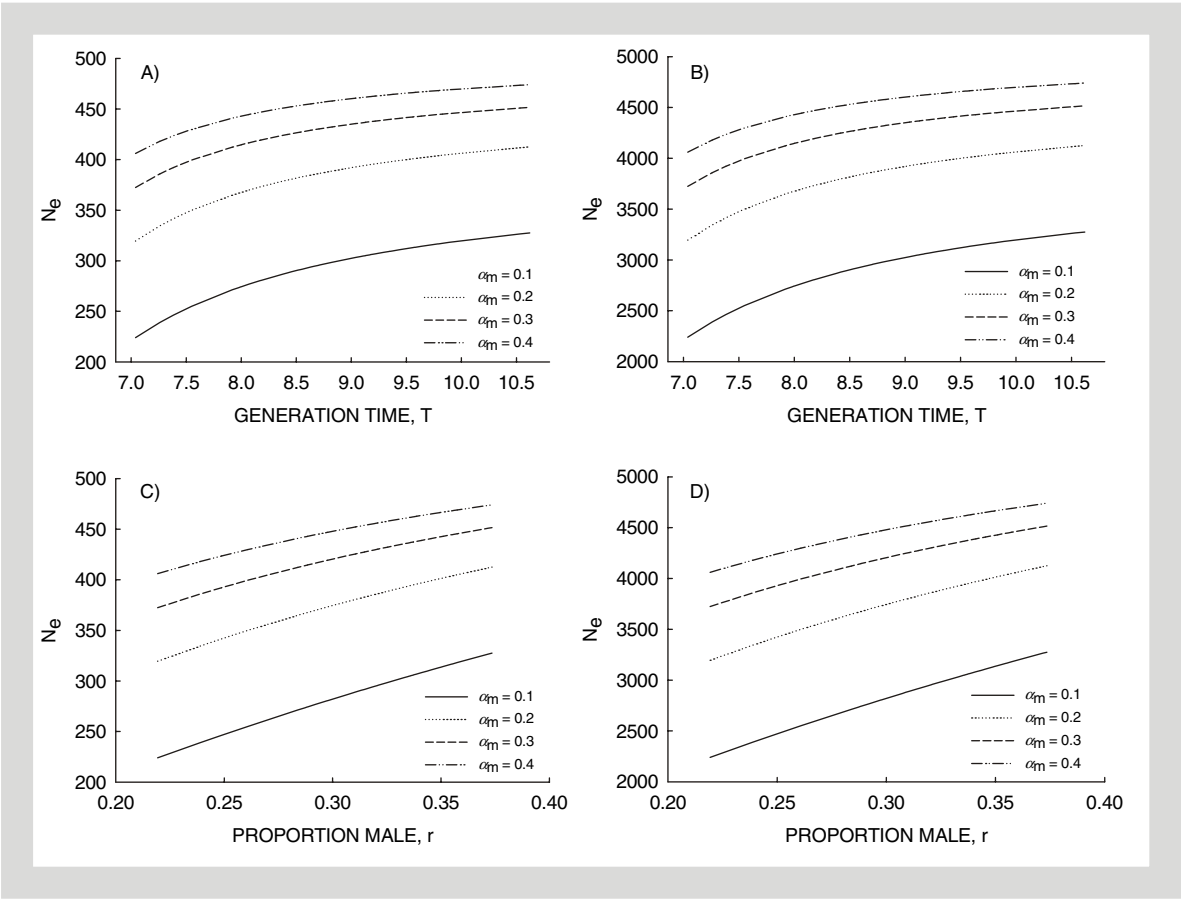


Figure 1. Effective population size, N_e, as a function of mean generation length for red deer populations of 1,000 (A) and 10,000 (B) breeding individuals under four proportions of harem-holding males (α_m). These proportions increase from 0.1 to 0.4 in increments of 0.1. Sex variation in survival is assumed. N_e as a function of sex ratio (i.e. male proportion) for red deer populations of 1,000 (C) and 10,000 (D) breeding individuals under four proportions of harem-holding males (α_m). These proportions increase from 0.1 (bottom curve) to 0.4 (top curve) in increments of 0.1. Sex variation in survival is assumed.

males that breed during the season, and their age structures (Bonenfant et al. 2004). We varied the male proportion from 0.1 to 0.6, and normal distributions of harem sizes, adult reproductive lifespans, and sex ratios were generated from these parameters (Table 1, Fig. 1). We based our simulations on a census size, N, of 1,000 adults, unless otherwise indicated. The simulation results are not very sensitive to changes in census size unless they are much larger or smaller (J.J. Hard, unpubl. data).

Because N_e is difficult to estimate in natural populations and age structures are often not available, considerable attention has focused on the N_e/N ratio as a means of estimating N_e from census data (e.g. Kalinowski & Waples 2002, Waples 2002). We used Nunney's (1993) model to compute this ratio from data for mean harem size, mean maturation age, reproductive lifespans of males and females and adult sex ratio.

Effects of selective harvest on size and correlated traits

We investigated short-term evolutionary effects of size-selective harvest on red deer by incorporating into a model of phenotypic evolution estimates of genetic and phenotypic parameters from the Isle of Rum (Scotland) red deer population (provided by Kruuk et al. 2000, 2002). The model predicts responses of correlated traits to size-selective harvest. Other models, notably those developed by Barton & Turelli (1991) and Kirkpatrick et al. (2002), provide more comprehensive means to predict evolution of polygenic characters under selection, and they incorporate the potential to evaluate a more comprehensive suite of factors that influence inheritance, including allelic interactions within and among loci, linkage and cytoplasmic inheritance. In this paper we use a simple additive genetic model because of the lack of empirical estimates for many of these factors, and be-

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

cause most quantitative genetic investigations of harvest-induced selection have employed this approach. Our objective was to determine whether size-selective harvest could produce appreciable short-term responses in body size and other red deer life-history characters that are likely to affect productivity, based on applying empirical genetic data to functional relationships based on a predictable mode of inheritance.

For the simple additive model, we used genetic and phenotypic variance component estimates to parameterize a set of equations determining multivariate response to directional selection (see Appendix I). An age- or stage-structured model (Law 1991, Charlesworth 1994) was not feasible because insufficient genetic and phenotypic data existed to parameterize such models (see Hard 2004 for a counterexample). We therefore relied on a discrete-generation form of the classic multivariate breeder's equation (Lande 1979, Falconer & Mackay 1996) relating mean phenotypes in generation t to the genetic (**G**) and phenotypic (**P**) covariance matrices and the vector of selection differentials resulting on each trait from harvest in generation t (Hard 2004, in press). We assumed that the covariance matrices and vector of selection differentials were constant over the number of generations simulated (10). To determine the selection differentials on the traits, we assumed that traits were subject to natural stabilizing selection with the mean trait value representing the selective optimum and fitness decaying weakly with deviation of the mean from this value; we computed the width of the fitness curve as 3-4 phenotypic standard deviations, based on published selection studies (Hoekstra et al. 2001, Kingsolver et al. 2001, Merilä et al. 2001). We assumed an annual harvest rate of males of 30%, based on estimates obtained from European red deer and North American wapiti. Equations for calculating selection differential on and fitness corresponding to each trait were taken from Law (1991) and Hard (2004).

For each trait, we computed the selection differential on red deer size (using leg length as a proxy for body size; Table 2), under the assumption that mean size in a cohort represents the mean size of its members susceptible to harvest. We estimated the correlated selection differentials on the means of the other traits from the relation of the phenotypic covariance between each pair of traits to the phenotypic variance of length (Falconer & Mackay 1996). For each trait, we calculated the fitnesses, selection differentials and responses to selection for males and females separately; we then combined these values to determine overall population responses.

Table 2. Means, standard deviations (SD), heritabilities ($h^2 \pm SE$), and correlations with fitness (r) for Isle of Rum red deer. Data are from Kruuk et al. (2000, 2002) in which descriptions of these terms can be found. Antler weight data (approximate mean and SD) are standardized to age seven; the heritability is age-corrected. Total fitness is expressed as lifetime reproductive success (LRS).

Trait	Mean	SD	h^2	SE(h^2)	r
Females					
Total fitness (LRS)	2.91	3.57	0.00	0.06	1.00
Adult breeding success	5.18	3.31	0.00	0.00	
Longevity	6.42	5.93	0.00	0.05	0.95
Adult longevity	11.52	3.85	0.00	0.00	
Fecundity	75.82	14.05	0.46	0.15	0.23
Age at first breeding	4.00	0.76			
Birth weight, kg	6.38	1.22	0.25	0.07	0.16
Leg length, mm	186.49	7.82	0.37	0.17	0.21
Males					
Total fitness (LRS)	2.09	5.57	0.02	0.06	1.00
Adult breeding success	6.45	8.25	0.08	0.08	
Longevity	3.14	3.27	0.01	0.09	0.61
Adult longevity	10.55	2.54	0.00	0.00	
Maximum annual breeding success	3.70	3.36	0.10	0.16	0.83
Age at first breeding	6.24	1.55	0.19	0.30	0.30
Birth weight, kg	6.69	1.24	0.11	0.07	0.18
Leg length, mm	193.57	7.73	0.07	0.14	0.43
Antler weight, g	~700	~165	0.33	0.12	-0.11

Genetic variation in life-history traits

The estimates of trait means and variation used to parameterize the model are summarized in Table 2; these estimates are from Kruuk et al. (2000, 2002). These assumptions reflect the typically low heritabilities for morphometric and life-history traits in wild populations. Kruuk et al. (2000, 2002) estimated genetic variances and heritabilities using maximum-likelihood methods with a mixed ('animal') model. An important advantage of this model is that it provides unbiased estimates of the parameters even in situations where family structure is unbalanced and the resulting covariance matrices are sparse (Shaw 1987, Hard et al. 1999), which is often the case for pedigrees of natural populations.

Unfortunately, Kruuk et al. (2000, 2002) provided few estimates of phenotypic or genetic covariances among the traits. Therefore, to employ these genetic data we estimated the phenotypic correlation between traits x and y (r_{xy}) as the product of the correlations of each trait with fitness (which Kruuk et al. did estimate), measured as lifetime reproductive success and the corresponding covariance (cov_{xy}) as $r_{xy} \cdot \sqrt{(var_x \cdot var_y)}$. We computed the genetic variance for each trait *x* as the product of the trait's heritability (h^2_x) and its phenotypic variance (var_x). We computed the genetic covariance between traits x and y as $\sqrt{h^2_x} \cdot \sqrt{h^2_y} \cdot cov_{xy}$.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

We used these variances and covariances in one scenario to seed the phenotypic and genetic covariance matrices in the selection model. One limitation of this method is that it does not allow for negative genetic correlations in the presence of positive phenotypic correlations (which are possible for any pair of traits), so the responses to selection predicted by the model are likely to be overestimated. In another scenario intended to evaluate the sensitivity of responses to higher heritabilities for female life-history characters and a tighter covariance structure, we assumed a heritability of 0.2 for each life-history character, a heritability of 0.5 for each morphometric character, and phenotypic and genetic correlations between traits estimated as described above.

Results

Effects of generation length and sex ratio on N_e

The effects of generation length on N_e are depicted in Figure 1, assuming census sizes of either 1,000 or 10,000 individuals, sex variation in adult survival, and varying proportions of males participating in breeding. These plots indicate that N_e declines monotonically with mean generation length, and more sharply as generation length declines below eight years. For harem polygyny, this pattern appears to reflect increasing variance in male reproductive success with decreasing generation length. For equivalent values of generation length, N_e tends to increase with the proportion of males holding harems, reflecting the substantial effect that variability in male reproductive success has on N_e. If generation length is very short, N_e may decline below 200 in a population of size 1,000, a value which could jeopardize long-term persistence (e.g. Mace & Lande 1991). When mean generation length is as low as seven years, N_e may be as low as 200 to 400, depending on variance in male reproductive success. An N_e of 350 for a population of 1,000 adults would correspond to a rate of loss of genetic variation per generation due to random genetic drift of 0.14%.

The effects of sex ratio on N_e, assuming sex variation in adult survival and under varying proportions of males participating in breeding, indicate that N_e declines monotonically with sex ratio, and becomes quite low as the proportion of males in the adult population approaches 0.2 (see Fig. 1). As in the case for variation in mean generation length, N_e increases with the proportion of males holding harems for a given sex ratio. Again, this pattern illustrates the substantial effect that variance in male reproductive success has on N_e. If the adult sex ratio is highly skewed toward females, N_e may decline below 200 in a population of size 1,000, if the proportion of males breeding is small. Assuming a sex ratio during the rut of 0.20, N_e for a population of 1,000 animals would vary between about 200 and 400, depending on the proportion of males holding harems. Harvest of males that results in an adult sex ratio during the rut much below this value will reduce effective size considerably by increasing variance in male reproductive success.

Effects of generation length and sex ratio on the N_e/N ratio

The effects of generation length and sex ratio on the ratio of N_e to the number of adults are summarized in Figure 2, for proportions of males holding harems of 0.1-0.6. Although the N_e/N ratio has no expected range (Nunney

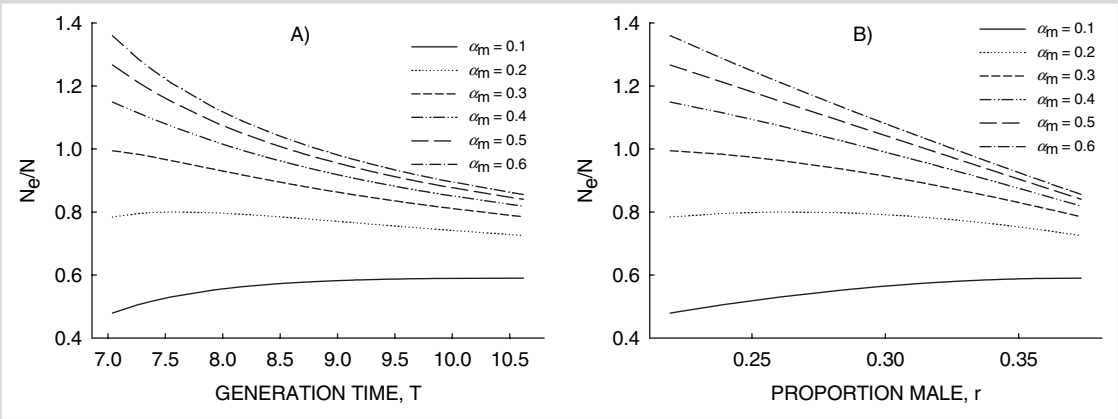


Figure 2. Ratio of N_e/N as a function of generation length (A) and sex ratio (B) for a red deer population under varying proportions of harem-holding males (α_m), from 0.1 (bottom curve) to 0.6 (top curve) Sex variation in survival is assumed. Note that N is not constant in these scenarios (see text).

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

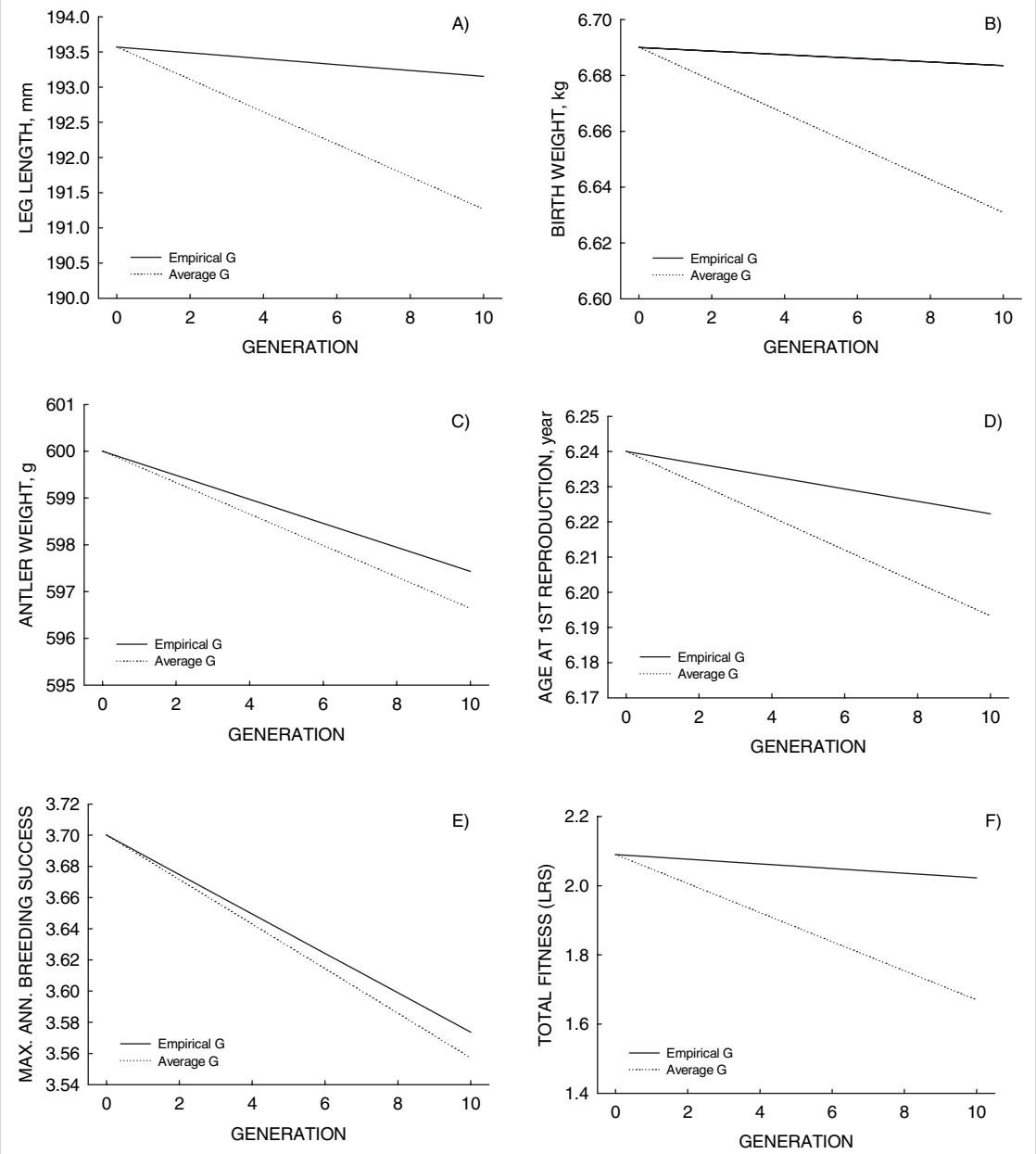


Figure 3. Simulated trajectories over 10 generations of means in the selected quantitative traits leg length (A; in mm), birth weight (B; in kg), antler weight (C; in g), age at first reproduction (D; in years) maximum animal breeding success (E) and total fitness (F) expressed as lifetime reproductive success (LRS) for male red deer under weak size-selective harvest assuming the empirical values in Table 2 (empirical G; ——) or assuming heritabilities for morphometric traits of 0.5 and for life-history traits of 0.2 (average G; ----).

1993), it generally varies from 0.1 to 0.5 in natural populations (Mace & Lande 1991, Frankham 1995a). The plots indicate that, if < 20% of males hold harems, the N_e/N ratio will not exceed 0.8, regardless of the generation length. The ratio declines more rapidly if the proportion of males holding harems is below 0.2 and generation length is below about eight years. If a small minority (~ 10%) of males holds harems, the N_e/N ratio is also rarely expected to exceed 0.6, regardless of the breeding sex ratio. The N_e/N declines rapidly if the sex

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

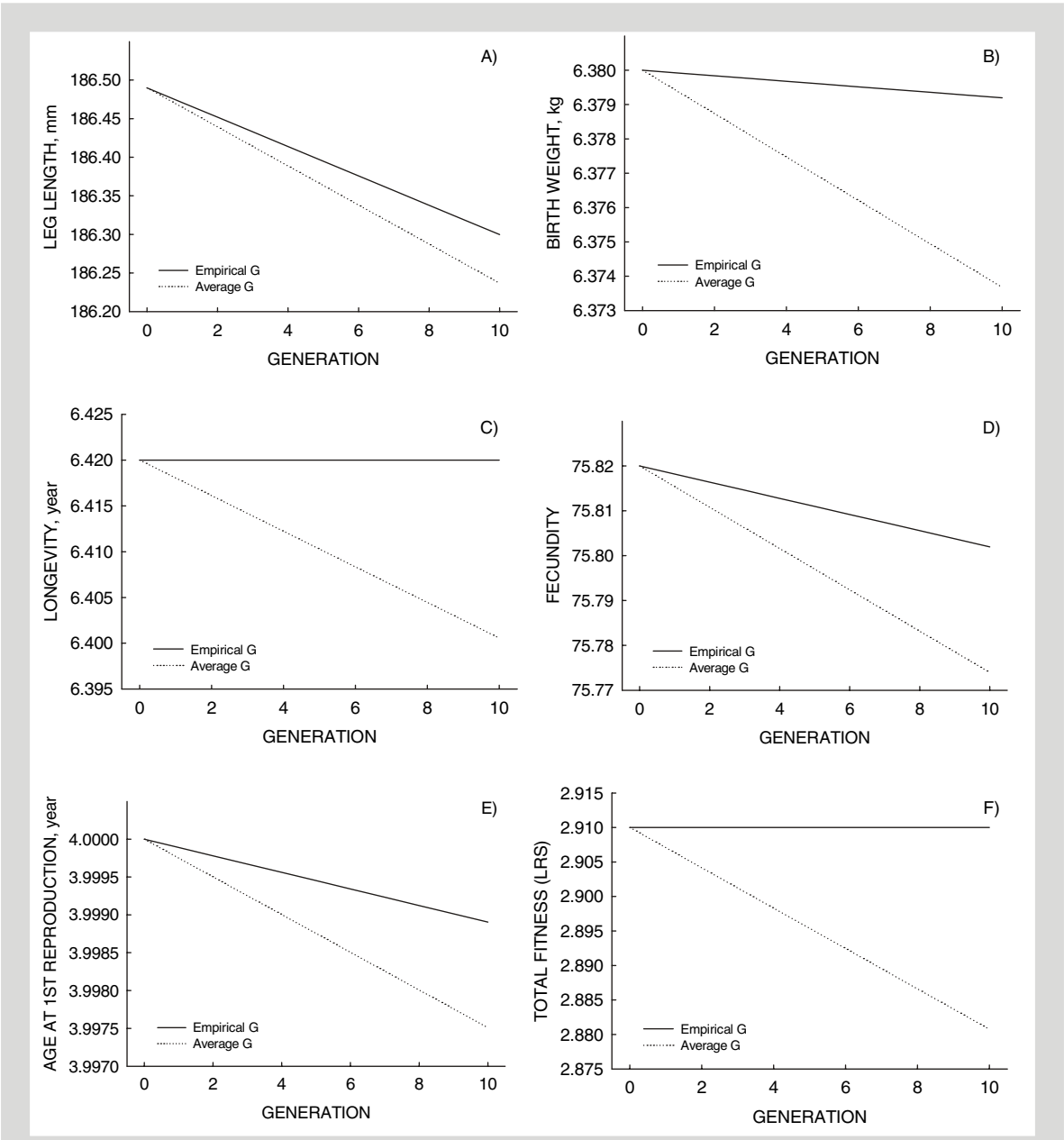


Figure 4. Simulated trajectories over 10 generations of means in the selected quantitative traits leg length (A; in mm), birth weight (B; in kg), longevity (C; in years), fecundity (D), age at first reproduction (E; in years) and total fitness (F) expressed as lifetime reproductive success (LRS) for female red deer under weak size-selective harvest assuming the empirical values in Table 2 (empirical G; ——) or assuming heritabilities for morphometric traits of 0.5 and for life-history traits of 0.2 (average G; ----).

ratio declines much below 0.2 (20 males:80 females, or 25 males:125 females), and if the proportion of males holding harems is below 0.1. Figure 2 indicates that the N_e/N ratio can increase at shorter generation lengths or lower proportion of males if the majority of males are holding harems, due to increasing participation of younger males in breeding and to reduced variance in male reproductive success. However, these relationships do not reflect a constant N; the N_e/N ratio is increasing in these situations because the total census size is decreasing more rapidly than is effective size. For a particular value of N, N_e always declines with declining generation length or deviation of the adult sex ratio from 1:1 (see Fig. 1).

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Responses of life-history traits to selective harvest

Based on the simulation modeling, the effects of size-selective harvest (male harvest rate of $1-\theta = 0.3$, with a threshold size for harvestable animals 1 SD above the mean; female harvest rate = 0.05) on red deer fitness and correlated life-history traits over 10 generations are summarized in Figures 3 and 4. With some notable exceptions, the results under either of the two scenarios modeled (empirical **G**, the **G** estimated from empirical heritabilities and correlations as described in the methods and shown in Table 2; average **G**, the **G** estimated as described in the methods) predict minor declines in the traits under weak directional selection imposed on size by a male harvest rate of 30%. The greatest effects are expected in maximum annual male breeding success and total male fitness, which are predicted to decline by 2 and 3.2%, respectively, if **G** reflects empirical values. If **G** reflects average values, at this harvest rate appreciable declines in male traits are predicted within 10 generations in longevity (3.1%), male adult breeding success (3.9%), maximum annual breeding success (2.7%), and total fitness (20.1%). Male antler weight is predicted to decline by < 1% over 10 generations. Under this harvest scenario, females are expected to show a decline in total fitness of at most 1% over 10 generations (see Fig. 4).

As expected, trends are more pronounced under a higher harvest rate, even if harvest is no more selective on size. For example, a harvest rate of 50% on males is expected to yield a decline in adult breeding success of > 5% and in total fitness of > 28% within 10 generations. Lower harvest rates on males produce smaller projected trends (data not shown), but trends in all reproductive traits remain downward, implying that even low harvest rates could depress productivity and fitness if population growth rate is already low.

Discussion

Sustainable harvest strategies result from consideration of both long- and short-term consequences of harvest practices. Harvest has the potential to alter the genetic and phenotypic characteristics of red deer populations as well as change fitness and population growth (Hartl et al. 1991, Harris et al. 2002; but see Kruuk et al. 2002). Harvest practices that sharply reduce adult longevity or skew adult sex ratios heavily toward females should be avoided because they may appreciably increase loss of genetic variability due to stochastic processes. Wedekind (2002) found that the demographic benefit of skewing toward females could increase the short-term population growth rate enough to prevent an immediate decrease in N_e; however, the models Wedekind (2002) used did not include any negative feedback (inbreeding depression or loss in adaptive traits) arising from the low initial N_e in the skewed populations.

The modeling results outlined here indicate that effective population size is nearly half the census size for red deer over a relatively wide range of generation lengths and adult sex ratios, but that N_e drops sharply at short generation lengths or adult sex ratios strongly skewed towards females. Therefore, variation in reproductive success, particularly of males, would be valuable information to monitor in managed red deer; if tissue samples from identifiable animals can be obtained, this variation could be measured quantitatively. Under an assumption of an isolated population, the model predictions are optimistic, as they do not account for all the annual variance in reproductive success in red deer. Gene flow from other metapopulation subunits would offset these losses of genetic variation to some degree, especially if dispersal involved older harem-holding males. Nevertheless, the potential consequences of low N_e for a population's ability to respond to future environmental challenges are serious, especially for small, relatively isolated populations. Over the short term, the reduction of effective population size due to harvest of older males could, in small populations, increase the demographic effects of inbreeding depression and thereby decrease the probability of population persistence (Mills & Smouse 1994).

Different population characteristics and environmental conditions will produce different demographic trajectories, and the interaction of factors such as starting population size, environmental variation and inbreeding cost on population growth rate make it impossible to give a single number for an optimal sex ratio in a management context. Also, the consequences of sex-ratio variation that might arise in natural populations from sex-ratio bias at birth and subsequent mortality (Flook 1970, Clutton-Brock & Iason 1986) is not considered, although this phenomenon is seldom reported for red deer. The findings reported here demonstrate potential disadvantages to red deer population growth that could arise from strongly skewing the male sex ratio in a relatively small, isolated population.

The modeling results imply that harvest management should strive to maintain at least a few older breeding males, perhaps 10-20% of all breeding males, in exploited populations. This is particularly important for smaller populations. Harvest regimes that drive mean age of males below three years or sex ratios below approximately 0.15 (18 males:100 females) should be avoided because they are likely to lead to evolutionary changes that

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

can reduce population viability in the short term, especially if the proportion of harem-holding males is low (< 20%). It should be kept in mind that these results assume that males successful in breeding each year are chosen at random from the population; the models do not account for annual variation in individual male breeding success, which has been documented (Clutton-Brock & Albon 1989, Rose et al. 1998). Consequently, the model underestimates the reductions in N_e that result from a decline in mean breeding age.

The selective harvest model indicates that size-selective harvest can alter mean values of life history traits affecting reproductive fitness, but the results depend heavily on genetic information that has not yet been published for most red deer populations (i.e. genetic and phenotypic covariance structures). That correlations among traits can influence response to selection has long been understood by plant and animal breeders, and in some cases this influence may be considerable. Consequently, our results should be viewed as initial approximations of consequences of harvest on demographics and morphology of red deer and are essentially hypotheses to be tested. The red deer data used in the model indicate that, in general, expected trends in adult size and reproductive traits are weak over 10 generations. However, trends in male lifetime reproductive success over this period may reach a loss of 3-20%, given the genetic parameters evaluated here.

Our results appear to contrast with the analyses of Coulson et al. (2003), who detected significant changes in early life-history traits of red deer on Rum occurring over three decades in the absence of hunting pressure. They attributed these changes to environmental variation acting on population characteristics largely through climate and deer density, and showed that the genetic covariance among traits is an important element of such changes. Our results, we believe, point to the importance of analyses like those of Coulson et al. (2003); indeed, such environmental factors are likely to mask any effects of harvest similar to the scenarios modeled here. In light of our work, the modeling results highlight the value of parameterizing the phenotypic and genetic covariance matrices (**P** and **G**, respectively; see Appendix I) with empirical variance and covariance data. They identify the additional and potentially detrimental effects that harvest may have on productivity, particularly when productivity is challenged by climate and density-dependent factors limiting population growth.

Under the simple scenarios considered here, predicted changes in life history resulting from directional selection are modest. However, the results depend heavily on the genetic and phenotypic covariances, and stronger responses are possible. Although insufficient data for red deer were available to fully evaluate the evolutionary consequences of harvest, nearly all trends reflected depressed productivity and fitness. The patterns suggest that current modes of harvest are unlikely to produce substantial life-history changes in red deer over 10 or fewer generations unless the genetic influences on red deer traits are considerably higher than those predicted here. However, it should be recognized that the population used in our analyses may not reflect the actual responses of many other populations, including those imperiled by harvest, habitat loss or other factors. The primary assumptions of the analysis are that genetic and phenotypic (co)variances are constant over time, that phenotypes are determined simply by a breeding value and an environmental deviation (i.e. additive gene action and no genotype-environment interaction), that harvest intensity and environmental influences on red deer demography do not vary, and that the distributions of breeding values, environmental deviations and phenotypes are multivariate normal and remain so under harvest.

Several additional caveats to recognize include: 1) the genetic data do not adequately capture the covariance structure of the important traits (in particular, no negative covariances exist in this model, a situation that could seriously bias predicted responses, and **G** is assumed constant under selection); 2) the discrete-generation model is likely to underestimate selection responses because it does not account for selection acting differentially on multiple ages within a cohort; 3) only weak harvest intensity is considered; 4) harvest selectivity may be more pronounced than that predicted from body size; 5) leg length may be a poor proxy for body size in evaluating size selectivity; 6) natural selection on these traits may be stronger than modeled, which could alter the responses to harvest; and 7) no changes in the variability of traits over time are permitted in the model, which will affect selection responses. Clearly, most of these assumptions are violated in wild red deer populations.

Departures from the first two conditions may have important implications for predicting harvest effects. For example, if **G** varies appreciably under selection, phenotypic changes resulting from selective harvest may erode quickly in traits with larger heritabilities, if selection is primarily directional. However, these changes may be offset by changes in the genetic correlations between traits that influence fitness, which are likely to become more negative under selection as positive genetic correlations with respect to fitness are removed, leaving more negative correlations maintained by antagonistic pleiotropy (Service & Rose 1985, Holloway et al. 1990). The net outcome is difficult to predict, and emphasizes the

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

value in estimating correlations among traits influencing reproductive fitness.

In addition, not accounting for age structure is also likely to affect responses to selection. If selection on traits varies, especially in direction but also in magnitude, among animals of different ages, predicted responses to selection may be more subtle than if age structure is not considered. The effects depend heavily on the degree to which heritabilities, genetic correlations, and selection differentials differ among animals of different ages in both sexes.

Nevertheless, the downward trends in life-history traits with respect to fitness highlight the need to be cautious about harvest methods that are selective, at least with respect to size. The consequences of variable natural selection for the distribution of adult size are likely to interact with those of size-selective harvest in a complex fashion. Empirical estimation of harvest selection differentials and responses to selection over several generations would help to determine how size-selective harvest affects variation in life history and productivity of antlered game. Where feasible, management biologists should strive to obtain additional data from red deer populations (as has been collected systematically for decades for a few European populations, such as the wild group on the Isle of Rum) that could provide key information on the genetic and demographic characteristics of these managed populations. Ideally, this information would include ages of adult males and females successfully mating and those excluded from mating, sex-specific reproductive lifespans and annual variation in individual breeding success, survival rates of calves born to parents of different ages, annual variation in reproductive success of harem-holding males of different ages, and tissues for genetic information sufficient to identify parent-progeny triplets. We recognize the difficulty in obtaining much of this information in freely ranging cervid populations; therefore, harvest managers should in the meantime adopt risk-averse management alternatives for red deer populations under harvest, such as hunts that reduce selectivity on size and age or permit a greater proportionate take of antlerless animals. By promoting less selective harvest methods, managers may be able to support higher sustainable harvest rates on an annual basis.

Acknowledgements - we thank J. Pierce and J. Nelson of the Washington Department of Fish & Wildlife (USA) for their advice, support, patience and encouragement of this work. M. Boyce (University of Alberta), E.O. Garton (University of Idaho), S. Kalinowski (Montana State University), and M. Ford and R. Waples (Northwest Fisheries Science Center) reviewed earlier drafts, for which we are grateful. The insightful comments of T. Coulson (Imperial College, London), A. Mysterud (University of Oslo) and an anonymous referee substantially improved the paper. This work was supported by the Washington Department of Fish and Wildlife, the Northwest Fisheries Science Center, U.S. National Oceanic and Atmospheric Administration, the University of Idaho, and the University of Montana.

References

Ashley, M.V., Willson, M.F., Pergams, O.R.W., O'Dowd, D.J., Gende, S.M. & Brown, J.S. 2003: Evolutionarily enlightened management. - Biological Conservation 111: 115-123.

Barton, N.H. & Turelli, M. 1991: Natural and sexual selection on many loci. - Genetics 127: 229-255.

Bonenfant, C., Gaillard, J-M., Klein, F. & Maillard, D. 2004: Variation in harem size of red deer (Cervus elaphus L.): the effect of adult sex ratio and age-structure. - Journal of Zoology 262: 1-9.

Bonenfant, C., Gaillard, J-M., Loison, A. & Klein, F. 2003: Sex ratio variation and reproductive costs in relation to density in a forest-dwelling population of red deer (Cervus elaphus). - Behavioral Ecology 14: 862–869.

Briton, J., Nurthen, R.K., Briscoe, D.A. & Frankham, R. 1994: Modelling problems in conservation genetics using Drosophila: consequences of harems. - Biological Conservation 69: 267-275.

Caughley, G. 1977: Analysis of vertebrate populations. - John Wiley and Sons, London, UK, 234 pp.

Charlesworth, B. 1994: Evolution in age-structured populations, 2nd edition - Cambridge University Press, Cambridge, UK, 306 pp.

Clutton-Brock, T.H. & Albon, S.D. 1989: Red deer in the highlands. - BSP Professional Books, Oxford, UK, 268 pp.

Clutton-Brock, T.H., Coulson, T., Milner-Gulland, E.J., Armstrong, H.M. & Thomson, D. 2002: Sex differences in emigration and mortality affect optimal management of deer populations. - Nature (London) 415: 633-637.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982: Red deer: behavior and ecology of two sexes. - University of Chicago Press, Chicago, IL, USA, 378 pp.

Clutton-Brock, T.H. & Iason, G.R. 1986: Sex ratio variation in mammals. - Quarterly Review of Biology 61: 339-374.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. 2003: Undesirable evolutionary consequences of trophy hunting. - Nature (London) 426: 655-658.

Connelly, J.W., Gammonley, J.H. & Peek, J.M. 2005: Harvest management. - In: Braun, C.E. (Ed.); Techniques for wildlife investigations and management. - The Wildlife Society, Bethesda, Maryland, USA, pp. 658-690.

Conover, D.O. & Munch, S.B. 2002: Sustaining fisheries yields over evolutionary time scales. - Science 297: 94-96.

Coughenour, M.B. & Singer, F.J. 1996: Elk population processes in Yellowstone National Park under the policy of natural regulation. - Ecological Applications 6: 573-593.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Coulson, T., Kruuk, L.E.B., Tavecchia, G., Pemberton, J.M. & Clutton-Brock, T.H. 2003: Estimating selection on neonatal traits in red deer using elasticity path analysis. - Evolution 57: 2879-2892.

Essington, T.E. 2001: The precautionary approach in fisheries management: the devil is in the details. - Trends in Ecology & Evolution 16: 121-122.

Falconer, D.S. & Mackay, T.F.C. 1996: Introduction to quantitative genetics, 4th edition. - Addison Wesley Longman, Ltd., Harlow, Essex, UK, 464 pp.

Flook, D.R. 1970: Causes and implications of an observed sex differential in the survival of wapiti. - Canadian Wildlife Service Report Series, No 11, 71 pp.

Frankham, R. 1995a: Conservation genetics. - Annual Review of Genetics 29: 305-327.

Frankham, R. 1995b: Effective population size/adult population size ratios in wildlife: a review. - Genetical Research (Cambridge) 66: 95-107.

Gaillard, J-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. 2000: Temporal variation in fitness components and population dynamics of large herbivores. - Annual Review of Ecology and Systematics 31: 367-393.

Ginsberg, J.R. & Milner-Gulland, E.J. 1994: Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. - Conservation Biology 8: 157-166.

Hamlin, K.L. & Ross, M.S. 2002: Effects of hunting regulation changes on elk and hunters in the Gravelly-Snowcrest Mountains, Montana. - Montana Fish, Wildlife and Parks, Helena, USA, 237 pp.

Hard, J.J. 2004: Evolution of chinook salmon life history under size-selective harvest. - In: Hendry, A. & Stearns, S. (Eds.); Evolution illuminated: salmon and their relatives. Oxford University Press, New York, NY, USA, pp. 315-337.

Hard, J.J. in press: Case study of Pacific salmon. - In: Dieckmann, U., Godø, O.R., Heino, M. & Mork, J. (Eds.); Fisheries-induced adaptive change. Cambridge Studies in Adaptive Dynamics, Cambridge University Press, Cambridge, UK.

Hard, J.J., Winans, G.A. & Richardson, J.C. 1999: Phenotypic and genetic architecture of juvenile morphometry in chinook salmon. - Journal of Heredity 90: 597-606.

Harris, R.B., Wall, W.A. & Allendorf, F.W. 2002: Genetic consequences of hunting: what do we know and what should we do? - Wildlife Society Bulletin 30: 634-643.

Hartl, G.B., Lang, G., Klein, F. & Willing, R. 1991: Relationships between allozymes, heterozygosity and morphological characters in red deer (Cervus elaphus), and the influence of selective hunting on allele frequency distributions. - Heredity 66: 343-350.

Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hoang, A., Hill, C.E., Beerli, P. &. Kingsolver, J.G. 2001: Strength and tempo of directional selection in the wild. - Proceedings of the National Academy of Sciences USA 98: 9157-9160.

Holloway, G.J., Povey, S.R. & Sibly, R.M. 1990: The effect of new environment on adapted genetic architecture. - Heredity 64: 323-330.

Kalinowski, S.T. & Waples, R.S. 2002: Relationship of effective to census size in fluctuating populations. - Conservation Biology 16: 129-136.

Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E., Hoang, A., Gibert, P. & Beerli, P. 2001: The strength of phenotypic selection in natural populations. - American Naturalist 157: 245-261.

Kirkpatrick, M., Johnson, T. & Barton, N. 2002: General models of multilocus evolution. - Genetics 161: 1727-1750.

Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guinness, F.E. 1999: Population density affects sex ratio variation in red deer. - Nature (London) 399: 459-461.

Kruuk, L.E.B., Clutton-Brock, T.H., Slate, J., Pemberton, J.M., Brotherstone, S. & Guinness, F.E. 2000: Heritability of fitness in a wild mammal population. - Proceedings of the National Academy of Sciences USA 97:698-703.

Kruuk, L.E.B., Slate, J., Pemberton, J., Brotherston, S., Guinness, F.E. & Clutton-Brock, T.H. 2002: Antler size in red deer: heritability and selection but no evolution. - Evolution 56: 1683-1695.

Kuehn, R., Schroeder, W., Pirchner, F. & Rottmann, O. 2003: Genetic diversity, gene flow and drift in Bavarian red deer populations (Cervus elaphus). - Conservation Genetics 4: 157-166.

Lande, R. 1979: Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. - Evolution 33: 402-416.

Lande, R. & Barrowclough, G.F. 1987: Effective population size, genetic variation, and their use in population management. - In: Soule, M.E. (Ed.); Viable populations for conservation. - Cambridge University Press, Cambridge, UK, pp. 87-124.

Langvatn, R. & Loison, A. 1999: Consequences of harvesting on age structure, sex ratio and population dynamics of red deer Cervus elaphus in central Norway. - Wildlife Biology 5: 213-223.

Law, R. 1991: On the quantitative genetics of correlated characters under directional selection in age-structured populations. - Philosophical Transactions of the Royal Society of London, B 331: 213-223.

Law, R. 2000: Fishing, selection, and phenotypic evolution. - ICES Journal of Marine Science 57: 659-668.

Lowe, V.P.W. 1969: Population dynamics of the red deer (Cervus elaphus L.) on Rhum. - Journal of Animal Ecology 38: 425-457.

Mace, G.M. & Lande, R. 1991: Assessing extinction threats: towards a reevaluation of IUCN threatened species categories. - Conservation Biology 5: 148-157.

Malo, A.F., Roldan, E.R.S., Garde, J., Soler, A.J. & Gomendio, M. 2005: Antlers honestly advertise sperm production and quality. - Proceedings of the Royal Society, Series B - Biological Sciences 272: 149-157.

Martinez, J.G., Carranza, J., Fernandez-Garcia, J.L. & Sanchez-Prieto, C.B. 2002: Genetic variation of red deer populations

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

under hunting exploitation in southwestern Spain. - Journal of Wildlife Management 66: 1273-1282.
Merilä, J., Sheldon, B.C. & Kruuk, L.E.B. 2001: Explaining stasis: microevolutionary studies in natural populations. - Genetica 112-113: 199-222.
Mills, L.S. & Smouse, P.E. 1994: Demographic consequences of inbreeding in remnant populations. - American Naturalist 144: 412-431.
Mysterud, A., Coulson, T. & Stenseth, N.C. 2002: The role of males in the dynamics of ungulate populations. - Journal of Animal Ecology 71: 907-915.
Noyes, J.H., Johnson, B.K., Bryant, L.D., Findholt, S.L. & Thomas, J.W. 1996: Effects of bull age on conception dates and pregnancy rates of cow elk. - Journal of Wildlife Management 60: 508-517.
Nunney, L. 1993: The influence of mating system and overlapping generations on effective population size. - Evolution 47: 1329-1341.
Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. & Dieckmann, U. 2004: Maturation trends indicative of rapid evolution preceded the collapse of northern cod. - Nature (London) 428: 932-935.
Peek, J.M., Lovaas, A.L. & Rouse, R.A. 1967: Population changes within the Gallatin elk herd, 1932-1965. - Journal of Wildlife Management 31: 304-316.
Rose, K.E., Clutton-Brock, T.H. & Guinness, F.E. 1998: Cohort variation in male survival and lifetime breeding success in red deer. - Journal of Animal Ecology 67: 979-986.
Ryman, R., Baccus, R., Reuterwall, C. & Smith, M.H. 1981: Effective population size, generation interval, and potential loss of genetic variability in game species under different hunting regimes. - Oikos 36: 257-266.
Schmidt, K.T., Stien, A., Albon, S.D. & Guinness, F.E. 2001: Antler length of yearling red deer is determined by population density, weather and early life-history. - Oecologia 127: 191-197.
Scribner, K.T., Wooten, M.C., Smith, M.H. & Johns, P.E. 1985: Demographic and genetic characteristics of white-tailed deer populations subjected to still or dog hunting. - In: Beasom, S.L. & Roberson, S.L. (Eds.); Game harvest management. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA, pp. 197-212.
Service, P.M. & Rose, M.R. 1985: Genetic covariation among life-history components: the effect of novel environments. - Evolution 39: 943-945.
Shaw, R.G. 1987: Maximum-likelihood approaches applied to quantitative genetics of natural populations. - Evolution 41: 812-826.
Taper, M.L. & Gogan, P.J.P. 2002: The northern Yellowstone elk: density dependence and climatic conditions. - Journal of Wildlife Management 66: 106-122.
Thelen, T.H. 1991: Effects of harvest on antlers of simulated populations of elks. - Journal of Wildlife Management 55: 243-249.
Ueckermann, E. 1987: Managing German red deer (Cervus elaphus L.) populations. - In: Wemmer, C.M. (Ed.); Biology and management of the Cervidae. Smithsonian Institution Press, Washington, D.C., pp. 505-516.
Wade, M.J. & Shuster, S.M. 2004: Sexual selection: harem size and the variance in male reproductive success. - The American Naturalist 164: E83-E89.
Waples, R.S. 2002: Effective size of fluctuating salmon populations. - Genetics 161: 783-791.
Wedekind, C. 2002: Manipulating sex ratios for conservation: short-term risks and long-term benefits. - Animal Conservation 5: 23-20.
White, G.C., Freddy, D.J., Gill, R.B. & Ellenberger, J.H. 2001: Effects of adult sex ratio on mule deer and elk productivity in Colorado. - Journal of Wildlife Management 65: 543-551.
Wright, S. 1938: Size of population and breeding structure in relation to evolution. - Science 87: 430-431.
Yoccoz, N.G., Mysterud, A., Langvatn, R. & Stenseth, N.C. 2002: Age- and density-dependent reproductive effort in male red deer. - Proceedings of the Royal Society of London, Series B - Biological Sciences 269: 1523-1528.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix I

Effective population size

Under an assumption of variation in sex ratio resulting from a bias in survival to adulthood, the effective population size, N_e, depends on the census size N, the adult sex ratio p_m (proportion male), the probabilities of male and female survival between breeding seasons (v_m and v_f, respectively), and harem size h (defined below) in the following way (Nunney 1993):

$$N_e = \frac{2N}{\left[2(v_m + v_f) + (1 - v_f)(h + 1)\right]}$$

if $pm \geq 1/(h + 1)$, or

$$N_e = \frac{2N}{\left[2(v_m + v_f) + (1 - v_m)(h + 1)/h\right]}$$

if $p_m < 1/(h + 1)$.

These equations compute changes in N_e under varying conditions of generation time, sex ratio and harem size. Assumptions are that all mature females mate once per season, that the harem bull does all breeding, that mean generation length is the sum of mean age at maturity and mean adult longevity (computed for each sex and then averaged), that the sex ratio can be computed from the ratio of mean male longevity to twice the mean adult longevity, and that harem size is equal to:

$$h = \frac{\alpha_f (1 - p_m)}{\alpha_m p_m}$$

where α_f is the proportion of females breeding during the season (assumed to be 1), p_m is the proportion of males among adults, and α_m is the proportion of males that breed during the season.

Nunney (1993) showed that, assuming sex variation in adult survival, the N_e/N ratio could be computed from:

$$\frac{\frac{M + A - 1}{A}}{\left[2 - \tfrac{1}{2}(A_m^{-1} + A_f^{-1}) + \tfrac{1}{2}\left|(hA_f^{-1} - A_m^{-1})\right|/H\right]}$$

where H = 1 for $p_m \geq 1/(h + 1)$, or else H = h (the mean harem size); M is the mean maturation age; A is the mean adult longevity; A_m and A_f are the longevities of males and females, respectively; p_m is the sex ratio; and h is the mean harem size.

Effects of selective harvest on size and correlated traits

We used genetic and phenotypic variance component estimates to parameterize a discrete-generation model determining multivariate response to directional selection on size. This additive genetic model, a multivariate form of the breeder's equation (Falconer & Mackay 1996), is expressed as (Lande 1979):

$$\Delta \mathbf{z}_t = \mathbf{G}\mathbf{P}^{-1}\mathbf{s}_t$$

where Δz_t is the vector of mean phenotypes in generation t, **G** is the genetic covariance matrix, **P** is the phenotypic covariance matrix, and $\mathbf{s}_t$ is the vector of selection differentials resulting on each trait from harvest in generation t. Mean fitness estimates under directional selection for trait x assuming normally distributed phenotypes are:

$$\hat{W}_x = \int_{-\infty}^{k_x} \frac{1}{\sqrt{2\pi(\sigma^2 + \omega^2)}} \exp\left[-\frac{y_x^2}{2(1+\omega^2)}\right] dy_x + \theta \int_{k_x}^{\infty} \frac{1}{\sqrt{2\pi(\sigma^2 + \omega^2)}} \exp\left[-\frac{y_x^2}{2(1+\omega^2)}\right] dy_x$$

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

where y_x is the phenotype scaled as a deviation from the mean value in standard deviation units (σ), k_x is the threshold size of harvestable red deer, ω is the width of the fitness function in units of σ, and θ is the probability of harvestable red deer escaping harvest (1-θ is therefore essentially the harvest rate, although it includes the survival of harvestable animals smaller than k_x as well; Law 1991). The selection differential on trait x, S_x, is

$$\hat{W}_x^{-1}\left\{-\frac{1-\theta}{\sqrt{2\pi(\sigma^2+\omega^2)}}\exp\left[-\frac{k_x^2}{2(1+\omega^2)}\right]\right\}\sigma_x$$

where σ_x is the trait's phenotypic standard deviation (Law 1991).

We estimated the correlated selection differentials on the means of the other traits, S'_y, from the relation:

$$S'_y = \frac{cov_{xy}}{var_x}S_x$$

where cov_{xy} is the phenotypic covariance between each pair of traits and var_x is the phenotypic variance of x (size) (Falconer & Mackay 1996).

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use