Selective harvest focused on sexual signal traits can lead to extinction under directional environmental change.

Authors: Robert J. Knell* and Carlos Martínez-Ruiz

Affiliation: School of Biological and Chemical Sciences, Queen Mary, University of London. Mile End Road, London E1 4NS, UK.

*Author for correspondence. Email R.Knell@qmul.ac.uk, telephone +44 2078827720

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Abstract

Humans commonly harvest animals based on their expression of secondary sexual traits such as horns or antlers. This selective harvest is thought to have little effect on harvested populations because off-take rates are low and usually only the males are targeted. These arguments do not, however, take the relationship between secondary sexual trait expression and animal condition into account: there is increasing evidence that in many cases the degree of expression of such traits is correlated with an animal's overall well-being, which is partly determined by their genetic match to the environment. Using an individual-based model, we find that when there is directional environmental change, selective harvest of males with the largest secondary sexual traits can lead to extinction in otherwise resilient populations. When harvest is not selective, the males best suited to a new environment gain the majority of matings and beneficial alleles spread rapidly. When these best-adapted males are removed, however, their beneficial alleles are lost, leading to extinction. Given the current changes happening globally, these results suggest that trophy hunting and other cases of selective harvest such as certain types of insect collection should be managed with extreme care whenever populations are faced with changing conditions.

Background

Humans harvest animal populations for many reasons. While many animal populations are harvested chiefly for food, others are targeted for recreational purposes, and in these latter cases the main targets for harvest are often males with large sexual ornaments. Some insect collectors, for example, will target particularly large and well-ornamented specimens of insects such as rhinoceros and stag beetles, and good specimens of some of these can sell for large sums of money (Fig. 1). Similarly, trophy hunters often specifically target male animals with exceptionally large antlers, horns, manes or other secondary sexual traits. A considerable amount of effort is sometimes expended by trophy hunters to take the largest and best ornamented males in a population, and Safari Club International, the main representative body for such hunters, awards prizes every year on the basis of measurements of these traits. Well-ornamented males are prized in some non-Western societies as well. As an example, the Huli "Wigmen" of Papua New Guinea use the plumes, and sometimes entire specimens, of male birds of paradise in the construction of their elaborate headwear [1]. Finally, illegal poaching of animals such as elephants for the ivory trade also targets animals with the greatest expression of secondary sexual traits [2].

The impacts of selective harvest have largely been studied with regards to trophy hunting. Hunting generally is a considerable cause of mortality for many populations [3] and uncontrolled hunting has caused some well-known extinctions such as the Quagga (*Equus quagga*) [4]. Trophy hunting of well-managed populations, however, is often thought to be unlikely to have serious consequences for the long-term population stability of the harvested animals, for two reasons. Firstly, well-managed trophy hunting often involves low off-takes from large populations [4]. Secondly, in many cases the animals targeted are males, and in the polygynous systems typical of the hunted animals, females will not have difficulty acquiring mates unless a large proportion of the males are removed [5]. Consequently, recruitment into the population should be unaffected by hunting, meaning that in the absence of other threats populations of animals that are primarily harvested for trophies or specimens should not be at risk of extinction [6,7]. Instead, more subtle effects from trophy hunting are found, such as changes in the sociobiological makeup of populations arising from the removal of males, as seen in hunted lion populations [8], and evolutionary changes arising from selection against desirable traits for hunters such as large horns or large body size [9–12], although the magnitude of this latter effect is the subject of some debate [13–15].

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This assumption that selective harvest is not especially threatening, however, does not take into account recent work which has found that sexual selection itself seems to have the capacity to have important effects on evolutionary processes such as adaptation to changing environments [16–19]. Traits used in sexual signalling and contests between males, including those which are often specifically targeted by humans such as the horns and antlers of bovids and cervids, are known often to show "condition dependence", whereby the degree of expression of the trait is strongly affected by the overall health and well being (the "condition") of the bearer [20–23]. This condition dependence means that trait expression and therefore mating success is associated with the genetic quality of the male in question - males carrying a heavy load of deleterious alleles will not be in good condition and will not be able to express their signal traits well, whereas those with a genetic makeup that makes them particularly able to acquire resources and to develop will have particularly large, loud or colourful secondary sexual traits and will acquire a disproportionate number of matings [24,25]. A series of studies over the last decade and a half have argued that as a consequence of this strong reproductive skew towards the fittest males, populations of strongly sexually selected animals should clear deleterious mutations faster and adapt to changing environments more quickly than populations where mating is less selective [16,19]. This benefit from sexual selection is consistently found in laboratory experiments which have shown that strong sexual selection leads to faster adaptation to novel foods [26] and to pesticides [27], to a reduced extinction risk from thermal stress [17] and to a reduction in inbreeding depression leading to improved persistence of small populations [18,28]. Field data, by contrast, mostly finds that strong sexual selection is either neutral or associated with higher extinction rates, but a recent modelling study which forms the basis of the present paper appears to resolve this - we found that when populations are very small, as is the case for many of the field populations that have been studied [29] the cost of growing and bearing secondary sexual ornaments appears to increase the risk of extinction arising from demographic stochasticity, but when populations are larger the increased adaptation rate more than compensates for this risk [19].

Given this benefit to mean population fitness arising from sexual selection, especially when the populations in question are under environmental stress, it is possible that selective harvest of well-ornamented males could have a much larger effect than might be expected from simple demographic considerations. If the environment is changing, then removing those males with the largest ornaments will have the effect of removing those individuals who are best adapted to the

new environment, potentially weakening, neutralising or even reversing the increase in adaptation rates and the reduction in extinction probability that sexual selection appears to bestow upon a population. We investigated the effect of selective harvesting on adaptation and extinction using a modification of an existing individual-based simulation model, previously used to investigate the relationships between demographic effects, sexual selection and environmental change (see supplementary material for full details). Individual-based models allow feedback between demographic and evolutionary processes and are well suited for investigating so-called "eco-evo" questions such as this [30,31].

Methods

The model used is a modification of the individual-based model used in [19] and is described in detail in the supplementary information, which also includes the full model code. The model is written in R [32] and allows the population dynamics and evolution of a spatially homogeneous, age-structured population of animals to be simulated, with the strength of sexual selection being specified for each population. The model proceeds as a series of timesteps of arbitrary length. These can be thought of as representing years but the model is not necessarily constrained to this time scale and we would caution against interpreting the output from this model as making specific predictions about the timescale of evolutionary or extinction events..

Individuals in the simulation are born as juveniles and mature aged 2. In the absence of other influences the probability of death is modelled as a quadratic function such that adults aged 5 or 6 years old experience the lowest probability of death, with young and old individuals both having an increased probability of dying. The probability of death is also related to population density, with an increasing likelihood of dying when the population approaches or exceeds the environmental carrying capacity.

The environment is modelled via a single variable, *environment*, which is assumed to represent a continuously variable environmental factor such as temperature or salinity. The *environment* can change randomly every year with the standard deviation of the changes being specified for each simulation, and larger random changes can also occur at intervals and with a magnitude which can be varied. For directional environmental change, the simulations begin with a period of 150 timesteps of stability with only a small amount of random noise altering *environment* to allow the population to reach "normal" levels of adaptation. After this, *environment* alters by a randomly

drawn value with a mean greater than zero each timestep: for the majority of simulations this value was 0.005 but for the simulations shown in fig. 3 and supplementary fig. 3 this value was varied. To allow for variability in individual responses to a particular environment, each individual experiences a different value for *environment* calculated as the current value plus a random number drawn from a normal distribution with mean zero and standard deviation equal to 0.2.

The fit to the environment for each individual is assumed to be a complex polygenic trait controlled by a large number of loci, and so is modelled as a continuous value called *genotype*. *genotype* is calculated from the mean value for the two parents, plus a random number drawn from a normal distribution with mean 0 and sd 0.05 which allows for stochastic effects and mutation. For both males and females, the square of the difference between the value for *genotype* and the value for *environment* (*mismatch*) determines the overall health and condition of the individual, with larger values for *mismatch* indicating worse condition. This then leads to reduced survival and reduced fecundity in females. Phenotype (*mismatch*) is thus controlled by genotype but is not completely equal to it because of the variability in individual environments, and throughout the simulation there is an optimal phenotype (*mismatch* = 0) which a population should track.

The expression of sexual display traits by males is calculated when they reach maturity, and is determined by several factors: a genetic variable controlling the degree by which such traits tend to be expressed (*t*) which was itself allowed to evolve during the simulation, the condition of the individual male (*mismatch*) and a constant (*α*) which specifies the extent by which expression of the sexual display trait scales with condition, such that trait expression for an individual male is calculated as:

$$Expression = \frac{t}{1 + mismatch * \alpha}.$$

α was set to 4 for the majority of simulations but the effects of varying it are shown in supplementary fig. 3.

Mate choice occurs by each female sampling a set number of males and choosing to mate with one, with the probability of choosing a particular male changing according to the difference between his display trait size and the median value for the group sampled, adjusted by the strength of female preference. The overall strength of sexual selection experienced by a population is determined by a

constant specifying the number of males that a female will assess before choosing a mate: if this number is 1 then mating is random, if it is greater than 1 then the population will experience sexual selection, with the degree of reproductive skew being greater as this value increases. Following this each female who has mated (it is possible for there to be no mature males in a population) produces a number of offspring determined by the parameter O which specifies maximum fecundity per female, adjusted by that female's condition (*mismatch*).

Harvesting was added to the model such that either removal of mature individuals of both sexes or of mature males only could be specified. To add selectivity to this process individual males were ranked according to their expression of secondary sexual traits and the probability of being removed weighted by:

$$weight_i = \left(\frac{1}{rank_i^s}\right) / \sum_{p=1}^{T} rank_p$$

Where S is a selectivity coefficient ('harvest_selectivity' in the model code) and T is the total number of adult males. This gives random sampling if $S = 0$ and increasingly selective sampling as S becomes larger (Supplementary Fig. 5).

Results

When environmental change is random, selective harvesting does not increase extinction risk, even when the amount of change is such that there is a reasonable risk of extinction (supplementary Fig. 1). With directional environmental change, however, increasing selectivity of harvesting is strongly associated with an increasing risk of extinction (Fig. 2, supplementary Fig. 2). When there is a low or medium probability that a changing environment will lead to extinction even in the absence of harvesting, selective harvest makes extinction a near-certainty. When the population is resilient to environmental change in the absence of harvesting, selective harvest can still lead to a high probability of extinction, especially when coupled with a relatively high harvest rate.

Selective harvesting reduces the ability of the population to adapt as the environment changes. Chevin *et al* [33] considered the question of how much environmental change a population can tolerate, and defined the Critical Rate of Environmental Change as "the maximum rate of sustained

environmental change that allows long-term persistence of a population". The stochastic nature of these simulations means that there is not a critical rate associated with each combination of parameter values, but whether we consider the rate of change at which no population, or 10% of populations, or 50% of populations become extinct to be a stochastic equivalent, we can see that the reduced capacity of selectively harvested populations to adapt means that this critical rate is reduced (Fig. 3). These effects are seen even when sexual selection is weak and the link between fitness and expression of the secondary sexual trait is not especially strong, and even a relatively mild degree of selectivity can increase the probability of extinction under some circumstances (supplementary Fig. 3).

We modeled two management scenarios that could ameliorate the possible negative effect of trophy hunting. Imposing a threshold population size below which harvest is not allowed does reduce the risk of extinction but only when the threshold is a large fraction of the population carrying capacity (Supplementary Fig. 4). Age restrictions on harvest, however, where males are only targeted once they are over a certain age, are effective in reducing the risk of extinction (Fig. 4) because the "high quality" males have opportunities to breed before being removed.

Discussion

It has been argued that human predation is qualitatively different from other forms of predation, with a strong bias towards the removal of large adults leading to different and more severe impacts on prey species than those caused by non-human predators [3]. Indeed, natural predation can actually enhance population persistence when prey populations are exposed to directional environmental change. This can occur via both 'selective push', whereby poorly-adapted individuals are removed by predators leading to more rapid adaptation, and also the 'Hydra effect', whereby removal of individuals from a population leads to increased recruitment and enhances adaptation because generation time is effectively reduced [34] – a phenomenon also seen in our model results when harvest is non-selective (Fig. 3, Supplementary Fig. 3). Our results here contrast notably with these effects of 'normal' predation and reinforce the point that the sorts of selectivity associated with human predation can lead to uniquely severe impacts on harvested populations.

This demonstration that selective harvesting can potentially push otherwise resilient populations to extinction when the environment changes is concerning. As mentioned earlier, it is widely believed

that selective harvest is unlikely to endanger well-managed populations, and this might well be reasonable when the environment is relatively stable, or changing at random – but directional environmental change is now a dangerous reality for considerable numbers of species [35], with global environmental change causing raised temperatures worldwide, increasing ocean acidification and changes in seasonal timing all becoming increasingly important. Populations with restricted geographical ranges, such as those on islands or which are confined to isolated habitat patches such as forest fragments or isolated conserved areas are unable to migrate to new environments. Given that phenotypic plasticity is unlikely to be sufficient to allow population persistence in many cases [36–38], these populations will have to adapt or they will become extinct.

Our results clearly show that age restrictions on harvest which allow males to breed before they are taken is effective at reducing the impact of selective harvest on adapting populations. Such management is already recommended for lions [39] and populations where these recommendations are followed are likely to be relatively unaffected by the removal of these males. Other well-managed trophy hunting schemes, such as those which follow the IUCN SSC Guiding Principles on Trophy Hunting [40], with low off-take and reactive management will also be somewhat resilient to the effects described here, although managers would need to consider the effects of removal of well-ornamented males if the population were faced with an altered environment. Poorly managed populations of hunted animals, however, with higher levels of off-take, a lack of monitoring and harvesting of males of all ages are likely to be vulnerable to problems caused by the removal of the fittest males even in the absence of other threats.

The present model does not consider two phenomena which might alter the effect of selective harvesting on adaptation. These are inbreeding and intralocus sexual conflict. In the case of the former, if selective harvest reduces the degree of reproductive skew in a population by removing the most attractive or dominant males then this will change the effective population size and potentially reduce the amount of inbreeding. In species which experience severe effects from inbreeding depression this could mitigate the negative effects of removing the best adapted males to some extent. How important this effect might be is not clear, and the situation is further complicated by the potential for a history of strong sexual selection to buffer a population against inbreeding depression [18]. There is a clear requirement for further research, both theoretical and empirical, to help us understand how inbreeding will interact with selective harvesting and how this might alter population mean fitness.

In the case of intralocus sexual conflict, different phenotypic optima for males and females could mean that in some cases females who mate with the most attractive males might actually have female offspring with reduced fitness [41,42], potentially reducing population mean fitness. It is possible, therefore, that removing those most attractive males from the system would reduce this effect and mitigate the other, negative effects of selective harvest to some extent. On the basis of current knowledge, however, we would suggest that this is unlikely, especially under directional selection: both empirical [43,44] and theoretical [45] research indicates that the negative effects of sexual conflict in changing environments are reduced because the phenotypic optima for both sexes are shifted in the same direction, leading to the selection gradients for both sexes becoming more similar [45]. Nonetheless, as with inbreeding, this is a complex question which remains an area for future research.

The outputs of this model are predicated on the assumption that sexually selected traits are condition-dependent and will respond to the environment in a way that allows sexual selection to affect adaptation and persistence. As discussed in the introduction, there is now a considerable amount of laboratory data supporting this assumption, but we must be cautious because these studies were all carried out on invertebrates, whereas the targets for selective harvesting are often vertebrates, which may well have rather more sophisticated breeding systems with important contributions from social selection as well as sexual selection [46]. Age is also important in sexual selection in many vertebrate systems, with the growth of sexual ornaments increasing throughout a male's life and only "prime" aged males being able to compete fully for access to females [21,39,47]. How this age effect might interact with adaptation and selective harvest is not clear, although removal of prime-aged males could potentially reverse the beneficial effects of only harvesting older males which we have found. As with all theoretical models, therefore, we do not claim that the effects found here will be universal, or even necessarily typical. Nonetheless, the effect of selective harvesting on extinction risk under environmental change appears to be strong and should at least be considered when strongly sexually selected species are harvested.

When properly regulated, trophy hunting is arguably a powerful force for conservation [4,48], with a greater area being conserved for hunting in Sub-Saharan Africa than is conserved in national parks [4]. Other forms of selective harvest such as insect collecting are much less well managed or studied. Unless a species of insect is specifically protected by national or international legislation,

collection is usually unregulated and populations are not managed: a search on Web of Knowledge for a variety of combinations of "insect", "collect*", "population" and "management" returns no relevant hits. This is unlikely to be a problem when populations are large and rates of off-take from collectors are low, but when populations are small and demand for particularly showy specimens is strong, as might well be the case for the larger lucanid and dynastid species in fragmented forests, there is a risk that collection targeted at these specimens might inadvertently cause local or even global extinction even when the proportion of animals collected seems insignificant.

Ethics statement

As this is a theoretical study no ethics clearance was necessary.

Data accessibility

The full model code is available in the electronic supplementary material.

Competing interests

We have no competing interests.

Author contributions

RK conceived the study. C M-R and RK wrote the model code and ran the simulations. RK wrote the manuscript and both authors gave final agreement for publication.
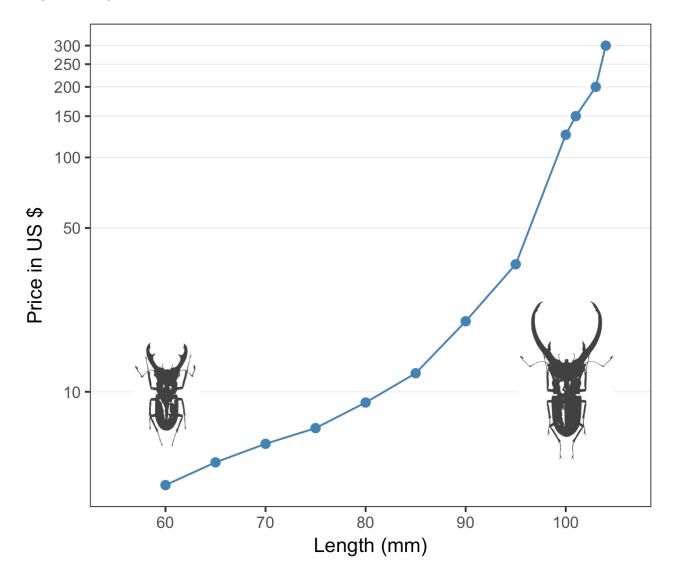
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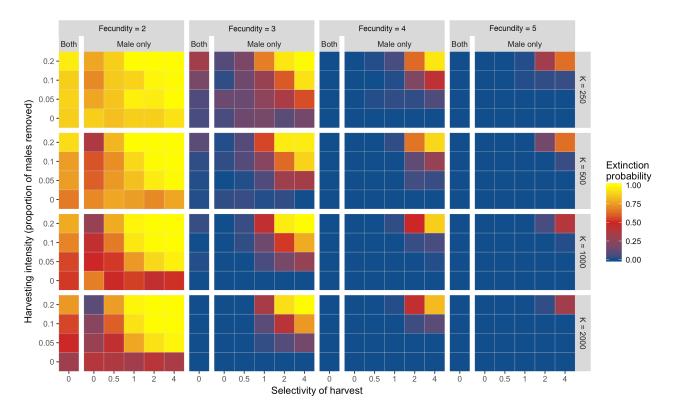
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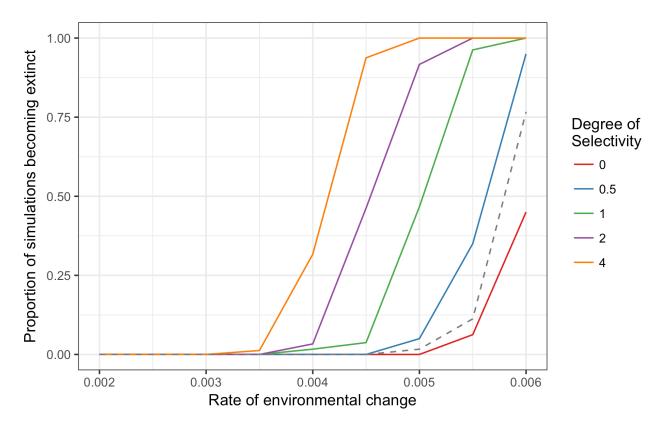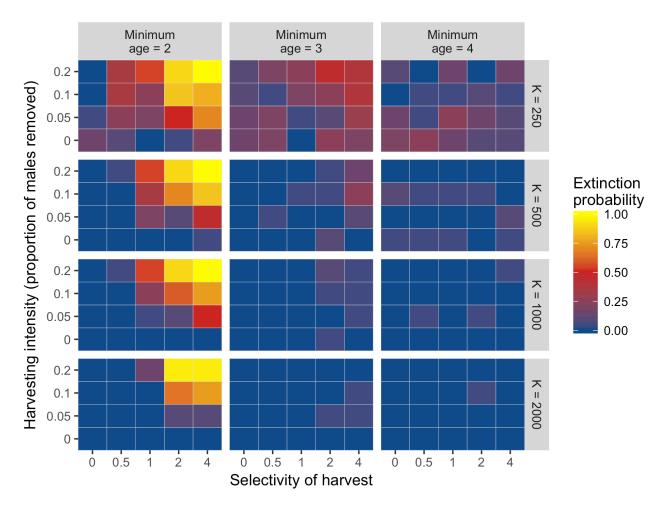
Figure legends

Figure 1. Insect collectors place a strong premium on males with extreme expression of secondary sexual traits. The figure shows prices quoted for specimens of the male stag beetles *Cyclommatus elaphus* plotted against the total length of the specimen. The pictured males are specimens 100mm and 60mm long and show that the very expensive large males are mostly differentiated from the cheap medium-sized males by the length of their mandibles. Note the log scale on the y-axis, and also that neither females nor males less than 60mm long were even offered for sale - some male *C. elaphus* can be as small as 30mm in length. Data taken from the website of an insect dealer specialising in Indonesian insects (http://www.giradis-insect.com/) on the 3rd April 2017.

Figure 2. When there is directional environmental change the probability of extinction increases with increasing selectivity and harvesting intensity. K indicates the carrying capacity of the environment, which will determine the population size when environmental change begins, and fecundity is the average fecundity of a female who is well adapted to the environment. The columns headed "Both" show probabilities of extinction when both male and female adults are harvested at random. The columns headed "Male only" show extinction probabilities when only adult males are harvested. The y-axes show harvesting intensity, expressed as the proportion of the male population removed per timestep (NB for the "Both" columns the harvesting intensity was reduced by 50% for each sex so that the same overall number of animals were removed). The x-axes show the degree of selectivity expressed as the coefficient S from the model, with 0 indicating that harvesting is random and the degree of selectivity increasing as the value increases such that a value of 4 indicates a strong preference for the most ornamented males – see supplementary information figure 2. All probabilities calculated from 80 runs of the model over 600 timesteps and with the increase in the environmental variable set to 0.005 per timestep. See the supplementary information for full details of the model.

Figure 3. Increasingly selective harvest leads to a decreased Critical Rate of Environmental Change. The y-axis shows the proportion of simulations in which the population became extinct before 600 timesteps had been completed, and the x-axis gives the amount by which the environment changes every timestep. Harvest is random for a degree of selectivity of zero and is very selective when the degree of selectivity is 4 (see figure S1). Because of the stochasticity in the model there is not a single critical rate for each set of parameter values, but this plot shows that a much lower rate of environmental change causes extinction when selectivity is high. All data compiled from 80 model runs at each combination of parameter values for 600 timesteps, with the harvest rate set to 0.2, a base fecundity of 3 and a carrying capacity of 1000. The dashed line shows the proportion of simulations becoming extinct when the harvest rate is set to zero – as can also be seen in figure 2, random harvest of males only (the situation when selectivity = 0) appears to protect the population to some degree against environmental change, probably because of the "Hydra effect" recently described by Osmond et al (Osmond *et al.* 2017).

Figure 4. Increasing the minimum age for harvest reduces extinction probability. In this model, males and females become sexually mature at age 2 and harvest is restricted to these mature individuals. If the minimum age for harvest is increased (as in the centre and right hand columns), the effect of selective harvest on extinction risk seems to be largely nullified. This is because the "high quality" males that would otherwise be removed from the population have an opportunity to breed and pass on their genes. Management of trophy hunts whereby older males only are targeted is already recommended for lion populations, albeit to reduce the effects of infanticide and lack of paternal care associated with removal of breeding age males(Whitman *et al.* 2004), and similar schemes should perhaps be considered for other hunted animals. Age-based management requires either an easy way of telling an animal's age or close management of a population whereby individuals are followed through time Neither of these are likely to be possible for many harvested populations, however: these include many mammal populations which are not intensely managed as well as, for example, insect populations where males with large secondary sexual traits are the focus of collection. For these populations it is difficult to recommend a simple management intervention that will avoid the effects detailed here, but close monitoring and

reactive management is likely to help and to give warning of declining numbers and potential problems.

All extinction probabilities calculated from 80 replicate runs of the simulation, with base fecundity = 3, the rate of environmental change set to 0.005 per timestep, strong sexual selection (strength of sexual selection = 5) and strong condition dependence (variable alpha = 4).