Selective harvesting: short- and long-term consequences for wild populations and their management

Selektiv høsting: kort- og langtidskonsekvenser for viltbestander og deres forvaltning

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Contents

Abstract

Human exploitation affects wildlife populations in many ways, including demographic, behavioral, and evolutionary. Selective exploitation – the intentional or unintentional bias for certain individuals or groups – seems particularly prone to alter populations and their evolutionary trajectory. The objective of my thesis is to provide an example of measuring harvesting selectivity, and, through various models, explore the processes underlying selective exploitation, its implications, and possible solutions.

The thesis consists of 5 articles. Two of these are descriptive, analyzing the harvest and vulnerability patterns of brown bears (*Ursus arctos*) in Sweden. The other 3 articles are concerned with concepts and utilize models to explore the mechanisms of selectivity and the role of management. I chose not to focus on one particular model species, but instead emphasize the processes. The subjects of the studies presented range from large carnivores, ungulates, and rodents, to purely theoretical constructs with the sole intent to show shifts in a hypothetical trait.

Selective harvesting and exploitation in general will continue to play a role in shaping wild populations and their communities. With an unprecedented human population size and continued growth, as well as increased efficiency in harvesting tools and methods, the need for considering both short and long-term sustainability of exploitation is paramount. With this thesis, I can offer a number of suggestions, the most important ones being:

- Quantification of harvest effects on wild populations should consider both information about the population itself, as well as cultural aspects of harvest and management.
- Harvest mortality must be viewed in the context of overall mortality, as it is the combined effect of all mortalities that determines viability.
- Selective harvesting, if sufficiently mild, may in some systems be accommodated using measures that compensate for its effect on the fitness surface.
- Adaptive behaviors can have substantial consequences for management, especially at high exploitation rates, such as those imposed during invasive species control.
- When making recommendations for mitigating or reversing the effects of selective harvesting, it is important to state explicitly the objectives for and conditions under which potential solutions may work.

It is the combined effect of the magnitude and the selectivity of human exploitation that determines its short- and long-term implications for wild populations and their communities. As man-made mortality schemes continue to augment or replace natural ones, knowing what individuals or groups are targeted can be as important as knowing how many individuals are killed. Where human exploitation patterns prove to be demographically, evolutionarily, or ecologically unsustainable, changes in exploitation magnitude and selectivity are necessary to reduce detrimental effects.

Sammendrag

Menneskets utnyttelse påvirker viltpopulasjoner på mange måter, inkludert demografisk, atferdsmessig og evolusjonært. Selektiv utnyttelse – det vil si tilsiktede eller utilsiktede skjevheter i forhold til enkelte individer eller grupper – synes særlig å ha en tendens til å endre populasjoner og deres evolusjonære bane. Målet med avhandlingen min er å gi et eksempel på måling av selektiviteten av høsting, og gjennom bruk av ulike modeller å utforske underliggende prosesser bak selektive utnyttelse, deres konsekvenser og mulige løsninger.

Avhandlingen består av 5 artikler. To av disse er beskrivende og analyserer høsting og sårbarhetsmønstre hos brunbjørn (*Ursus arctos*) i Sverige. De 3 andre artiklene handler om begreper og bruker modeller for å utforske selektivitetsmekanismer og forvaltnings rolle. Jeg valgte å ikke fokusere på en bestemt modellart, men i stedet legge vekt på prosessene. Gjenstandene for studiene spenner fra store rovdyr, hovdyr, og gnagere, til teoretiske utlegninger med eneste hensikt å vise endringer i et hypotetisk trekk.

Selektiv høsting og utnyttelse generelt vil fortsette å påvirke viltpopulasjoner og deres samfunn. Med dagens høye befolkningstetthet, som fortsatt er økende, og økt effektivitet av innhøstingsredskap og metoder, er behovet for å vurdere både den kortsiktige og langsiktige bærekraften av menneskets utnyttelse svært viktig. Med denne oppgaven legge jeg fram en rekke forslag, de viktigste er:

- Kvantifisering av høstingseffekter på viltpopulasjoner bør ta i betraktning informasjon om selve populasjonen, så vel som kulturelle aspekter ved høsting og forvaltning.
- Høstingsdødelighet må ses i sammenheng med total dødelighet, fordi det er den kombinerte effekten av all dødelighet som avgjør levedyktighet.
- Forsiktig selektiv høsting kan tilpasses til noen systemer dersom man i tilleg anvender metoder som kompenserer for denne høstings-selektiviteten.
- Adaptiv atferd kan ha betydelige konsekvenser for forvaltningen, særlig ved høy uttaksrate, slik som de som anvendes for å kontrollere invaderende arter.
- Når man gir anbefalinger for å minske eller reversere effektene av selektiv høsting, er det viktig å gi klart uttryk for hva målene er, og under hvilke betingelser de mulige løsningene kan fungere.

Det er den kombinerte effekten av høstingens størrelse og høstingens selektivitet som avgjør de kort- og langsiktige konsekvensene for viltpopulasjoner og deres samfunn. Ettersom menneskeskapt dødelighet fortsetter å øke eller erstatter naturlig dødelighet, kan det å vite hvilke individuer eller grupper som er mest utsatt være like viktig som å vite hvor mange individuer som blir felt. Der hvor menneskelige utnyttelsesmønstre viser seg å ikke være demografisk, evolusjonært eller økologisk bærekraftige, er endringer i omfang og selektivitet av høsting nødvendig for å redusere skadelige effekter.

Zusammenfassung

Menschliche Nutzung beeinflusst Wildtierpopulationen auf vielfältige Weise, vor allem bezüglich deren Demografie, Verhalten und Evolution. Selektive Jagd – der absichtliche bzw. unabsichtliche Vorzug bestimmter Individuen oder Gruppen – scheint besonders geneigt zu sein, Populationen und deren evolutionäre Tendenz zu verändern. Das Ziel der vorliegenden Arbeit ist, ein Beispiel für die Erfassung von Jagdselektion vorzulegen und durch verschiedene Modelle die mit derartiger Selektion verknüpften Prozesse hinsichtlich ihrer Auswirkungen und möglicher Lösungsansätze zu untersuchen.

Die Arbeit basiert auf fünf Publikationen. Zwei davon sind deskriptive Publikationen, die die Jagd und Mortalität von Braunbären (*Ursus arctos*) in Schweden betrachten. Die anderen drei Publikationen beschäftigen sich mit Konzepten und verwenden Modelle um die Mechanismen der Selektierung und den Einfluss des Wildtiermanagements zu untersuchen. Dabei habe ich mich nicht auf eine bestimmte Modellspezies beschränkt, sondern stattdessen das Augenmerk auf die Untersuchung von Prozessen gerichtet. Die Objekte der vorgelegten Studien reichen von Großraubtieren über Huf- und Nagetiere bis hin zu ausschließlich theoretischen Konstrukten mit dem alleinigen Ziel, Verschiebungen in der Verteilung eines hypothetischen Merkmals zu verdeutlichen.

Jagdselektion und Jagd generell werden auch in Zukunft Wildtierpopulationen und -gemeinschaften beeinflussen. Das extreme Wachstum der Weltbevölkerung einerseits und die Effektivitätssteigerung von Jagdgerät und -methoden andererseits erfordern, dass sowohl Kurz- als auch Langzeiteinflüsse von Fang- und Jagdabläufen zu beachten sind. Mit der vorgelegten Arbeit möchte ich eine Reihe von Empfehlungen unterbreiten, zu deren wichtigsten die nachfolgenden gehören:

- Bei der Erfassung von Jagdeffekten auf Wildtierbestände sollten sowohl Informationen über die betroffenen Populationen als auch über die kulturellen Aspekte der Jagd und des Wildtiermanagements berücksichtigt werden.
- Jagdmortalität muss im Zusammenhang mit der Gesamtmortalität betrachtet werden, da der gemeinsame Effekt aller Mortalitäten die Überlebensfähigkeit bestimmt.
- Geringfügige jagdselektive Effekte könnten möglicherweise in manchen Systemen durch kompensatorische Maßnahmen ausgeglichen werden.
- Verhaltensanpassungen können – insbesondere bei hohen Fang- bzw Jagdraten – wichtige Auswirkungen auf das Wildtiermanagement haben, so z. B. jene durch die Kontrolle invasiver Arten.
- Vorschläge zur Vermeidung oder Umkehrung der Effekte selektiver Jagd sollten immer auch die Zielstellungen und die Bedingungen potentieller Lösungen enthalten.

Die Kurz- und Langzeitkonsequenzen für Wildtierpopulationen und -gemeinschaften werden durch den Umfang und die Selektivität der Nutzung durch den Menschen bestimmt. Wenn künstliche Mortalitätsschemata die natürlichen verstär-

ken oder ersetzen, ist die Kenntnis der betroffenen Individuen oder Gruppen ebenso wichtig, wie die der Zahl getöteter Individuen. Wo der Eingriff des Menschen demographische, evolutionäre oder ökologische Nachhaltigkeit negiert, müssen Anpassungen des Ausmaßes bzw. der Selektivität der Wildtiernutzung nachteilige Effekte mindern.

List of articles

Article I

Bischof, R., R. Fujita, A. Zedrosser, A. Söderberg, and J. E. Swenson. 2008. Hunting patterns, the ban on baiting, and harvest demographics of brown bears in Sweden. Journal of Wildlife Management 72:79-88.
doi: 10.2193/2007-149

Article II

Bischof, R., J. E. Swenson, N. G. Yoccoz, A. Mysterud, and O. Gimenez. 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. Journal of Animal Ecology 78:656-665.
doi: 10.1111/j.1365-2656.2009.01524.x

Article III

Mysterud, A., and R. Bischof. 2009. Can compensatory culling offset undesirable evolutionary consequences of trophy hunting? Journal of Animal Ecology. Published online in advance of print.
doi: 10.1111/j.1365-2656.2009.01621

Article IV

Bischof, R., and A. Zedrosser. 2009. The educated prey: consequences for exploitation and control. Behavioral Ecology 20:1228-1235.
doi: 10.1093/beheco/arp124

Article V

Bischof, R., A. Mysterud, and J. E. Swenson. 2008. Should hunting mortality mimic the patterns of natural mortality? Biology Letters 4:307-310.
doi: 10.1098/rsbl.2008.0027

Synopsis

1. Introduction

Throughout human history, we have had a tremendous impact on the wildlife that we exploit. We caused, or at least contributed to the extinction of species with stone-age hunting weapons and methods (Flannery, 2001; Brook and Bowman, 2004; but see Owen-Smith, 1988). As an agent of evolutionary change, we have altered their appearance (Law, 2001), their life history (Festa-Bianchet, 2003), and behavior (Sasaki et al., 2009). We demoted top carnivores and installed ourselves as such (Ray et al., 2005), albeit generally with lower competence (Berger, 2005). We altered community structures and trophic systems (Steneck and Sala, 2005). We have modified species distributions, in part through persecution and in part through intentional translocations, so that we could hunt familiar species in new places (Kraus, 2003). This list is by no means complete.

Humans have not only been hunting for a long time, but have been doing so selectively. Archeological records suggest size-selective harvesting since at least the Middle Stone Age (Klein et al., 2004). Specifically, bias towards larger sizes was likely facilitated by their greater detectability and the higher payoff per unit effort (Fenberg and Roy, 2008). Evidence of the dramatic effects of such selectivity has been found in several prehistoric marine systems (reviewed in Steneck and Sala (2005)). More recently, size-selective commercial fishing has been identified as a likely cause for the collapse of northern Atlantic cod (*Gadus morhua*) stocks (Olsen et al., 2004). In terrestrial systems, trophy hunting has been the practice most prolific in yielding examples of negative evolutionary and demographic effects of selective harvesting (Coltman et al., 2003; Barnes and Kapela, 1991; Whitman et al., 2004). The attention directed at the effects of selective harvesting is illustrated by a splurge of reviews on the subject during the past decade (Law, 2001; Ratner and Lande, 2001; Harris et al., 2002; Stockwell et al., 2003; Birkeland and Dayton, 2005; Hairston et al., 2005; Milner et al., 2007; Allendorf et al., 2008; Coltman, 2008b; Fenberg and Roy, 2008; Allendorf and Hard, 2009; Darimont et al., 2009). The following list gives an overview of some important effects of selective harvesting:

1. direct demographic effect: This is the reduction in survival as a result of the removal of individuals, leading to changes in the population growth rate - the effect that wildlife managers have traditionally been the most concerned with (Williams et al., 2002; Caughley, 1994). Selectivity can play an important role, because the magnitude of the influence depends in part on the relative vulnerability of sex and age/size groups and the sensitivity of the population growth rate to changes in individual vital rates (Benton and Grant, 1999). Overall, underharvesting, following the disturbance of natural community structures and trophic systems, can contribute to habitat degradation, whereas overharvesting has led to severe reductions and many extinctions. Example: high harvest pressure on large mature fish, especially in slow-growing and long-lived species has a disproportionally negative effect on population growth, in part because their fecundity (number of larvae produced) and quality of their larvae (larval survival) are greater than in younger, smaller fish (reviewed by Birkeland and Dayton, 2005).

2. indirect demographic effects: These include effects on the population growth rate (often through a reduction in recruitment), due to changes in the age

and sex structure of the population, the removal of key individuals, as well as the resulting destabilization of social structures. Indirect demographic effects have been reviewed by (Milner et al., 2007). Example: in some brown bear populations, it appears that the killing of adult males indirectly affects recruitment, due to the influx of other, potentially infanticidal males (Swenson et al., 1997; Wielgus and Bunnell, 2000).

3. evolutionary effects: These refer to changes in heritable traits (physical and life history traits, as well as unobservable genetic substructure) in the population as a result of selective pressure exerted through harvesting (most recently reviewed by Allendorf and Hard, 2009). Their importance was first recognized in fisheries, followed by ecologists and managers of terrestrial systems (Harris et al., 2002). In fact, it appears that persecution by humans causes significantly greater and more rapid change in traits in wild populations than other factors (Darimont et al. 2009). Example: one of the best-supported examples of evolutionary change due to selective harvesting is the decline in body weight and horn size in bighorn rams (*Ovis canadensis*) at Ram Mountain, Alberta, Canada following intense trophy hunting (Coltman et al., 2003).

4. ecological effects: These are the effects of harvesting on community structure and ecosystem functioning (reviewed by Fenberg and Roy, 2008), going beyond just the target species. The selective removal of large and/or dominant individuals can negatively impact the ability of a predatory or competing population/guild to play its functional role in the trophic network (Berger et al., 2003). Example: the selective exploitation and removal of cod and other large vertebrate predators in marine coastal zones resulted in an increase in invertebrates, including crabs and sea urchins. Particularly the overabundance of the latter led to overgrazing of marine algae to the point of leaving wide-spread barrens (Steneck and Sala, 2005).

I began this PhD study with the intent to help narrow the large gap between the tasks and skill set of the applied wildlife manager and the knowledge that has been accrued by scientists in ecology, evolutionary biology, conservation, and natural resource use. Having worked as a wildlife manager, I know that managers are often either not aware of effects 2, 3 and 4, or do not consider them important enough to include them in management plans. This thesis is about hunting, selective in one way or another, and it is my objective to highlight some of the implications of biased harvesting, as well as possible solutions. The scope of the 5 articles that make up the thesis helps illustrate the diversity of issues involved. Article I describes the Swedish brown bear (*Ursus arctos*) harvest using solely hunting data, whereas Article II relies on long-term individual-based monitoring data to estimate brown bear vulnerability to hunting and other mortality causes. Article III takes on the evolutionary changes in red deer (*Cervus elaphus*) antler sizes due to trophy hunting and, with the help of a simulation model, investigates the feasibility of compensatory culling to make trophy hunting sustainable. Article IV addresses non-lethal effects of hunting by theoretically evaluating the role of individual learning and behavioral adaptation in exploited populations and the implications for hunting and invasive species control. Article V points out caveats associated with the management recommendation that hunting should mimic the patterns of natural mortality. In the remainder of the synopsis, I discuss each article within the wider context of selective harvesting and offer my thoughts about the implication for management and exploitation.

2. Brown bear hunting in Sweden: quantifying selectivity

When evaluating the effects of hunting, it is convenient to start with an assessment of its extent from the perspective of hunters and managers. This means analyzing harvest data, such as bag sizes, catch per unit effort, demography of killed animals, and similar measures that can be obtained from hunter surveys and hunter-killed individuals. Although harvest data have limitations when it comes to drawing conclusions about the exploited population and can be fraught with biases (Bunnefeld et al., 2009; Martínez et al., 2005), they should not be discounted, as they can provide insights into hunting patterns (Mysterud et al., 2006) and temporal trends in wild populations (Cattadori et al., 1999). A distinct advantage of harvest data is that they are generally much easier to obtain than direct measurements on the target population. Such is the case for brown bears in Sweden, where all successful hunters must present their bear carcasses to an officially appointed inspector on the day of the kill and provide information about harvest methods, the sex of the harvested bears, body mass, kill location, as well as various samples to the authorities. In Sweden, brown bears are hunted during a 1-2 month fall hunting season. Currently, harvest quotas are county- (län) specific. Bears are hunted by sit-and-wait (still hunting), stalking, with dogs, and over bait (meat-based). In 2000, the Swedish Environmental Protection Agency (Naturvårdsverket, 2000) issued a ban on baiting for bears to start in 2001, mainly because of concerns about human safety and a perceived greater vulnerability of bears to this method.

Article I in this thesis describes the analysis and interpretation of harvest data, using the Scandinavian brown bear hunt as an example. The main objective was to gain a general overview of the Swedish brown bear harvest, including the demographic composition of killed bears and the contribution of the different hunting methods. Results indicated that the relative prevalence of methods that yielded bears varied depending on the harvest region and whether a hunter was hunting specifically for bears or not. Apparently, hunting over bait was more important for bear-oriented hunters, whereas hunters going after moose shot bears incidentally most often while still hunting. A particularly important component of the study was the comparison of pre and post bait-ban patterns in hunting methods and demographic makeup of harvested bears. When comparing the 4 years immediately prior to the ban on baiting with the 4 years following the ban, we found no differences in average age of harvested bears, sex ratio, or proportion of bears killed with the various methods, suggesting that the ban on baiting in Sweden had no immediate effect on patterns of brown bear harvest demography and remaining hunting methods.

Harvest data by themselves are generally insufficient to quantify the impact of hunting on the population. For example, without information about the demographic makeup of the population, it is difficult, if not impossible, to distinguish whether differential vulnerability or higher frequency in the population is the cause for greater prevalence of a certain population segment among hunter-killed animals. Article II complements the information gathered in Article I by illuminating the effect of hunting from the bear's perspective, i.e. it assesses risk. Because individual viability is determined by the combination of all causes of death, a comprehensive look at hunting survival requires that it be evaluated within the context of the magnitude and selectivity of all mortality causes. For this reason, we also considered mortalities due to causes other than legal hunting, such as natural (mainly intraspecific kills), damage control and self defense, illegal hunting, and traffic accidents. At the time of this study, 23 years of individual-based data on 525 brown bears were available. Many bears had been monitored since they were yearlings until their death, presenting a rare opportunity to estimate viability in a large carnivore. We fit multi-state capture mark recapture models (Hestbeck et al., 1991; Brownie et al., 1993) to capture histories in order to estimate cause-specific risk to hunting and other mortalities of Swedish brown bears. The trick to estimate cause-specific mortalities was to model mortalities as transitions to "newly dead" states, one for legal hunting mortality and one for all other mortalities; see Schaub and Lebreton (2004) for another example of this approach. As with the harvest analysis (Article I), the evidence for age and sex selectivity of legal hunting was weak, with a trend towards greater male vulnerability. Although hunting is the single-most important source of mortality among Swedish bears, it became clear that the combined mortalities other than legal hunting are also important contributors to bear mortality in Sweden, and as such should not be ignored during demographic analyses. Furthermore, these non-hunting mortalities showed a greater age bias than legal hunting.

It appeared that hunters harvesting bears in Sweden are less selective than their North American counterparts (e.g., brown bear: McLellan and Shackleton, 1988; black bear: Kohlmann et al., 1999), possibly due to differences in the hunting system. Limited encounters with bears, Swedish hunting traditions, and the hunting system – no individual bag limits and no specific license requirement – provide little motivation and opportunity for hunters to be deliberately selective when shooting bears (other than the avoidance of family groups, which are protected). Thus any biases that may be present in the harvest would most likely be a result of passive selectivity, e.g. a result of differential vulnerability due to heterogeneities in life history, behavior, and mobility rather than active selection by the hunter. Similarly, Bunnefeld et al. (2009) suggested that in red grouse (*Lagopus lagopus scoticus*) in Northern England selectivity for younger birds in the harvest is unintentional, as individuals cannot be distinguished during the hunt based on sex or age class. As the demographic and evolutionary side-effects of selective harvesting receive growing attention, wildlife managers should be aware that differences in harvest systems between jurisdictions may cause qualitative and quantitative differences in harvest biases.

The lack of strong obvious selectivity of legal hunting for certain sex and age classes should not be taken as an indication that hunting does not exert selective pressure on brown bears in Sweden. Firstly, although hunting may show no or limited bias for sex and age, there could be other untested or unmeasured traits/features that distinguish between more and less vulnerable individuals. This also shows the difficulty of identifying or attempting to implement unbiased harvest - unless all possible sources of bias are identified and controlled for, harvest may be (and probably is) selective. Secondly, even unbiased harvesting can put selective pressure on certain life history traits and consequently physiological traits. This can occur through an increase in overall mortality and reduced life expectancy, which in turn selects for younger age and smaller size at the time of first reproduction, as future reproduction is discounted (Fenberg and Roy, 2008; Proaktor et al., 2007; Heino and Godo, 2002; Kuparinen and Merilä, 2007).

Finally, although we found no noticeable age-bias of hunting and only a trend of a sex bias (Article II), there is another form of bias, which is a direct result of current bear hunting regulations: family groups – mothers and their dependent young – are protected from legal hunting. Therefore, legal hunting is strongly biased for females that are not part of a family group during the hunting season. In the short term, the protection of mothers with dependent young is bound to have positive demographic effects. As Miller (1990) suggested, protection of family groups is a way of steering hunters away from the female segment of the population. In species where a solitary individual's sex cannot easily be identified by a hunter, as is the case with brown bears in Scandinavia (Bischof et al., 2008), association with dependent young provides the means for correctly identifying females and hence affording adult females some protection. Furthermore, mothers with dependent young may be more vulnerable to certain harvesting methods than other adult segments of the population (Article I), in which case protection has an even greater impact.

With respect to the protection of family groups from hunting, there are additional considerations beyond short-term and direct demographic implications. It seems plausible that such strong selectivity in our study population and in other systems with similarly selective harvesting may, in the long run, have consequences for the evolution of female life history strategies. What precisely these consequences could be is the subject of another ongoing investigation, but there are some suggestions I can offer for our study system now. Whereas survival is positively affected by family association, there is an implicit tradeoff involved. Longer association with the mother, i.e. higher weaning ages, while reducing risk for both the mother and cubs, also decreases female fecundity, because a female will typically not enter estrus unless she has weaned or lost her young prior to or during the mating season (Dahle and Swenson, 2003). If viability selection favors individuals that wean their young later in order to decrease exposure to legal hunting, an evolutionary response and increase in average weaning age could lower the per capita birth rate, since inter-litter intervals would increase. In such a way, the evolutionary shift in a trait (duration of maternal care) could have demographic consequences.

Hunting bears in Scandinavia and elsewhere in Europe may have already shaped today's Eurasian brown bear in terms of life history and behavior. This notion is supported by some evidence of differences in aggression towards people (Swenson and Sandegren, 1999) and diurnal behavior (summarized in Kaczensky et al., 2006) between brown bears in Europe vs. North America, where bears have a much shorter history of human persecution. Also, in a comparison of brown bear populations with and without long-histories of human exploitation, Zedrosser (2006) found that the latter exhibit greater and earlier reproductive investment, arguing that this is an evolutionary response to elevated adult mortality.

Box 1. Bear hunting in Sweden today

The following description is based on personal observations during the 2008 bear hunting season and conversations with hunters, wildlife managers, and the Scandinavian Brown Bear Research Project's field leader S. Brunberg between spring 2007 and summer 2009. A common setup for a bear hunt in central Sweden is a hunting team, consisting of several sedentary hunters arranged around the area that is to be hunted. One or more dog teams (handlers and one to several dogs) will work the area, with the dogs either on or off leash. If the hunt is successful, a bear is held at bay by the dog(s) and shot by the hunter following the dog, or it is shot by one of the hunters posted on the periphery as it attempts to leave the area. Most Swedish hunters consider killing a bear a once-in-a-life-time opportunity and harvested animals are treated as trophies. Aside from the taxidermy of the pelt and skull, the meat is also used by the hunter or sold to specialty food retailers or lodges. A detailed description of brown bears and their pursuit from the perspective of the Swedish hunter is provided in Boström and Lännbjer (2008).

Today's Swedish bear hunter could be mistaken for member of a special-ops team. He is equipped with a walkie-talkie and ear-piece to communicate with his fellow hunters in the field, with a mobile phone to stay in touch with the world beyond his hunting grounds, and a GPS unit to track his own and his dog's movements. The dog sports a harness with a GPS unit, VHF transmitter, and perhaps even a built-in barking indicator. I have met hunters who carry along gun-mounted video cameras to record their shots and even attach an action cam to their dog's harness to get that perspective of the hunt. As a side effect, many hunters spend a fair amount of time monitoring their electronic equipment, not only the forest.

The antennas protruding from the hunter can be a nuisance to him, but the effectiveness and accuracy with which he can collect and evaluate the information about the hunt make the troubles well worth it. Seeing on a screen how the dog moves through the landscape, working (or not) in different sized loops away and back to the hunter can help assess the effectiveness of the dog and its training and also detect a response quickly. Staying in touch with fellow hunters, positioned throughout the forest, not only allows a free flow of information about the game seen or not seen, but also heightens the level of safety, as each hunter knows were he is in relation to everyone else. These technological advances go hand-in-hand with an increase in experience and effectiveness of the average Swedish bear hunter, which is bound to have an effect not only on his success, but ultimately on the bear population as well.

photo: R. Bischof, 2008

The Swedish bear may or may not be evolving, but its hunter's gear and methods definitely are. The Swedish bear hunter was a moose hunter during most of the 20th century. While moose hunters continue to shoot bears incidentally, some hunters have adjusted their methods and gear (i.e. dogs) to hunt specifically for bears, as the species became more common in Sweden. The increased proficiency with which bear hunters harvest bears in Sweden (Box 1) is bound to have consequences for the population, or at the very least for the time it takes to meet annual quotas. Furthermore, bear density has increased substantially over the past 25 years (Saether et al., 1998; Kindberg et al., 2009) and it remains to be seen whether this and correspondingly greater encounter rates will result in greater hunter selectivity in the future (see also the Discussion in Article I).

The near-extinction of bears due to extensive persecution until the late 1900s was followed by a recovery (Bjärvall, 1990; Swenson et al., 1995) that lead to today's population in Sweden, which exceeds that of the mid-1800s (Kindberg et al., 2009; Swenson et al., 1995). Still, these continue to be dynamic times for brown bears in Sweden. Aside from the potential for evolutionary effects mentioned above, there are direct demographic impacts due to rapidly increasing quotas over the past decade that may now be reaching or even exceeded sustainable levels, at least in central Sweden (Bischof et al., 2009), as well as indirect demographic effects of killing adult males, which may facilitate sexually selected infanticide (Swenson et al., 1997).

Past and current management regimes will continue to determine the makeup and dynamics of the Swedish brown bear population. The management of exploited populations involves complex decisions at various levels: there are decisions about the research questions that scientists will focus on, decisions by managers about what goals to establish and how to use their experience and scientific information to achieve them. There are also important decisions by the individual hunter, for example where to hunt, when to hunt, how to hunt, and whether to take a shot or not. All these decisions in concert create the harvest patterns that we observe, so it is clear that the maintenance of brown bear hunting in Sweden as a sustainable recreational activity and effective management tool requires the continued interaction among managers, scientists, and hunters. It is as important for managers to understand and appreciate the more subtle elements of selective harvesting as it is for researchers to be aware of the constraints and objectives under which managers operate.

Attempts to quantify the magnitude and selectivity of harvesting should draw from harvest data, as well as information about the population that is being exploited; estimation of vital rates is essential to assess differential vulnerabilities, whereas knowledge about the harvesting regimes and the cultural aspects of management can provide the context that simplifies the interpretation of observed patterns of vulnerability and exploitation. Furthermore, harvest mortality should be considered in the context of overall mortality, in part to determine its direct relative population dynamic importance and in part to evaluate its contribution to viability selection. Although harvesting selectivity can be intentional through regulations or culture, the potential for unintentional selectivity as a result of intrinsic differential vulnerability should not be underestimated, and is a further reason to not rely solely on harvest data to assess the impact of exploitation. In fact, management programs that continue to rely on harvest data for detecting demographic trends in populations should be challenged to evaluate the harvest for potential unintentional biases (Bunnefeld et al., 2009; Martínez et al., 2005).

3. Trophy hunting and the utility of compensatory selection

Trophy hunting, with its strong bias for exceptional specimens, is perhaps the most noticeable selective harvesting regime with long-term consequences (e.g., African elephant: Jachmann et al., 1995; Rasmussen et al., 2008; Barnes and Kapela, 1991; African lion: Whitman et al., 2004). Among the most desired trophies are antlers in cervids and horns in bovids and there is convincing evidence that sizes of these sexual ornaments have declined in some populations (Coltman et al., 2003; Garel et al., 2007; Loehr et al., 2007). Having been convinced of the detrimental effects of selective harvesting by abundant empirical and some theoretical evidence (Ratner and Lande, 2001; Law, 2001; Thelen, 1991), an obvious question is how to deal with the problem. One solution is to stop trophy hunting altogether. This, albeit effective, is unlikely to happen as long as affected populations appear to persist at least numerically, giving the appearance of sustainability. Importantly, trophy hunting bestows economic benefits upon rural communities and can contribute to species conservation (Festa-Bianchet, 2003; Milner et al., 2006), although it needs to be added that these benefits are neither universal nor unchallenged (Lindsey et al., 2007; Hussain, 2003). Are there ways trophy hunting can be made ecologically sustainable, or at least help sustain the activity itself?

Red deer (*Cervus elaphus*), with their highly priced antlers, have been an important target of recreational hunters for centuries. Consequently, the species has been studied extensively and much is now known about its population dynamics, ontogeny, and life history (e.g., Coulson et al., 2004; Catchpole et al., 2004), as well as some of the genetics underlying antler development (e.g., Kruuk et al., 2002). In Article III, we made use of the accumulated knowledge, and, with the help of an individual-based model (IBM), explored the utility of compensatory culling of low-quality yearling males in order to compensate for the trait-changing effect of trophy hunting of adult male red deer. We simulated a population of red deer stags with empirically based demographic and trait attributes (e.g. heritability and antler growth). We then allowed natural mortality, hunting mortality and age and antler-size dependent reproduction to occur, so that an optimal strategy, in terms of antler size, could emerge under a given management regime. One of these management regimes consisted of trophy hunting of adult stags paired with selective culling of yearlings with small antlers, indicative of smaller antler size as adults. Simulation results showed that, given heritability and yearling-to-adult correlation of antler size, compensatory selective culling of yearlings can help compensate for the trait-changing effect of trophy hunting adults, as long as trophy pressure is reasonably low (i.e. around 10% of trophy-quality males).

As is often the case, the development of the model provided as many or more insights into the system under study than the predictions from the final model. The model described in Article III is not the first IBM of an ungulate population (see for example Collier and Krementz, 2007; Proaktor et al., 2007), nor is it the first IBM focusing on red deer antler quality (Thelen, 1991). To my knowledge, however, it is the first such model incorporating trait-based selective hunting in yearling males in order to compensate for trophy hunting effects in adults. It quickly became apparent that the complexities involved are daunting. The system modeled was one with overlapping generations, age-dependent survival and reproductive rates, combined viability and fecundity selection, as well as density-dependent effects on antler size and survival. In addition to the numerous interactions between trait development, breeding success and survival, there is the differentiation between evolutionary effects vs. short-term effects. The latter means that managers may observe shifts in the distribution of antler sizes that are due to change in the age structure or the persistence of individuals, rather than a change in average breeding values due to selection on a heritable trait.

In a comparison of trait and life-history changes in human-harvested and natural populations, Darimont et al. (2009) reported greater life-history trait changes in response to human exploitation than changes in morphological traits. It is thus possible that the obvious shifts in the quality of sexual ornaments or body size in populations under trophy hunting pressure may be accompanied by even greater changes in life history. As we used an individual-based model in Article III that simulated growth, aging, and reproduction on an individual level, this aspect is likely accounted for, at least in part. Nonetheless, we must be aware that changes in morphological traits may be just one sign of more substantial alterations at the core of a species' life history. The concept of compensatory culling is limited in that it is aimed at addressing one aspect of trophy hunting, namely its selectivity for higher quality sexual ornaments or body size. As such it may only serve as a Band-Aid, rather than a comprehensive solution to a complex problem.

Managers are typically concerned with immediate or short-term effects of management (Harris et al., 2002; Stockwell et al., 2003). Genetic concerns are being considered and addressed in some cases (Allendorf et al., 2008; Drechsler, 1992), but generally it is difficult to interest terrestrial wildlife managers in the long-term evolutionary consequences of certain management regimes. With a conventional view on evolutionary time frames, it is hard to see how current management regimes will be maintained for the thousands of years it may take to obtain a noticeable response. The point however is that it may not take that long. As shown by Darimont et al. (2009), trait changes in wild populations are much more rapid when humans are involved. There are now several examples of rapid evolution under exploitation pressure (review in Hairston et al., 2005). Following comparison of hunted and unhunted populations of the Japanese mamushi snake (*Gloydius blomhoffii*), Sasaki et al. (2009) attributed differences in body size, reproductive investment, and behavior to evolutionary responses to harvesting pressure. Other examples are the already mentioned early-maturation trends in Atlantic cod attributed to size-selective commercial fisheries (Olsen et al., 2004) and the declining horn sizes in big horn rams as a result of trophy hunting (Coltman et al., 2003). Displeased with the lack of a clear definition of what"rapid" is within the context of rapid evolution, Stockwell et al. (2003) introduced the term "contemporary" evolution to refer to evolutionary changes "observable over less than a few hundred years". Our simulations (Article III), with the assumption of moderate heritability of antler size ($h^2 = 0.329$), also indicated that noticeable phenotypic changes are possible within 5 - 10 generations. Narrowing the timeline within which evolutionary change is possible should give managers a greater sense of urgency when it comes to considering the evolutionary implications of current management regimes. The argument of a relatively fast response could also make managers more inclined to consider actions that are intended to reverse or compensate for evolutionary change that has already occurred. Such reversal has been documented as a result of the interplay of natural selection and changing harvest intensities in a population of pike (*Esox lucius*, Edeline et al., 2007; see also Coltman, 2008a). Caution is advised nonetheless; through experimental exposure of silverside fish (*Menidia menidia*) populations to different forms of size-selective fishing, Conover et al. (2009) found that, although evolutionary change in their laboratory system was reversible, it required more than twice the time than the original selection period. This and the potential loss in genetic variation through strong selective pressures suggests that, whenever possible, we should emphasize proactive approaches to evolutionarily sustainable harvesting rather than attempting to fix things after they are broken.

4. Behavioral effects: learning to fear the hunter

Up to this point, this thesis has been concerned with the lethal effects of hunting. Predators, human and non-human alike, not only affect populations by removing individuals. Behavioral responses of prey to predation such as modification of foraging rates, habitat use, and activity patterns (reviewed by Berger, 2005) have population and community-level importance. Human hunters, like natural predators, can cause alterations in the behavior of survivors or non-targets. For example, various studies have shown effects of hunting on habitat utilization and food intake in waterbirds (reviewed by Tamisier et al., 2003) and mourning doves (*Zenaida macroura*, Roy and Woolf, 2001). As another behavioral effect, hunted ungulate populations exhibit greater flight-initiation distances than non-hunted populations (reviewed by Stankowich, 2008).

An interesting combination of non-lethal effects and harvesting selectivity is the reduced vulnerability of individuals who have survived and learned from an encounter with a hunter and subsequently are less likely to be harvested. This is a special situation, because the non-lethal effect of hunting – i.e. the "education" of individuals that escaped an attempt – subsequently leads to unintentional selectivity, which in turn affects both population dynamics and harvesting efficiency. There are many examples of this happening; first-generation toxicants for the control of pest and invasive species have been replaced by newer drugs and delivery systems, partially because of concerns over learned taste aversion after the ingestion of sub-lethal doses (Towns and Broome, 2003). Hunters and trappers perceive an increased difficulty with which some animals are harvested once they have been educated to hunters or a certain trap type. Finally, although different in terms of its outcome for the individuals targeted, capture responses (trap happiness or shyness) in capture-mark-recapture studies are acquired as a consequence of previous experience with a capture method or tool (Pradel, 1993).

Article IV explores the potential implications of learned recognition or avoidance behaviors in the context of exploitation by humans. We present a multistate exploitation model that accounts for improved defenses to exploitation as a result of experience and make predictions about the implications for harvesting of wildlife populations and for invasive species control. These implications can be substantial, especially when harvest rates are high, as is the case with invasive species control. For example, the time required to extirpate a population of invasives can increase several-fold if a small proportion of targeted individuals survives the initial encounter with a control device and then learns to avoid subsequent exposure to the device. Among the findings are the modulating role that the speed of life history plays; learned avoidance has a greater impact in longer-lived species, and some non-intuitive effects; in the presence of response loss over time, harvest yield or the ability to control an invasive species can actually decline as exploitation pressure increases. We demonstrated the latter, seemingly counterintuitive effect, in theoretical systems where response loss is possible, because for certain parameter values the benefits of increased control effort are outweighed by the cost of turning naïve individuals into educated ones and meanwhile continuously re-educating (i.e. preventing response loss in) educated individuals.

Predator recognition and learned avoidance behaviors are ecologically relevant for reasons beyond immediate survival benefit. Fitness tradeoffs are a major component of the theory of inducible defenses, which generally postulates that without costs, defensive traits will be fixed (Tollrian and Harvell, 1999). Although fitness tradeoffs were not modeled explicitly in Article IV, they can easily be incorporated into the model by using different vital rates (natural mortality and/or fecundity) for naïve and educated individuals. Negative demographic effects are likely if individuals must trade-off reproduction or natural survival for predator avoidance, e.g. through reduced foraging time (Tollrian and Harvell, 1999), and there are examples of this being the case in systems exploited by humans (Roy and Woolf, 2001; see also review by Frid and Dill, 2002).

Aside from adding a behavioral component to selective harvesting, Article IV expands the treatment of human exploitation to include the removal of individuals for control purposes (e.g. invasive or pest species), not only commercial reasons or recreation. Exotic species invasions are now one of the primary drivers of biodiversity loss worldwide (Stockwell et al. (2003) and references therein) and managers are routinely charged with the control and eventual eradication of invading species (Rodda et al., 1999; Towns and Broome, 2003). Although the demographic and evolutionary consequences of selective harvesting are generally disadvantageous in the context of sustainable exploitation, it is conceivable that they can be turned into assets in the fight against invasive species. Intentional phenotypic and life history trait shifts as a result of biased control, targeting of those groups whose survival has the greatest impact on population growth, and demographic and social instability due to selective removal of key individuals are some examples of how the woes of game managers could become the allies of managers targeting invasive species.

5. Conventional wisdom and selective harvesting. Are there practical solutions?

The evidence for detrimental population dynamic and evolutionary effects of size-selective harvesting continues to accumulate from both terrestrial and aquatic/marine systems (Allendorf et al., 2008; Allendorf and Hard, 2009; Stockwell et al., 2003; Birkeland and Dayton, 2005; Darimont et al., 2009; Fenberg and Roy, 2008; Milner et al., 2007). The issue of evolutionary consequences of selective harvesting also has found its way into popular literature (e.g. Newsweek, February 2, 2009). Meanwhile, trophy hunting (or fishing) traditions on land and sea continue, backed by a relatively small but influential lobby and more or less unabated by concerns over the ecological sustainability of the activity. In many cases the warning against picking out the largest, fittest individuals is just being ignored, in others selectivity for the large ones is actually encouraged with the argument of ecological sustainability. The latter is rooted in the persistent perception that targeting larger, older individuals gives young, small animals a chance to grow large (see also Birkeland and Dayton, 2005). This indicates that many consumptive users of wildlife, as well as some wildlife managers – as is evident from the widespread use of lower size limits, still see the harvest of wildlife akin to the picking of fruit. From this perspective, wildlife dynamics are reduced to a kind of ripening process; individuals become ready for harvest in a conveyor-belt-fashion where large and old individuals that are removed by the harvester make room for and are continuously replaced by new individuals.

Even the most pragmatically anthropomorphic view on harvesting and its implications must yield an appreciation of the relevance of issues addressed in this thesis. The reduction in trophy traits due to trophy hunting undermines the activity itself (Article III). The evolutionary effects on life history traits due to extreme size-selective harvesting may have caused or at least contributed to the worldwide collapse of cod stocks (Olsen et al., 2004),with important implication for fisheries. Purely from an economic or recreational perspective, doing business as usual does not appear to have a future. As selectivity, intentional or not, is shaping up to play an increasing role in our ability to exploit and control wildlife populations, we need to search for strategies that balance our desire for high yield or trophy quality with long-term sustainability.

An essential step prior to any mitigating management is the recognition that selective harvesting has implications that go beyond direct demographic effects that are usually the primary concerns of managers and resource users, and that these effects can be severe enough to deserve consideration in management plans (Conover and Munch, 2002; Ratner and Lande, 2001; Harris et al., 2002). Various strategies have been proposed for minimizing or reversing the negative selective effects of harvesting, some of which I will address in more detail here, as they are prevalent in the literature and pertinent to the examples in this thesis.

1. One of the most effective ways to reduce the impact of selective harvesting is to lower overall harvest pressure (Allendorf et al., 2008; Ernande et al., 2004; Kuparinen and Merilä, 2007). However, tolerance for such reduction is generally low, because management regimes often operate with the objective to obtain something close to maximum sustainable yield, especially for commercially exploited species or highly sought-after game species.

2. Another logical response is to remove bias from the harvest (Allendorf and Hard, 2009; Allendorf et al., 2008; Law, 2001), but there are several problems with this: (i) completely unbiased harvest is hardly achievable, as it requires full knowledge of every aspect of the population, an assessment of individuals encountered during the hunt relative to the population, and full control over the harvest itself, (ii) it will be difficult to completely overcome the human desire for the rare and elusive, and (iii) even unbiased harvest can put selective pressures on life history strategies if it raises overall mortality (Law, 2000; Heino and Godo, 2002).

3. Especially in fisheries management, several authors have recommended a shift from lower size limits to upper size limits (Conover and Munch, 2002; Birkeland and Dayton, 2005; Allendorf et al., 2008), partially in order to afford greater protection to the most fecund individuals (i.e. the larger, older ones) and those with the greatest natural survival. However, when evolutionary considerations enter in, lower size limits are recommended by some (Gårdmark and Dieckmann, 2006; Ernande et al., 2004; Kuparinen and Merilä, 2007), because these are believed to reduce the selection pressure for earlier maturation.

Another, and arguably prudent, take on sustainable harvesting has been to recommend that harvest, in terms of its selectivity, mimic the patterns of natural mortality in the affected population (Milner et al., 2007; Loehr et al., 2007; Bergeron et al., 2008). In Article V, the general validity of this recommendation is evaluated, and it is endowed with disclaimers. Simulations showed that biased hunting mortality, added to equally biased natural mortality will increase the overall bias in viability. There is nothing surprising or profoundly intriguing about this finding, as also recognized in a commentary (O'Hara, 2009) to Article V, but it helped highlight the need for clarifying one's objectives when talking about controlling the negative impacts of biased harvesting (see also Bischof et al., 2009). Some authors use the recommendation to mean that the final outcome (in terms of post-mortality trait distributions) in the presence of hunting should resemble that in its absence, when only natural mortality is acting (Harris et al., 2002; Garel et al., 2007). This is probably the more accurate formulation, because, if implemented, it would leave risk-ratios unchanged.

As we dig deeper into the effects of harvesting on wild populations, we uncover and appreciate its complexity, with its impact on demography and evolution of the target species, as well as on their biological communities. Perhaps we are beyond scratching the surface of the role of human exploitation, but it is safe to assume that the list of evidence for detrimental direct and indirect effects and their interactions will continue to grow. How can we make recommendations for effective and realizable adjustments to our role as exploiters that will improve the sustainable use of wildlife in the short and long-term? How can the insights gained so far be distilled into some general rules for the exploiter?

Article V pointed out that a single best solution may not exist to the problems of selective harvesting. Yet, and despite the complexity of harvest effects on wildlife and our ability to come up with correspondingly complex solutions, we must formulate simple and clear solutions whenever feasible, because accomplishments are limited by our ability to communicate and implement our objectives. Even if there is not a universally optimal solution, we would benefit from a general guiding principle for how we approach the exploitation of wildlife, which can then form the basis for more system- and case-specific strategies. I suggest that, unless population control or severe reduction is desired, a general rule for harvesting should be to harvest what is common at a sustainable rate and to harvest none or next to none of what is rare. This assumes that we know what is common and what is rare, in many cases a realistic premise. This simple rule should be applied to heterogeneity at different levels of organization, for example at the species level (selection based on genotype, phenotype, sex and age), at the level of the guild (selection based on species, average adult body size, etc.), or at the level of the ecological community (selection based on guilds). Whether selection is intentional or un-intentional, the direction and magnitude of selection first must be identified. Once that has been accomplished, adjustments may be possible to harvesting regimes, methods, and hunter behavior (e.g. through regulations).

6. Considerations for research and management

With demographically sustainable exploitation regimes, it is easy to think of hunting as the removal of something that will grow back. However, this is likely too simplistic a view. For example, depending on stochastic events and the selectivity of hunting, killed individuals could be replaced by more or less fit individuals, and we can make an educated guess as to how the population may be affected on the demographic level. Ultimately, we have to accept that harvesting wildlife, selective or not, changes the population - the hunted population will not be the same as the population without hunting, even if exploitation is sustainable in terms of population size. Allendorf et al. (2008) make an even more specific recommendation, namely that we should assume that "some genetic change due to harvest is inevitable". Since humans are part of the natural world and the processes that change it, we do not necessarily have to attach value to this observation, but we ought to be preoccupied with avoiding at least the most detrimental effects.

Ecologists and evolutionary biologists have amassed evidence for short and long-term consequences of selective harvesting. They have unraveled some of its inner workings, better understood the processes involved, and come up with potential solutions for how to cope with or reverse the effects. Despite the wealth of accumulated information and large number of empirical and theoretical studies, the dominant impression that I emerged with from this thesis work is an appreciation of the complexities involved and for the abundance of questions left unanswered. This fuzziness, while somewhat frustrating, can serve as a partial map to help direct future research efforts.

One important complication is that hunting may be selective with respect to multiple dimensions in the same system, such as sex, age, physical appearance, life history, behavior, or even genetic sub-structure without noticeable expression (see for example Bristol Bay sockeye salmon fisheries described in Allendorf et al. (2008)). In addition, some or all of these dimensions may interact or covary with each other and the environment (Kruuk et al., 2002), further complicating the decision about the most important selective effects that research and management ought to target. Take the case of red deer trophy harvest; should management focus on mitigating the trait-changing effect of harvesting stags with the largest antlers (Article III), the effect on age structure and life-history evolution of targeting prime-aged individuals instead of juveniles (Proaktor et al., 2007), the sex-ratio altering effect of a highly male-biased harvest (Ginsberg and Milner-Gulland, 1994), or all of the above? Many questions remain, and answering them will require a more comprehensive approach than the focus on a single trait, as was done in Article V.

This ambiguity is perhaps one of the reasons why biologists are still not in agreement about some of the recommendations for dealing with selective harvesting effects. One example is the contradictory recommendation on the use of size limits for commercial and recreational fisheries. Whereas some recommend the shift from lower size limits to upper size limits (Conover and Munch, 2002; Birkeland and Dayton, 2005; Allendorf et al., 2008), others argue that lower size limits are needed to reduce the pressure for earlier size/age at maturation (Gårdmark and Dieckmann, 2006; Ernande et al., 2004; Kuparinen and Merilä, 2007). This is partially due to a difference in objectives (minimizing demographic effects vs. preventing evolutionary change), and illustrates the need for more comprehensive theoretical and empirical research on the combined role of selectivity on life history and demography.

One of the weaknesses of the study described in Article III is that we did not explicitly model processes that have the potential to maintain genetic variation in sexual ornaments (reviewed by Radwan, 2008). Instead, variation in the model is maintained through a permanent individual error introduced in each individual's "inherited" size. Consequently, we were not able to make quantitative predictions about the change in additive genetic variation under different management regimes in our simulations. Yet, any harvesting regime, selective or not, has the potential to alter not only mean trait values but also trait variances (Law, 2001), which in turn can influence the effectiveness and outcome of mitigating actions. For example, compensatory culling of "poor" quality yearling stags could plausibly be expected to lead to a "squeezing" of the antler size distribution (i.e. a loss of the extremes on both ends of the distribution), and the resulting loss in genetic variation may outweigh any benefit gained from offsetting the effect of trophy hunting on mean antler size. As Roff (2002) pointed out, phenotypic perspectives (e.g. ESS approach) and quantitative genetics methods are being increasingly combined by evolutionary ecologists. Evolutionary studies exploring the implications of selective harvesting will benefit from more movement in that direction and a closer look at effects on other moments of the focal trait distribution, not only its mean.

As pointed out in Articles I and II, and as others have noted (e.g., Milner et al., 2006), the cultural backdrop of an exploitation system needs to be considered when evaluating that system. Understanding the reasons behind intentional selectivity, such as the prestige or monetary value associated with a trophy, can be essential when assessing the extent of harvesting selectivity and predicting the outcome of management actions. Harvesting is generally conducted by individuals or small groups of individuals. Just as the vital rates of individuals are the constituents of the demographics of wild populations, the patterns of exploitation are the result of individual harvesters' actions. Within (and sometimes outside) the boundaries set by laws and regulations, individual decisions lead at least in part to the population-level patterns observed. For this reason, a closer look at the human dimension of exploitation, particularly decision making, may yield the kind of insights that have been gained from similar approaches in such fields as economics and social sciences.

There is an obvious dichotomy in methodology in this thesis. Articles I and II are descriptive, focusing on a real-life brown bear population and its harvest. The other three articles are concerned with concepts and utilize models – more or less empirically based – to study mechanisms underlying real processes. Similarly, most studies on the effects of selective harvesting or harvesting in general are either descriptive or theoretical, with very few examples of controlled experiments (e.g., Conover et al., 2009; Pedersen et al., 2004). However, it is the latter that have the greatest potential to help explain patterns observed and to validate model assumptions and predictions. Properly designed and replicated experiments in the future would help remove some of the guesswork and conjecture that this field is currently fraught with and help solidify its foundation. That said, due to the length of time that even "rapid" evolutionary processes require, modeling will continue to occupy a prominent place in the toolbox of those who investigate and predict the long-term effects of selective harvesting.

The increasing sophistication and invasiveness with which we could and sometimes do manage wild populations leads to another important, albeit less tangible issue of the inherent value of wild things in wild places. Compensatory culling of "poor" quality yearling red deer stags may help compensate for trophy hunting as suggested in Article III, but it also represents a highly invasive interference with a population's natural dynamics. How far can we as managers go and still call a population "wild"? The same question can be asked with respect to wildlife surveys and monitoring. In parts of the Swedish brown bear range, the Scandinavian Brown Bear Research Project has been radio-monitoring between 80%-100% of the female population for over 25 years now. With individuals recaptured every 2-3 years and associated intense presence of field staff during parts of the year for a slough of studies, it is likely that monitoring and bear research are substantial components of a bear's life within the study area. Control areas (remote sensing of collared bears, but no on-the-ground field work) were established in 2007 (J. E. Swenson, pers. comm.); future comparisons may show whether there are differences between intensely studied vs. control areas. As we gain the knowledge and tools to accommodate our current patterns of using wildlife (such as trophy hunting), will it come at the cost of wildness? With this question in mind, it is debatable whether any activity should be considered ecologically sustainable, if it requires invasive and intensive countermeasures to ensure that it can continue.

With the world's human population approaching 7 billion, hunting, at least recreationally, is no longer a right, but a privilege. Regardless of how practical the strategies are that we come up with to address the issue of selective harvesting, it will not be sufficient to just lay down the law. We need not only hunting regulations that are implemented and enforced to facilitate responsible harvesting (Gordon et al., 2004), but also a shift in hunting ethic. As Hardin (1968) put it,"the population problem has no technical solution; it requires a fundamental extension in morality". In the context of intentionally selective harvesting, we have to teach ourselves to go against what seems to be a basic human behavior: we have to choose the common, not the rare; the average, not the exceptional.

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Articles

Article I

Management and Conservation Article

Hunting Patterns, Ban on Baiting, and Harvest Demographics of Brown Bears in Sweden

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ABSTRACT We analyzed harvest data to describe hunting patterns and harvest demography of brown bears (*Ursus arctos*) killed in 3 geographic regions in Sweden during 1981–2004. In addition, we investigated the effects of a ban on baiting, instituted in 2001, and 2 major changes in the quota system: a switch to sex-specific quotas in 1992 and a return to total quotas in 1999. Brown bears ($n = 887$) were harvested specifically by bear hunters and incidentally by moose (*Alces alces*) hunters. Both hunter categories harvested bears 1) using dogs (37%), 2) by still hunting (30%), 3) with the use of bait (18%), and 4) by stalking (16%). The proportion of bears killed with different harvest methods varied among regions and between bear- and moose-oriented hunters. We found differences between male (52%) and female bears (48%) with respect to the variables that explained age. Moose-oriented hunters using still hunting harvested the youngest male bears. Bears harvested during the first management period (1981–1991) were older and had greater odds of being male than during the subsequent period. It appears that hunters harvesting bears in Sweden are less selective than their North American counterparts, possibly due to differences in the hunting system. When comparing the 4 years immediately prior to the ban on baiting with the 4 years following the ban, we found no differences in average age of harvested bears, sex ratio, or proportion of bears killed with stalking, still hunting, and hunting with dogs, suggesting that the ban on baiting in Sweden had no immediate effect on patterns of brown bear harvest demography and remaining hunting methods. As the demographic and evolutionary side effects of selective harvesting receive growing attention, wildlife managers should be aware that differences in harvest systems between jurisdictions may cause qualitative and quantitative differences in harvest biases. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):79–88; 2008)

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KEY WORDS age, baiting, brown bear, demography, hunting, sex, Sweden, *Ursus arctos*.

Brown bears (*Ursus arctos*) in Scandinavia have experienced a drastic decline in numbers to near extinction by the early 1900s as a result of aggressive persecution (Swenson et al. 1995). This decline was followed by a period of recovery, due to protective measures that were implemented in Sweden as early as the late 1800s (Bjärvall 1990, Swenson et al. 1995). Brown bears are currently hunted through most of their range in Sweden, with the annual harvest in 2005 estimated at ranging from 4.1% to 5.1% of the total population estimate (2,350–2,900; Kindberg and Swenson 2006). Bear populations have a relatively low rate of increase and are vulnerable to over-harvest (Miller 1990), so information about the harvest and the relative vulnerability of sex and age groups to different harvest methods is relevant to our understanding and management of the Swedish brown bear population and bear populations in general.

Demographic data derived from harvested animals are typically biased and should be used with caution when drawing conclusions about the sex and age composition or density of the population from which the sample was collected. Despite this caveat, harvest data should not be discarded (Martinez et al. 2005, Mysterud et al. 2006); even with biases, and sometimes because of them, harvest data are important for management-oriented research and life history studies. Several studies on bears (e.g., McLellan and Shackleton 1988, Derocher et al. 1997, Noyce and Garshelis 1997, Kohlmann et al. 1999, McLellan et al. 1999) have shown that harvest is demographically biased and that biases could at least in part be explained by heterogeneities in the bear population (e.g., behavior, mobility, and morphology) and interplay of these heterogeneities with differences in harvest methods, hunter selectivity, and regulations. Although results differ between studies investigating bias and vulnerability in bear harvests, persistent findings shared by most investigations have been 1) harvest is generally biased towards males, 2) young and subadult animals (particularly young M) are more vulnerable than older animals, and 3) harvest sex and age biases differ among harvesting methods. The explanations offered for these biases are wide-ranging. For example, male bias in the harvest is generally explained with greater male mobility, hence greater probability of encountering hunters (Litvaitis and Kane 1994, Noyce and Garshelis 1997, Kohlmann et al. 1999, McLellan et al. 1999), but male bias also has been attributed to the legal protection of females with dependent young (McLellan and Shackleton 1988, Kohlmann et al. 1999, McLellan et al. 1999), longer denning periods for pregnant females and thus reduced availability for harvest (Derocher et al. 1997), active hunter selection for larger-bodied animals, which are more likely males (McLellan et

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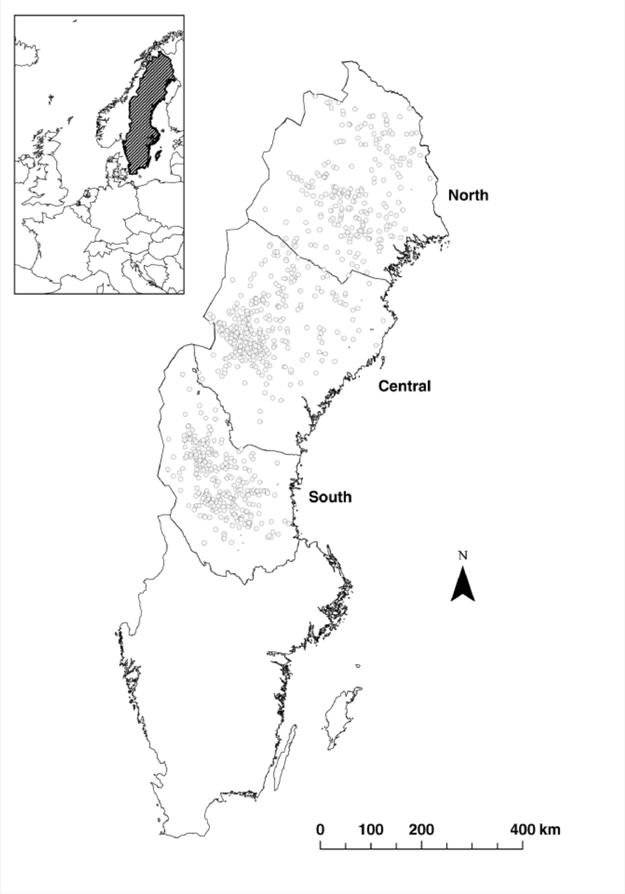

Figure 1. Map of Sweden, showing the 3 regions of our study area (northern, central, and southern) and harvest locations for 883 brown bears with sufficient spatial information from 1981 through 2004 (circles).

al. 1999), and greater male tolerance towards feeding near other bears and humans (Noyce and Garshelis 1997).

Brown bears in Sweden are hunted in the fall by sit-and-wait (still hunting), by stalking, with dogs, and with bait. In 2000, the Swedish Environmental Protection Agency issued a ban on baiting for bears to start in 2001, mainly because of concerns about human safety (Naturvårdsverket 2000). Additional issues regarding the impact of baiting on bear management had also been raised, namely 1) the perceived increasing prevalence of baiting in the annual brown bear harvest and 2) the suspicion that certain age and sex groups were more vulnerable to baiting than others (Naturvårdsverket 2000). On the other hand, proponents of baiting have argued that, among the available hunting techniques, baiting actually allows for a more deliberate selection due to increased visibility and the more controlled setting that it provides, reducing the risk of inadvertently shooting females with dependant young (Fujita 2000). The ban on baiting was and continues to be controversial among hunters and wildlife managers, in part because of the scarcity of quantitative information about the consequences of this or other harvest methods on bear populations, particularly brown bears. We also note that the legality of the ban according to Swedish law is currently being evaluated by the Swedish court system.

We examined the demographic composition of harvested brown bears in Sweden in relation to harvesting methods from 1981 to 2004, with added emphasis on hunting over bait and the ban on baiting. Specifically, we ask the following main questions: 1) What is the age and sex composition of harvested bears and is it affected by harvest method? 2) Did the ban on baiting affect the prevalence of bears taken by different hunting techniques and the age and sex composition of harvested bears? 3) Did changes in the quota system (i.e., sex- vs. non–sex-specific quotas) during the study period coincide with changes in demographic composition of the harvest?

STUDY AREA

Our study area consisted of 3 contiguous regions in Sweden (northern, central, and southern), spread over 292,000 km^2, approximately the northern 65% of the country, from about 60° to 69° N (Fig. 1). We based the region delineation on 3 genetically distinct subpopulations that matched 3 geographical clusters of bears with no or very little interchange of females (Manel et al. 2004). All 3 regions occurred within the southern, intermediate, and northern boreal vegetation zones, which were dominated by coniferous forests on primarily granite and gneiss bedrock, with small adjoining alpine zones on the western edge and the Baltic Sea to the east of each region. The area was cool and moist, with 120–160 days per year $\geq 6°$ C and primarily 500–700 mm annual precipitation. The dominating tree species were Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), but birches were also common (*Betula* spp.). The primary land use throughout this area was clear-cut forestry (Nordisk ministerrådet 1984, Bernes 1994).

METHODS

Brown Bear Hunting in Sweden

During our study (1981–2004), the brown bear hunting season occurred annually in the fall in Sweden, generally starting in late August or early September and lasting 1–2 months. No specific license was required for harvesting brown bears; all hunters with hunting rights on a hunting ground and a legal weapon for big game hunting could harvest bears. During 1981–1985, cubs of the year and females with cubs of the year were protected; after 1985 family groups were protected, regardless of the cubs' age. Bears were shot by hunters who were hunting specifically for bears and by hunters who were hunting primarily for moose (*Alces alces*; Swenson et al. 1998). Both bear- and moose-oriented hunters harvested bears 1) by stalking, 2) by still hunting (generally waiting for moose), 3) with dogs, and 4) by hunting over bait. Although the requirements for training and stamina differ between moose and bear dogs (Sandegren and Swenson 1997), methods for hunting bears with dogs were typically identical for bear- and moose-oriented hunters and generally consisted of on- or off-leash pursuit with 1–3 dogs, after which the dog or dogs (off-leash) kept the bear in place until it was shot by the hunter. Baiting used by bear hunters generally consisted of deliberately placing meat bait (often domestic animal carcasses or slaughter remains from wild and domestic animals) to attract bears at a location chosen by the hunter. Bears shot incidentally by moose hunters over bait were attracted to moose entrails left after a previous moose hunt in the same area.

Guided hunts, financially motivated by trophy hunting, are rare in Sweden. There was no limit on the number of bears that an individual hunter was allowed to harvest in a given year, and the hunting season continued each year until the scheduled season end date or until the harvest quota was reached (whichever came first). The authorities informed hunters of the number of bears that remained on the harvest quota via the media and a 24-hour telephone number (beginning in the mid-1990s). During 1981–1991 (management period 1), harvest quotas (nonspecific for sex) were based on political units (municipalities or groups of municipalities), rather than biological units (subpopulations). During 1992–1998 (management period 2), a double quota system, with a total quota and a female quota (between 29% and 33% of the total quota) in each of 4 subpopulations recognized at that time regulated the maximum number of bears that were harvested annually (Swenson et al. 1994). This sex-specific quota system stipulated that the bear season ended if either the female quota or the total quota was filled, whichever came first. In 1999 (management period 3, 1999–2004), the hunting system changed again; female quotas were removed and quotas were set at the county (i.e., län) level, rather than by subpopulation. A ban on hunting bears over bait was implemented starting with the 2001 hunting season and was in place throughout the remainder of our study.

Reporting

Successful brown bear hunters were required to present bear carcasses to an officially appointed inspector on the day of the harvest and to provide information about harvest methods, sex of harvested bears, body mass, and harvest location to the Swedish Hunters Association (1986–2001) and the National Veterinary Institute of Sweden (after 2001). If the inspector was suspicious of the accuracy of information provided by the hunter, the hunter was required to take the inspector to the reported harvest site. In addition, hunters had to submit a premolar tooth from harvested bears for age determination via cementum annuli counts (Mattson's Inc., Milltown, MT; Craighead et al. 1970). The information and samples were archived by the National Veterinary Institute of Sweden.

Analysis

We analyzed data from hunter reports collected between 1981 and 2004. No data were available for unsuccessful hunts or hunters, therefore, our analysis was restricted to data associated with harvested bears, without a measure of harvest effort. We excluded from analysis bears harvested outside of regular harvest activities. We used log-linear analysis to evaluate the effect of harvest method, hunter category, and population on the number of bears harvested between 1981 and 2000. We used linear regression to detect temporal trends in arcsine-transformed proportions (e.g., proportion of F in the harvest), after ensuring that the data were not autocorrelated over years. We used generalized linear models (GLM) to test effects of independent variables and meaningful 2-way interactions between variables on the log-transformed age of harvested bears. Preliminary analysis of our data and review of the literature suggested differences between male and females with respect to the effect of age on vulnerability to hunting, hence we calculated separate models for each sex. The independent variables used in the initial model for each sex were 1) method (baiting, dog hunting, still-hunting, stalking), 2) hunter category (moose-oriented, bear-oriented), 3) region (north, south, central), 4) management period (periods 1, 2, and 3), and 5) year (covariate).

We used logistic regression to test effects of the above independent variables, age (log-transformed covariate), and meaningful 2-way interactions between variables on sex of harvested bears. We did not include the ban on baiting (before and after) in these models because the ban was defined by the presence or absence of baiting, already a model component as a level of the categorical variable "method." Prior to including the harvest year as a covariate, we looked for autocorrelation in proportion of females and average age, using autocorrelation factor plots, and found no indication of autocorrelation among years. For all models, we removed model terms in a stepwise fashion until we arrived at the model with the lowest Akaike's Information Criterion (AIC) value. For the final GLMs with age as the dependent variable, we inspected the residuals for normality and found no gross deviations. For the age analysis, we excluded age data from the years 1981–1985 because ages from those years were only available for a small subset (3–12%) of harvested bears and are unlikely to represent random samples of the harvest. To test whether geographic differences on a scale smaller than the study region were important enough to be included in final age models, we initially included commune (a political unit below county level) as a random effect in the age model. We omitted the random effect from final age models because its impact was negligible and did not improve model fit (e.g., for M: AIC = 745.192 for model including commune as a random factor vs. AIC = 743.192 for model without the random factor).

To test effects of the ban on baiting on harvest demography and harvest patterns, we compared the 4 years immediately prior to the ban on baiting (1997–2000) with the 4 years immediately following the ban (2001–2004). We felt that this comparison would 1) enhance balance, in terms of years and sample size, and 2) make the comparison more robust, because shrinking the overall time frame reduced (although not eliminated) the opportunity for potentially confounding temporal changes in environmental conditions, harvest effort, and population attributes. To verify that our data were sufficiently independent (i.e., that we did not have

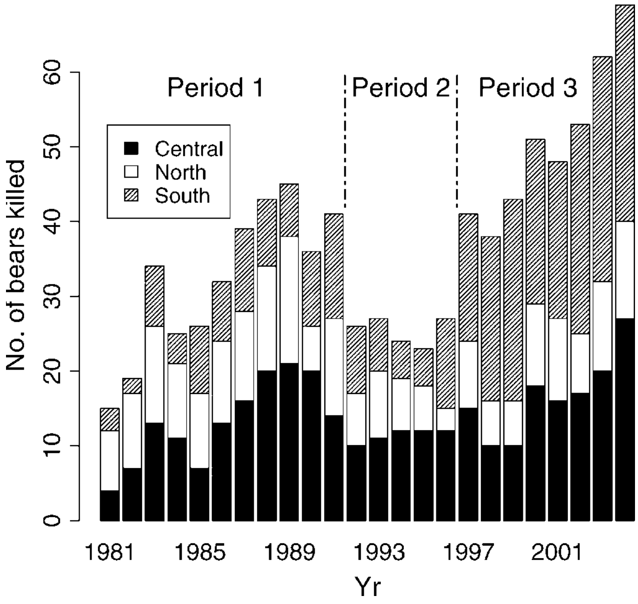

Figure 2. Number of brown bears killed per year within the northern, central, and southern study areas in Sweden between 1981 and 2004. Periods with different quota systems are separated by hatched lines. A noticeable depression in total harvest coincides with management period 2, during which sex-specific harvest quotas were implemented. $n = 887$.

a few hunters taking a large portion of bears harvested), we calculated the number of bears shot per individual hunters for years for which hunter identity data were available (1981–2003). We used the statistical programming language and environment R 2.4.0 for statistical analysis (R Development Core Team 2006).

RESULTS

During 1981–2004, hunters reported harvest of 1,053 brown bears in Sweden. We used data from 887 bears with sufficient information for our analysis. Of these, 232 (26%) were harvested in the north, 336 (38%) in the central region, and 319 (36%) in the south. As a result of increasing quotas, the number of bears harvested or lethally wounded annually increased during our study, from 16 bears in 1981 to 101 in 2004, attributable mainly to harvest increases in the southern region and to a lesser degree in the central region (Fig. 2). Only 3.1% of hunters (22 of 700) harvested >1 bear during 1981–2003, with 2, 3, 4, 5, and 17 bears harvested by 16, 2, 2, 1, and 1 hunter(s), respectively. On 14 occasions 2 bears were shot by a hunter in one year, and on one occasion a hunter shot 3 bears during the same year. The one hunter that harvested 17 bears did so within the same municipality over a period of 18 years (1986–2003, never >2 bears/yr) and shot bears both incidentally while hunting for moose and specifically, using stalking and baited hunting.

Harvest Patterns

Of the 887 bears we used in our analysis, 159 (18%) were harvested using baiting, 329 (37%) by using dogs, 137 (16%) by stalking, and 262 (30%) by still hunting. We identified hunter category for 771 bears, of which 351 (46%) were harvested by bear-oriented hunters and 420 (55%) by moose-oriented hunters. Only the saturated log-linear model (containing all possible interactions among model terms) sufficiently explained the observed number of bears harvested (pre-bait ban, Table 1) relative to hunting method, hunter category, and population (3-way interaction: deviance = 15.385, df = 6, $P[\chi^2] = 0.018$). Inspection of predicted values from the model and associated standard errors suggested 1) bear-oriented hunters harvested more bears with baiting in the south than with any other technique in any of the 3 regions (between 1.7 and 7.7 times more, depending on method and region), 2) moose-oriented hunters harvested more bears in the central region with still hunting than with any other technique in any of the 3 regions (between 1.7 and 10.5 times more, depending on method and region), and 3) still hunting in all 3 regions was more important for moose hunters than for bear hunters but was least important in the north (18 bears vs. 34 in the south and 63 in the central region; Fig. 3).

We used linear regression analysis to test whether the relative importance of baiting had increased during 1981–2000 and found that, contrary to one of the arguments made by opponents of baiting, the proportion of bears harvested by baiting was stable prior to the bait ban for bear hunters

Table 1. Number of brown bears harvested by moose- and bear-oriented hunters in 3 regions using 4 methods in Sweden before the ban on baiting (1981–2000) and after (2001–2004).

		Hunter category							
		Bear-oriented				Moose-oriented			
Period	Method	North	Central	South	Total	North	Central	South	Total
1981–2000	Bait	23	20	54	97	25	17	6	48
	Dog	18	29	31	78	31	37	28	96
	Stalk	12	18	12	42	23	19	6	48
	Still	7	11	10	28	18	63	34	115
	Total	60	78	107	245	97	136	74	307
2001–2004	Dog	7	24	33	64	10	11	18	39
	Stalk	3	2	8	13	7	3	4	14
	Still	0	13	16	29	13	26	21	60
	Total	10	39	57	106	30	40	43	113

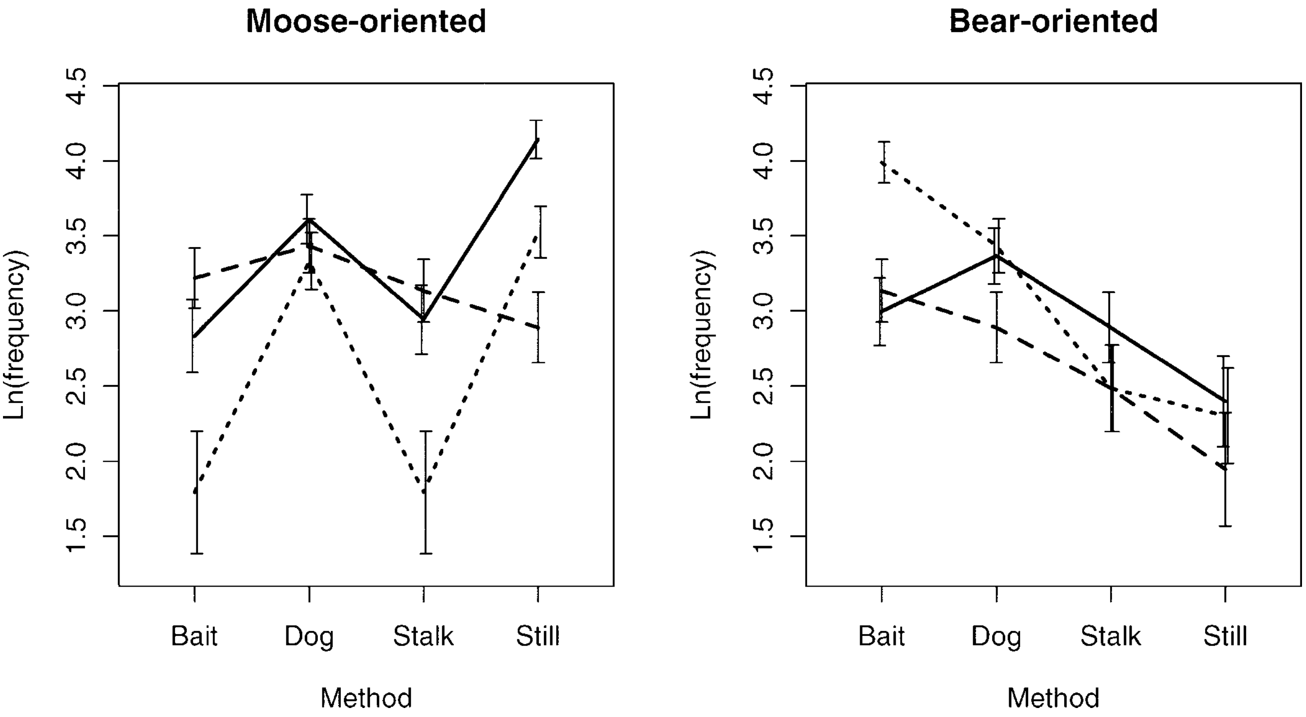

Figure 3. Predicted brown bear harvest frequencies in Sweden (log-transformed) and standard error bars from the log-linear model with hunting method, hunter category, and region (solid = central, dashed = north, dotted = south) as model factors, during 1981–2000. Because model selection (Akaike's Information Criterion [AIC]) resulted in the saturated final model (3-way interaction between the predictor variables), predicted and observed frequencies are identical. We added a small amount of noise to the location of error bars along the x-axis to allow distinction of overlapping error bars.

and had decreased during the same period for moose hunters at a rate of approximately 1% per year (Table 2, Fig. 4).

Harvest Demography

Of the 887 bears we used in the analysis, 422 (48%) were female and 465 (52%) were male. Regression analysis showed no temporal trend in the proportion of females (arcsine-transformed) in the harvest during our study (linear regression, $F_{1,22} = 0.268$, $\beta = 0.002$, $P = 0.61$). Age information was available for 644 bears. Male and female age distributions were similar (M: $\bar{x} = 4.823$ yr, SD = 4.142, min. = 1, max. = 22 yr; F: $\bar{x} = 5.048$ yr, SD = 4.907, min. = 1, max. = 33 yr; Fig. 5), although there was some indication of an elevated male:female ratio in the harvest among the 4- to 7-year-olds. Subadults (1- to 3-yr-olds) made up 51.6% of the harvest ($N = 644$). The 4 oldest animals (23 yr, 24 yr, 32 yr, and 33 yr) were females.

Table 2. Regression results for temporal trends in the proportion (arcsine-transformed) of brown bears harvested by moose- and bear-oriented hunters in Sweden while using bait, dogs, stalking, and still hunting during 1981–2000.

Method	β	SE	$F_{1,18}$	P
Bear-oriented				
Bait	0.001	0.009	0.006	0.941
Dog	0	0.008	<0.001	0.985
Stalk	−0.012	0.014	0.701	0.414
Still	0.015	0.007	4.649	0.045
Moose-oriented				
Bait	−0.024	0.007	10.76	0.004
Dog	0.015	0.007	5.231	0.035
Stalk	−0.018	0.005	10.7	0.004
Still	0.014	0.007	4.085	0.058

Variable selection resulted in different final GLMs for males and females (Tables 3, 4). For males, region, management period, and method modified by hunter category were variables predicting age (Table 3). Male bears shot by moose hunters using still hunting were 24–50% younger than males shot with other methods, although there seemed to be no recognizable difference among ages of males shot with the different methods by bear hunters. Inspection of model residuals and histograms over age by hunter category and method suggest differences in the age distribution among the groups, most notably a bias towards yearling males by moose hunters using still hunting (Fig. 6). Harvested males were approximately 32% younger in the north than in other regions. For females, region, management period, and hunter category modified by year remained in the final model (Table 4). Region did not have an effect on age but remained in the model as an adjusting variable. The interaction between hunter category and year indicated that average age of females harvested by moose hunters increased during our study, whereas there was no linear temporal trend in the average age of females harvested by bear-oriented hunters. Both males and females harvested during management period 1 were older than during the subsequent period.

Management period, age modified by hunter category, and

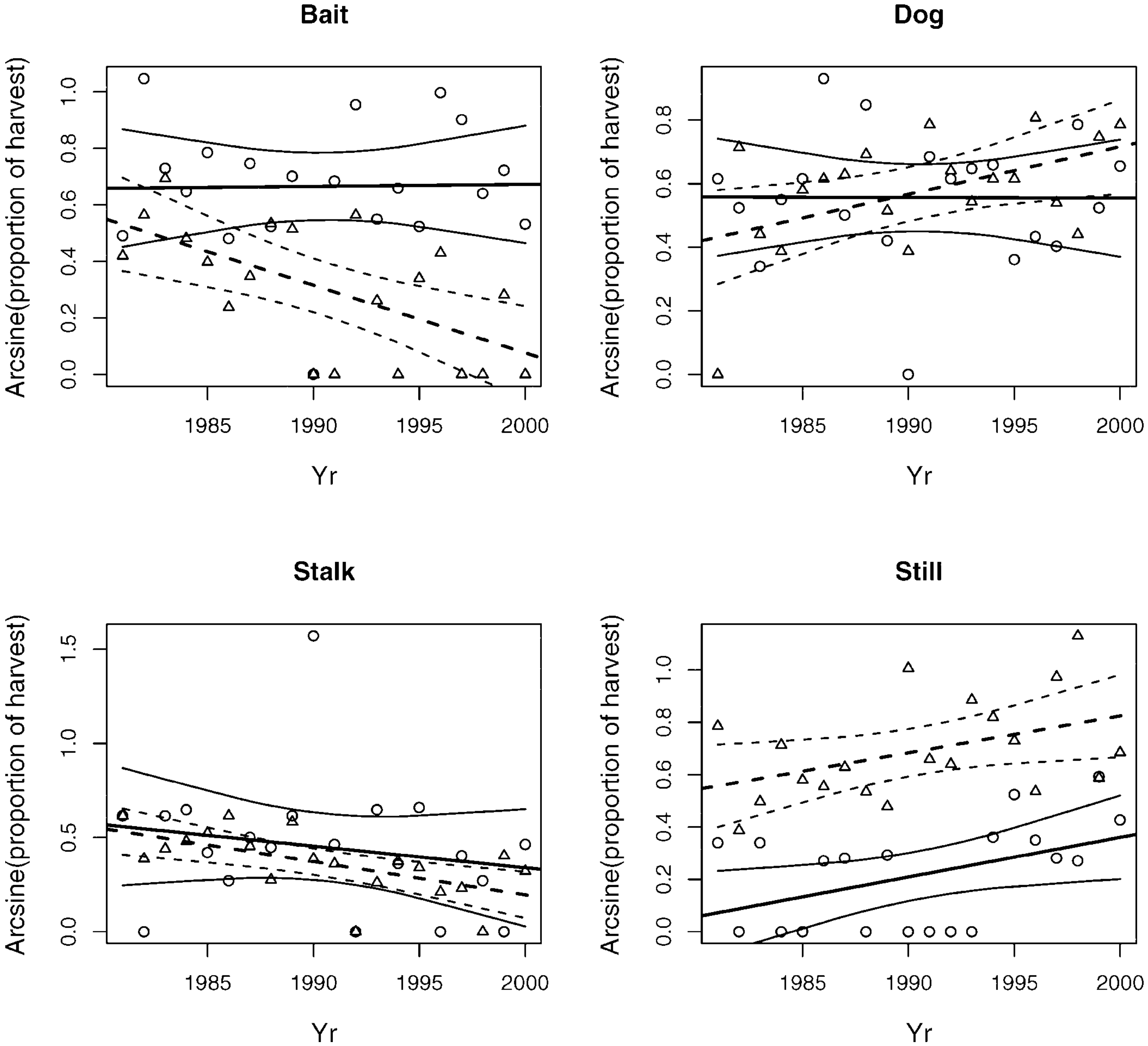

Figure 4. Proportion (arcsine-transformed) of brown bears killed annually with each of 4 hunting methods by bear- (circles and solid lines) and moose-oriented hunters (triangles and dashed lines) in Sweden between 1981 and 2000, including linear regression lines (bold lines) and 95% pointwise confidence bounds (thin lines) for the fitted lines.

age modified by region remained as predictors in the final logistic regression model with sex as the dependent variable (Table 5). Odds of a harvested bear being male were greatest during management period 1 (between 24% and 33% greater than during the other 2 management periods). The interaction between age and region suggests decreasing odds with increasing age that bears harvested in the northern region were male, which is consistent with the findings of the GLM with age as the dependent variable for males. Neither method nor harvest year were predictors for the sex of harvested bears.

Effects of the Ban on Baiting

We found no difference between the 4 years before and the 4 years after the ban on baiting with respect to relative importance (representation in the harvest) of stalking, still hunting, and hunting with dogs ($\chi^2 = 0.202$, df = 2, $P = 0.904$). There was no difference in the proportion of males and females harvested between the 2 periods (bear hunters: $\chi^2 = 0.012$, df = 1, $P = 0.914$; moose hunters: $\chi^2 = 0.209$, df = 1, $P = 0.648$; combined: $\chi^2 = 0.284$, df = 1, $P = 0.594$). We also found no difference between pre- and postban years in the age (log-transformed) of bears harvested (F: $t = 1.204$, df = 184, $P = 0.23$; M: $t = 0.799$, df = 193, $P = 0.425$; combined: $t = 1.439$, df = 379, $P = 0.151$). The removal of baiting as a harvest method in 2001 did not reduce the ability of hunters to reach the annual harvest quota (Table 6), as would have been expected if baiting were substantially more efficient than the remaining hunting methods.

Before the ban, baiting was most prevalent in the southern

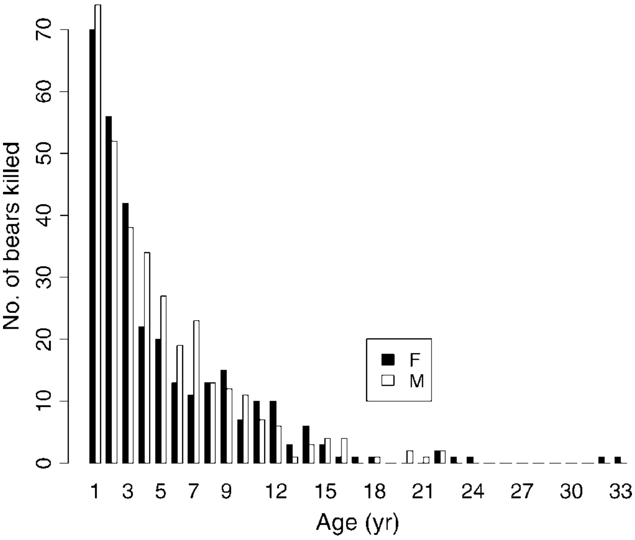

Figure 5. Number of female ($n = 310$) and male ($n = 334$) brown bears killed by age in Sweden during 1981–2004.

area (Table 1); hence we speculated that the southern area may be where impacts of the ban on baiting on the relative proportion of harvest methods would be the most pronounced, particularly for bear-oriented hunters. However, we found no difference between the 4 years before and after the ban on baiting with respect to the proportion of bears harvested by hunting with dogs, stalking, and still hunting in the southern area by bear-oriented hunters ($\chi^2 = 0.593$, df = 2, $P = 0.744$).

Table 3. Parameter estimates and test statistics for the generalized linear model[a] explaining age (log-transformed) of male brown bears harvested in Sweden during 1986–2004. We based model selection on Akaike's Information Criterion. One level of each categorical variable serves as a contrast ($\beta = 0$) for the remaining levels of that variable.

Explanatory variables	df	β	SE	*t*	*P*(>|*t*|)
Method	3				
Dog		0			
Bait		0.199	0.19	1.049	0.295
Stalk		−0.048	0.236	−0.204	0.839
Still		0.071	0.19	0.373	0.71
Hunter category	1				
Bear-oriented		0			
Moose-oriented		0.153	0.166	0.921	0.358
Region	2				
South		0			
Central		0.054	0.114	0.477	0.634
North		−0.366	0.132	−2.77	0.006
Management period	2				
1986–1991		0			
1992–1998		−0.317	0.142	−2.237	0.026
1999–2004		−0.182	0.135	−1.349	0.179
Method:hunter category	3				
Bait:moose-oriented		−0.238	0.296	−0.804	0.422
Stalk:moose-oriented		−0.259	0.321	−0.807	0.421
Still:moose-oriented		−0.702	0.24	−2.929	0.004

[a] Model $R^2 = 0.14$.

Table 4. Parameter estimates and test statistics for the generalized linear model[a] explaining age (log-transformed) of female brown bears harvested in Sweden during 1986–2004. We based model selection on Akaike's Information Criterion. One level of each categorical variable serves as a contrast ($\beta = 0$) for the remaining levels of that variable.

Explanatory variables	df	β	SE	*t*	*P*(>|*t*|)
Hunter category	1				
Bear-oriented		0			
Moose-oriented		−146.8	44.36	−3.31	0.001
Region	2				
South		0			
Central		−0.165	0.129	−1.277	0.203
North		0.183	0.153	1.193	0.234
Management period	2				
1986–1991		0			
1992–1998		−0.666	0.317	−2.104	0.036
1999–2004		−0.83	0.496	−1.674	0.095
Yr	1	0.006	0.036	0.157	0.876
Hunter category:yr	1				
Moose-oriented		0.074	0.022	3.31	0.001

[a] Model $R^2 = 0.08$.

One of the arguments of proponents of baiting was that females with cubs were easier to identify as such over bait and thus less likely to be harvested. Due to the low sample size, we were not able to carry out statistical tests; however, 5 of the 6 females with known dependent offspring were harvested with the use of dogs, and 3 of them were harvested after the ban on baiting. In addition, of the 12 cubs-of-the-year harvested during hunting (not included in the other analyses), 8 were harvested using dogs, 3 by still hunting, and one over bait. Of the 12 cubs, 6 were harvested after the ban on baiting was implemented, 2 with dogs and one with still hunting.

DISCUSSION

Differences in age and sex composition among harvest methods in Sweden were not as pronounced as the differential biases that similar investigations have shown to exist for brown and black bear (*Ursus americanus*) harvests in North America (e.g. McLellan and Shackleton 1988, Kohlmann et al. 1999). For example, we found no effect of method on the sex of harvested bears and few age-specific biases. In addition, our models explained only a small proportion of the overall variation in age (14% for M, 8% for F), which we attribute in part to differences in hunter selectivity. Active hunter selectivity of bears based on sex or age is unlikely to be a major factor causing demographic bias in the Swedish harvest. Given a relatively low probability of encountering a bear, the lack of individual bag limits, combined with a harvest that is limited by season quotas, there is little incentive for Swedish hunters to pass up a shot at a legal brown bear they encounter, other than a fee that has to be paid to the owner of the hunting rights (the landowner). The low encounter rate is further illustrated by the small proportion of hunters (3.1%) that shot >1 bear during our study. It remains to be seen whether a growing bear population in Sweden (and correspondingly increasing

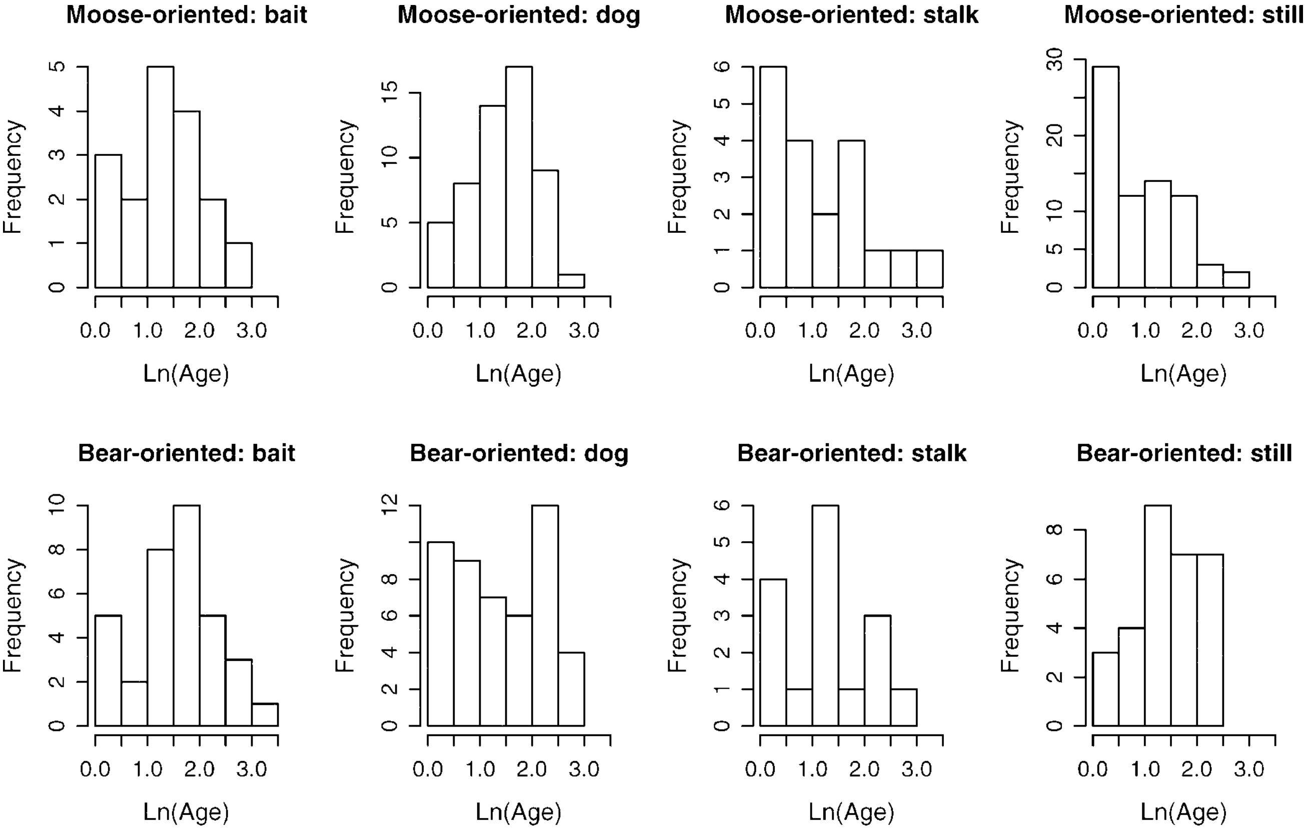

Figure 6. Histograms of male brown bear ages (log-transformed) harvested by moose and bear oriented hunters using 4 different methods from 1986 to 2004 in Sweden.

encounter rates) will result in greater hunter selectivity in the future. We found that hunters in Sweden did not distinguish between male and female brown bears when encountering them in the field, because sex-specific quotas that were meant to encourage hunter selectivity did not have that effect. We recognize that active hunter selectivity accounts for only a portion of the demographic patterns observed during harvest analyses of other bear populations, and differential vulnerability of sex and age groups to harvest methods would not be eliminated solely by lack of hunter selectivity. Thus, another explanation for the comparatively small difference in age and sex composition among different methods in our results could be that differential vulnerabilities among sex and age groups are not as pronounced in the Scandinavian bear population as in North America and that a larger sample size than the one available to us is needed to detect them.

The ban on baiting had no recognizable effect on harvest patterns and demographic composition of the harvest, at least when comparing the 4 years leading up to the ban with the 4 years following it. We note that we only had 4 years of postban data to evaluate. Data from future harvest years may be required to uncover delayed or small, but long-term, impacts on harvest demographics.

Our models suggested that average age was highest for bears harvested during management period 1 (most pronounced in comparison with management period 2) and that odds of a harvested bear being male were greater during management period 1 than during the subsequent periods. Interpretation of these results is difficult, because our analysis does not allow us to distinguish potential temporal effects, perhaps associated with a changing population, from effects of changes in the quota system. The percentage of the annual quota that was filled showed an upward trend during the study period, with a noticeable depression during 1992–1998 (Table 6), because hunters reached the female quota, and hence ended the season, prior to reaching the total quota during the time period with sex-specific quotas.

We found that younger male bears (particularly yearlings) were more vulnerable to still hunting (when used by moose-oriented hunters) than to other hunting methods. Method-specific vulnerabilities are more likely to show up with incidentally shot bears (moose-oriented hunters), because they are not as prone to be masked or confounded by other factors associated with active targeting or seeking of bears (bear-oriented hunters). Others have attributed harvest bias towards young animals (particularly M) to their greater mobility compared with other sex and age cohorts, increasing the probability of encountering a hunter (Litvaitis and Kane 1994, Noyce and Garshelis 1997, Kohlmann et al. 1999, McLellan et al. 1999). In our case, because still hunters are sedentary, vulnerability of bears to still hunting is likely to increase with increasing mobility of bears.

Table 5. Parameter estimates and test statistics for the logistic regression model explaining sex (F = 0, M = 1) of brown bears harvested in Sweden during 1981–2004. We based model selection on Akaike's Information Criterion (AIC). One level of each categorical variable serves as a contrast (β = 0) for the remaining levels of that variable.[a]

Explanatory variables	df	β	SE	*z*	LCL	OR	UCL	*P*(>|*z*|)
Age (log)	1	0.256	0.166	1.546	0.934	1.292	1.788	0.122
Hunter category	1							
Bear-oriented		0						
Moose-oriented		0.861	0.315	2.734	1.276	2.366	4.386	0.006
Region	2							
South		0						
Central		−0.539	0.354	−1.523	0.292	0.584	1.167	0.128
North		0.809	0.408	1.981	1.009	2.245	4.996	0.048
Management period	2							
1981–1991		0						
1992–1998		−0.631	0.281	−2.248	0.307	0.532	0.922	0.025
1999–2004		−0.500	0.262	−1.906	0.363	0.607	1.014	0.057
Age:hunter category	1							
Moose-oriented		−0.353	0.207	−1.704	0.468	0.702	1.054	0.088
Age:region	2							
South		0						
Central		0.309	0.233	1.330	0.864	1.362	2.149	0.184
North		−0.803	0.274	−2.930	0.262	0.448	0.766	0.003

[a] LCL = lower 95% CL; UCL: upper 95% CL; OR = odds ratio.

The average age of male bears was lowest for animals harvested in the northern region of the study area, which was not likely a result of distribution of hunter categories and harvest methods, because still hunting, the technique we found to be biased towards younger animals compared with other methods, comprised a smaller portion of the harvest in the north than elsewhere. Instead, this regional bias towards younger males in the harvest may represent a difference in age structure of the male population or greater subadult male vulnerability in the north (Zedrosser et al. 2007).

Table 6. Annual harvest quota and number of brown bears killed or lethally wounded by hunters in Sweden during 1981–2004. We show female quotas and the number of females harvested for the time period with sex specific quotas (1992–1998). The number of brown bears harvested exceeded the quota in some years, due to a small time lag between the filling of the quota and the announcement of the end of the season.

Yr	Quota	No. harvested	F quota	F harvested
1981	36	16		
1982	35	21		
1983	42	34		
1984	42	27		
1985	40	27		
1986	45	35		
1987	57	41		
1988	60	45		
1989	59	49		
1990	58	42		
1991	51	46		
1992	50	34	16	8
1993	50	34	16	18
1994	50	30	16	16
1995	50	36	16	14
1996	58	30	17	18
1997	69	48	23	24
1998	78	49	26	27
1999	55	51		
2000	56	57		
2001	60	63		
2002	64	62		
2003	74	75		
2004	101	101		

We found differences in the relative importance of the 4 hunting methods used for harvesting brown bears in Sweden, as well as regional and temporal variation in harvest patterns and differences between bear- and moose-oriented hunters. The complex interaction between hunting method, hunter category, and harvest region in terms of the number of bears harvested means that conclusions about the effect of either factor can only be drawn when the remaining 2 factors are also considered. Differences among regions in the prevalence of bears harvested with different hunting methods are attributable at least in part to regional differences in hunting traditions and the ratio of bear- to moose-oriented hunters and likely also to variation in the demographic structure of the different populations.

We found anecdotal evidence that cubs and females with dependent young may be more vulnerable to be harvested when hunted using dogs than by other methods, but our sample size was too small to determine the magnitude of this effect, if in fact it exists. Females with dependent young could be more vulnerable to dog hunting than other hunting methods, if they move slower and through more accessible terrain, leave a wider scent trail, and if they are more likely to face their attackers in order to protect their cubs. In addition, it is possible that hunters will not recognize a female with dependent young as such if she is separated from her cubs (e.g., by sending them up a tree) before they are noticed by the hunter. We recommend that future studies investigate the vulnerability of females with dependent young at bait stations (e.g., do females take their young with them when visiting bait stations?) and when hunted with dogs (e.g., are hunters able to see and recognize the cubs when a female pursued with dogs has dependent young?).

Milner et al. (2006) recommended that harvesting regimes mimic natural mortality patterns more closely to minimize demographic side effects as well as evolutionary consequences of selective harvesting. If and when hunting regimes closer to natural mortality patterns become an objective for the management of the Scandinavian brown bear, it will require information about the demography and natural mortality patterns in unhunted brown bear populations, preferably in Scandinavia. In addition, to further identify and to explain biases in Swedish brown bear harvest and to account for potentially confounding variation in bear populations and harvest effort over time and space, future analyses should provide context through information about population(s) from which the harvest sample is drawn, as well as some measure of harvest effort.

MANAGEMENT IMPLICATIONS

Wildlife managers can expect to find differences in harvest biases among jurisdictions with different harvest systems. Biases in Swedish brown bear harvest primarily reflect differences in inherent vulnerability, whereas in North America investigators often have to distinguish between biases that are a result of active hunter selectivity and those that are caused by differential vulnerability of sex and age groups in the population. Furthermore, we found no demographic effect of the ban on baiting in Sweden on the harvest, hence an evaluation of the advantages and disadvantages of the ban should continue to concentrate on the human dimensions of hunting using bait. These include concerns about human safety (for example if bears are accustomed to forage on food provided by humans or if hikers inadvertently stumble onto a bear at a bait station), as well as ethical issues, such as discussions about fair chase (Loker and Decker 1995).

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The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears

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Summary

1. The population dynamic and evolutionary effects of harvesting are receiving growing attention among biologists. Cause-specific estimates of mortality are necessary to determine and compare the magnitude and selectivity of hunting and other types of mortalities. In addition to the logistic and financial constraints on longitudinal studies, they are complicated by the fact that nonhunting mortality in managed populations usually consists of a mix of natural and human-caused factors.

2. We used multistate capture–recapture (MCR) models to estimate cause-specific survival of brown bears (*Ursus arctos*) in two subpopulations in Sweden over a 23-year period. In our analysis, we distinguished between legal hunting and other sources of mortality, such as intraspecific predation, accidents, poaching, and damage control removals. We also tested whether a strong increase in harvest quotas after 1997 in one of the subpopulations affected vulnerability to legal hunting.

3. Although only a fraction of mortalities other than legal hunting could be considered natural, this group of causes showed a general pattern of demographic selectivity expected from natural mortality regimes in populations of long-lived species, namely greater vulnerability of young animals. On the other hand, demographic effects on hunting vulnerability were weak and inconsistent. Our findings support the assumption that hunting and other mortalities were additive.

4. As expected, an increase in hunting pressure coincided with a correspondingly large increase in vulnerability to hunting in the affected subpopulation. Because even unbiased harvest can lead to selective pressures on life-history traits, such as size at primiparity, increasing harvest quotas may not only affect population growth directly, but could also alter optimal life-history strategies in brown bears and other carnivores.

5. Legal hunting is the most conveniently assessed and the most easily managed cause of mortality in many wild populations of large mammals. Although legal hunting is the single-most important cause of mortality for brown bears in Sweden, the combined mortality from other causes is of considerable magnitude and additionally shows greater selectivity in terms of sex and age than legal hunting. Therefore, its role in population dynamics and evolution should not be underestimated.

Key-words: carnivore, compensatory mortality, competing risks, M-SURGE, wildlife management

Introduction

In many naturally regulated populations of large mammals, age-specific mortality has been shown to follow a similar U-shaped pattern irrespective of the proximate causes of mortality (Caughley, 1966; Gaillard, Festa-Bianchet & Yoccoz, 1998; Gaillard *et al.*, 2000). This is not expected to hold for populations that are heavily affected by human exploitation, where prime-aged individuals that otherwise survive well can also be targeted. Indeed, the selective pressures in harvested marine and terrestrial populations have recently raised concern regarding their long-term evolutionary consequences (Coltman *et al.*, 2003; Kuparinen & Merilä, 2007). It is thus not surprising that science dealing

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with the management and conservation of wild populations focuses increasingly on the effects of hunting on population dynamics and evolution.

We further suspect that the spotlight that hunting is receiving, particularly in large mammals, may be motivated partially by the relative ease with which it can be assessed (hunter surveys, tagging systems, etc.) and that it is arguably the most easily influenced by wildlife managers (e.g. through hunting seasons, quotas, and bag limits). Natural mortality is usually more difficult to detect and hence to estimate. Furthermore, natural mortality schemes are often disturbed and at times replaced by human-caused mortalities other than hunting (vehicle accidents, wildlife damage control, poaching, etc.). This makes the otherwise intuitive separation of 'harvest' and 'natural mortality' (Anderson & Burnham, 1976) less useful, even if cause-specific vulnerability estimates are desired. Yet, because survival is determined by the combination of all causes of death, a comprehensive look at survival requires estimates of the magnitude and selectivity of all mortality causes, including those due to proximate causes other than hunting. Additionally, comparing mortality patterns for different age and sex classes can yield insight into deviations from natural mortality patterns and therefore contemporary selection pressures, and may also help determine the degree of compensation in mortality (Otis & White, 2004; Pedersen *et al.*, 2004; Schaub & Lebreton, 2004a; Lebreton, 2005).

Estimating and contrasting cause-specific mortality in long-lived species requires longitudinal studies, which additionally provide opportunities to evaluate how management actions, such as a major change in harvest quotas, may affect vulnerability patterns. The difficulties and costs associated with such studies may explain why they are rare in large mammals. The most well-known longitudinal studies have been performed on ungulate populations, such as red deer (*Cervus elaphus*) on the island of Rum (Clutton-Brock, Guinness & Albon, 1982) and Soay sheep (*Ovis aries*) on the island of St. Kilda, Scotland (Clutton-Brock & Pemberton, 2004). To our knowledge, no study on large carnivores has yet compared harvest and other mortality patterns under contrasting management regimes.

The Scandinavian Brown Bear Research Project has collected an extensive data set with information on 525 marked brown bears (*Ursus arctos*), spanning 23 years of intensive monitoring. Many of the individuals have been followed from the age of 1 to death, which presents a rare opportunity to assess cause-specific vulnerabilities in a large carnivore species. Our first objective was to estimate age- and sex-specific vulnerability to legal hunting in this population and determine if they are comparable to the patterns observed in other harvested bear populations in North America, where there is evidence for selectivity for younger, inexperienced individuals, especially males (Derocher, Stirling & Calvert, 1997; Noyce & Garshelis, 1997; McLellan *et al.*, 1999). In Bischof *et al.* (2008a), we documented differences between males and females in terms of the variables that explained the age of harvested bears, but could not address vulnerability directly, because that analysis was based solely on harvested bears.

In addition to legal hunting, brown bears in Sweden die from a variety of other causes, such as intraspecific predation, vehicle collision, depredation control, and poaching (Swenson *et al.*, 1997; Swenson & Sandegren, 1999; Swenson, Dahle & Sandegren, 2001; Sahlén *et al.*, 2006). Consequently, our second objective was to compare the magnitude and demographic selectivity of legal hunting mortality with other mortality sources. We use multistate capture–recapture modelling to estimate and compare the magnitude and demographic selectivity of legal hunting with other mortality causes and discuss our findings in the context of carnivore population dynamics and evolution.

Finally, the potential for compensatory mortality is an important consideration for the management of exploited populations. The effect of changes in harvest intensity (i.e. quotas) is dependent on the degree of compensation this causes in other mortality sources, may they be natural or human caused. A dramatic increase in quotas starting in the mid-1990s in one of our two subpopulations enabled us to look for evidence of compensation by monitoring changes in the vulnerability to hunting and other causes of death before and after hunting pressure increased.

Methods

STUDY AREA

Our two study areas were located in northern and south-central Sweden. The northern study area ('north', 67°N, 18°E) encompasses 12 000 km^2, the other site ('south', 61°N, 18°E) is 11 500 km^2 in size. These areas are based on genetically distinct subpopulations that match geographical clusters of bears with no or very little interchange of females (Manel *et al.*, 2004). Both study areas occur within the southern, intermediate, and northern boreal vegetation zones (Nordiska inisterrådet, 1984; Bernes, 1994). The study areas are described in detail in Zedrosser, Dahle & Swenson (2006).

Protective measures, implemented in Sweden as early as the end of the 19th century, brought the brown bear population back from the brink of extinction (Swenson *et al.*, 1995). In 2005, the population size of brown bears in Sweden was estimated to be between 2350 and 2900 (Kindberg & Swenson, 2006). Hunting brown bears is legal in Sweden, where a fall season results (in recent years) in the harvest of approximately 5% of the estimated population (Bischof *et al.*, 2008a).

DATA COLLECTION

Most bears were captured from a helicopter with immobilizing darts during the spring (20 March–10 June) from 1984–2006. Captured bears were measured and weighed, and blood, tissue, and hair samples were collected. Unless they were followed from birth, the first premolar was extracted and sent to Matson's, Inc., Milltown, MT, USA for age estimation using counts of cementum annuli layers (Matson *et al.*, 1993). Bears designated for radiotelemetry ($N = 388$) were equipped with collar-mounted radiotransmitters, radio-implants, or both. All bears, including non-instrumented ones ($N = 137$), were marked individually with tattoos (inside of the upper lip), ear tags, and passive integrated transponder (PIT) tags placed subcutaneously between the shoulder blades. Radio-marked bears were recaptured every 2–3 years to collect new measurements and to exchange used radiotransmitters for ones with new batteries. Great effort was made to capture all yearlings accompanying radio-marked females. Non-instrumented animals were (re)captured opportunistically based on priorities and available funding. Radio-marked bears were located once every 1–2 weeks during the active period (March–November) and sporadically throughout the denning period with standard triangulation from the ground or from a fixed wing aircraft or helicopter. The radiotelemetry portion of the study has generally focused more on females than males. Arnemo *et al.* (2006), Zedrosser *et al.* (2007), and Dahle & Swenson (2003b) provide additional information about the capture of bears, monitoring, and data collection procedures. Capture, manipulation, marking and monitoring of bears complied with current laws regulating the treatment of animals in Sweden and Norway, where a few bears were captured, and were approved by the appropriate ethical committees in both countries.

Recoveries

The main sources for recoveries of bears (outside of regular monitoring activities of radio-tagged bears) were mandatory hunter reporting, dead bears discovered and reported by members of the public, and bears killed as part of damage control activities. By regulation, successful brown bear hunters in Sweden were required to notify the police on the day of the kill, present their bear carcass to an officially appointed inspector and provide information about harvest methods, the sex of the harvested bear, body mass, and kill location. The Swedish brown bear hunt and reporting of hunter-killed bears are described in Bischof *et al.* (2008a). Between 1984 and 2006, 124 marked bears were shot during legal hunting, accounting for 59·6% of all marked bears recovered dead ($N = 208$). Confirmed mortalities of marked bears due to causes other than legal hunting included the following (in order of prevalence and with the proportion of deaths in parentheses):

1. Natural ($N = 28$, 13·5 %, mainly intraspecific kills)
2. Damage control removal and self-defense ($N = 23$, 11·1%)
3. Cause unknown ($N = 15$, 7·2 %)
4. Death as a result of capture ($N = 7$, 3·4%)
5. Confirmed illegal hunting ($N = 7$, 3·4%)
6. Accident (including traffic) ($N = 4$, 1.9%)

Although a breakdown into these causes would increase resolution in terms of cause-specific mortalities, in our case data limitations and resulting parameter estimation problems for the various transitions (see below), made such distinction unfeasible. It is worth noting that natural mortality (in the sense of nonhuman-caused mortality) constituted only a small portion (13·5%) of confirmed deaths of marked animals and 1/3 of bears dying due to causes other than legal hunting.

MULTISTATE CAPTURE—RECAPTURE ANALYSIS

Model and parameter description

Modelling of movement was the main motivation for the initial development of multistate capture–recapture (MCR) models (Hestbeck, Nichols & Malecki, 1991; Brownie *et al.*, 1993). Their usefulness for modelling transitions between other types of states, e.g. behavioural and reproductive states (Barbraud & Weimerskirch, 2005; Weladji *et al.*, 2008), has since become apparent, and Lebreton, Almeras & Pradel (1999) showed how multistate models can be used to combine live recaptures and dead recoveries by designating separate states for alive and newly dead, each state with its respective detection probability. Following Schaub & Pradel (2004b), we extended Burnham's (Burnham, 1993) model (presented as a three-stratum model in Lebreton *et al.*, 1999) for combined analysis of tag recovery and recapture data. Our model (Fig. 1) included an additional cause of mortality and the possibility of return for animals that had left the study area, resulting in four possible states: (1) alive inside the study area, (2) alive outside the study area, (3) newly dead due to legal hunting, and (4) newly dead due to other causes.

State transitions probabilities are defined in the following matrix (row, states of departure; column, states of arrival):

$$T = \begin{bmatrix} (1-h-w)F & (1-h-w)(1-F) & h & w \\ (1-h-w)R & (1-h-w)(1-R) & h & w \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \qquad \text{eqn 1}$$

with h being the probability of dying due to legal hunting during the time period t to $t + 1$, w the probability of dying due to causes other than legal hunting during the same time period, and $1 - h - w$ the probability of surviving. F, a fidelity term, represents the probability of remaining within the study area, and R is the probability of returning to the study area for animals that are outside. The mortality parameters associated with the transition to states 3 and 4 are true mortalities, whereas the parameters in the other two states are only local survival. Detection probabilities differ depending on the cause of mortality among animals newly dead, but the model assumes that dead animals are detected with equal probability inside and outside the study area, as does Burnham's model (Burnham, 1993). Equal detection probability inside and outside our study areas is a reasonable assumption given that animals killed by legal hunting were all detected by definition, and bears that died due to other causes were either detected because they were followed by radiotelemetry, or incidentally encountered. The weakest part of the assumption is equal detection of instrumented bears dead due to causes other than legal hunting, regardless of

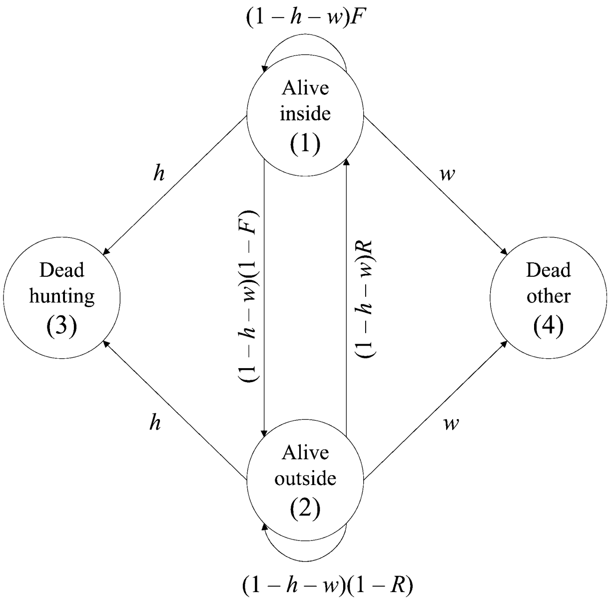

Fig. 1. Fate diagram illustrating MCR model state transitions of marked brown bears in Sweden. Bears can die due to two competing risks (legal hunting and all other mortality causes) or stay alive. Bears alive inside or outside the study area may remain in their current location or move out of or into the study area, respectively.

location in- or outside the study area. This potential lack of realism is necessitated by the need for parameter identifiability (Gimenez, Choquet & Lebreton, 2003; Hunter & Caswell, 2009).

Schaub & Pradel (2004) demonstrated the use of multistate models to assess the relative importance of different sources of mortality. Our approach is similar to theirs, however, whereas they estimated the probability of death being caused by a certain source of mortality conditional on having died during the interval, we estimated the cause-specific probability of dying conditional on being alive at the beginning of the interval.

We constrained the capture probability (p) for state 3 to equal 1, recognizing that all legally shot bears had to be reported to the management authorities in Sweden. Consequently, we only estimated capture probabilities in states 1, 2 and 4. Being able to constrain capture probability in state 3 supplied a significant benefit, by allowing for the separate estimation of the capture probability in state 4 and transition probabilities from the live states to state 4. As Lebreton *et al.* (1999) pointed out, in cases where recoveries are obtained from specific causes of death (with associated cause-specific mortality m_{cause}), hence $m_{cause} \neq 1 - s$ (s, survival), the detection probability cannot be identified separately from a specific type of mortality. For this reason, the pair of parameters (s, p) is often replaced by [s, $(1 - s)\, p$]. In our case, constraining the capture probability in state 3 to 1 made p identifiable.

To construct capture histories, we pooled captures and live resightings for each individual during the spring capture season (20 March–10 June), using a capture interval of 1 year. We used an extended period (3·5 months) as a single occasion, because the biases associated with parameters derived from pooled estimates are minimal if mortality during the capture interval does not exceed about 50% (Hargrove & Borland, 1994). Animals encountered alive and inside the study area during the capture season were assigned to state 1, live animals outside the study area were assigned to state 2. Animals killed by legal hunting during the hunting season preceding capture occasion $i + 1$ (regardless of whether or not they were shot inside or outside the study area) were assigned to state 3 at occasion $i + 1$, and animals discovered as having died for reasons other than legal hunting between the end of capture occasion i and the end of capture occasion $i + 1$ were assigned to state 4 at occasion $i + 1$. We assigned animals encountered in the 'newly dead' states (3 and 4) between capture occasions i and $i + 1$ to occasion $i + 1$, instead of the previous occasion (as is carried out in combined tag recovery and live recapture data; Barker, White & McDougall, 2005), because we were estimating survival indirectly as a transition probability from occasion i to occasion $i + 1$. Whereas direct survival estimates at occasion i are interpreted as having survived from occasion i to occasion $i + 1$, transition probabilities at occasion i are interpreted as having made a transition during the interval between $i - 1$ to i. Animals not encountered alive at occasion $i + 1$ and not discovered dead between the end of occasion i and the end of occasion $i + 1$ received a 0 in the capture history at occasion $i + 1$. Capture histories were constructed for 464 individuals.

Model selection and parameter estimation

We used the program M-SURGE (Choquet *et al.*, 2004; Choquet *et al.*, 2006) for model fitting and parameter estimation. We assessed the effects of the following variables in the multistate modelling framework:

1. Sex (male, female; symbol: s) – for transition and capture
2. Age class (yearlings = 1y, subadults = 2–4y, adults = 5y +; symbol: a) – for transition and capture
3. Subpopulation (north, south; symbol: p) – for transition and capture
4. Radiocollar (yes, no; symbol: r) - for capture
5. Harvest intensity (low, high; symbol: i) – for transition

The symbols for explanatory variables defined above were used in the M-SURGE notation presented later and are not italicized to avoid confusion with variables used earlier in the text. We implemented and compared several candidate MCR models, with the most complex model including all of the above variables and biologically meaningful/interpretable interactions between them (full model, Table 1). No tests are currently available to test the goodness-of-fit (GOF) of multistate models to data consisting of a combination of recaptures and recoveries. Nevertheless, because most of the information about cause-specific mortality came from dead recoveries, we carried out a GOF test using only the recovery data (Brownie *et al.*, 1985), and the fit was found to be satisfactory ($X^2_{53} = 65.23$, $P = 0.12$). Because data demands are high for multistate models and the number of parameters increases quickly with increasing number of states and groups (Lebreton & Pradel, 2002), we did not consider the fully time-dependent model, but instead used time periods we believed to be relevant for survival , i.e. two time periods representing a change in harvest intensity due to a 3·4-fold increase in average annual quotas in the south, beginning with the 1998 hunting season (from 11·4 bears in 1984–97 to 38·6 bears after 1997). Similarly, age was defined as a categorical variable with cuts roughly identified based on splines in a preliminary Cox proportional hazards regression model (Lunn & McNeil, 1995).

We estimated capture probabilities separately for instrumented and non-instrumented bears, as bears equipped with radio transmitters can be expected to have much greater recapture probabilities than bears without (e.g. Amstrup, McDonald & Stirling, 2001). Because convergence on local minima is a concern in multistate models (Choquet *et al.* 2006), we either re-ran models at least three times with random starting values for unconstrained parameters, or (when available) re-ran models with starting values from a well-defined simpler model (Choquet *et al.* 2006). As mentioned above, identifiability is a crucial issue in multistate models combining dead recoveries and live recaptures (Gimenez *et al.*, 2003), both in terms of model selection and interpretation of parameter estimates. We relied on M-SURGE which implements up-to-date algorithms to check for parameter identifiability (Choquet *et al.*, 2004). Model selection was based on Akaike's information criterion values corrected for small sample sizes (AIC$_c$; Burnham & Anderson, 2002).

Results

Sex, age, subpopulation, and harvest intensity were retained as variables predicting survival in the best MCR models (Table 1). Demographic effects were relatively mild, with a trend towards greater vulnerability of male bears to legal hunting, at least in the north. The best-performing models indicated no differences in vulnerability between age categories, except that cause-specific risk to hunting was estimated to be 0 for yearlings in the north. However, due to a small sample size and a lack of mortalities in that age category in our sample, standard error could not be estimated for the parameter. During the period with increased harvest quotas (1998–2006) in the south, the average cause-specific risk of dying due to legal hunting was 2·8 times higher than during the preceding low-pressure period (Fig. 2, Table 2). Harvest intensity had no significant effect on vulnerability in the north, where there was no corresponding increase in harvest quotas.

Table 1. Model ranking and fit parameters[a] with respect to the focal transitions (mortality parameters *h* and *w*) for Swedish brown bears. Parameters were estimated using multistate capture–recapture (MCR) modelling in M-SURGE. Shown are the most complex model considered and representative candidate models, including three top models that differ only slightly in AIC$_c$ value (w_i = AIC$_c$ weights). Regression terms are shown for transition probabilities of the MCR model. Following M-SURGE notation, interactions are signified by a period between the interacting factors. The last two columns indicate the model for immediate comparison ('comp.') and the term(s) targeted ('effect'). Model terms for capture probabilities and conditional movement in and out of the study areas are shown separately in Table 3.

	Mortality (*h* and *w* in Transition, Ψ)		Model performance					
	Legal hunting	Other	NP	Deviance	ΔAIC$_c$	w_i	Comp.	Effect
Full model:								
	a + s + p + i + a.s + p.s + p.a + p.i	a + s + p + i + a.s + p.s + p.a + p.i	52	3164.7	15.5	0.0002		
Other candidate models:								
1	a + s + p + i + p.a + p.i + p.s	a + s + a.s	41	3176.4	0	0.3804		
2	a + s + p + i + p.a + p.i	a + s + a.s	40	3180.4	1.6	0.1709	1	p.s. on hunting
3	a + s + p + i + p.a + p.i	a + s + p + a.s	41	3178.4	2	0.1400	2	p on other
4	a + s + p + i + p.a + p.i	a + s + p + a.s + p.s	42	3176.9	2.9	0.0892	2	p.s. on other
5	a + s + p + i + p.a + p.i + a.s	a + s + a.s	42	3177	3	0.0849	2	a.s. on hunting
6	a + s + p + i + p.a + p.i	a + s + p + a.s + p.a	43	3175.6	4	0.0515	2	p.a. on other
7	a + s + p + i + p.a + p.i	a + s + p + i + a.s + p.i	43	3176.6	5	0.0312	3	i + p.i. on other
8	s + p + i + p.i + p.s	a + s + a.s	37	3191.3	5.3	0.0269	1	a + p.a. on hunting
9	a + s + p + i + p.i + p.s	a + s + a.s	39	3187.5	6.3	0.0163	1	p.a. on hunting
10	a + s + p + i + p.a	a + s + a.s	39	3189.1	7.9	0.0073	2	p.i. on hunting
11	a + s + p + p.a	a + s + a.s	38	3196.8	13.2	0.0005	10	i on hunting
12	a + s + p + i + p.a + p.i	a + s + a.s	39	3194.5	13.3	0.0005	2	s on hunting
13	a + s + p + i + p.a + p.i	a + s	38	3199.5	15.9	0.0001	2	a.s. on other

[a]Symbol interpretation: age (a), sex (s), subpopulation (p), harvest pressure (i).

Table 2. Estimates of cause-specific mortality for brown bears monitored in Sweden between 1984 and 2006. Parameter estimates are from the best-fitting candidate multistate model, with the following effects on mortality transition probability in M-SURGE notation: $\Psi_{\text{from(12)to3(intensity subpop+subpop age+subpop sex)+from(12)to(4)(sex age)+others}}$. The age categories are defined as follows: yearlings = 1y, subadults = 2 – 4y, adults = 5y +. The vulnerability of yearling brown bears to legal hunting in the north was estimated to be 0 (not shown here), but no confidence interval could be constructed due to the small sample size and lack of hunting mortalities in that group. Nonetheless, legal hunting mortality for yearling bears in the north can be expected to be relatively small, for reasons outlined in the main text. The top-performing model for mortalities other than legal hunting did not distinguish between subpopulations and periods of harvest intensity.

Cause	Subpop.	Age category	Sex	Harvest intensity	Estimate	95% lCI	95% uCI	SE
Hunting	North	Subadult	f	low	0.036	0.014	0.089	0.017
			f	high	0.023	0.009	0.058	0.011
			m	low	0.103	0.052	0.193	0.035
			m	high	0.068	0.033	0.136	0.025
		Adult	f	low	0.019	0.007	0.051	0.010
			f	high	0.012	0.005	0.031	0.006
			m	low	0.067	0.027	0.154	0.030
			m	high	0.043	0.018	0.100	0.019
	South	Yearling	f	low	0.019	0.008	0.045	0.008
			f	high	0.054	0.028	0.103	0.018
			m	low	0.034	0.015	0.073	0.013
			m	high	0.092	0.051	0.163	0.028
		Subadult	f	low	0.021	0.010	0.043	0.008
			f	high	0.058	0.034	0.097	0.016
			m	low	0.023	0.011	0.045	0.008
			m	high	0.063	0.038	0.102	0.016
		Adult	f	low	0.031	0.017	0.057	0.010
			f	high	0.086	0.058	0.126	0.017
			m	low	0.040	0.023	0.071	0.012
			m	high	0.109	0.075	0.157	0.021
Other	North/south	Yearling	f	high/low	0.177	0.121	0.251	0.033
			m		0.086	0.039	0.179	0.034
		Subadult	f		0.060	0.036	0.099	0.016
			m		0.183	0.134	0.244	0.028
		Adult	f		0.066	0.047	0.092	0.012
			m		0.107	0.076	0.148	0.018

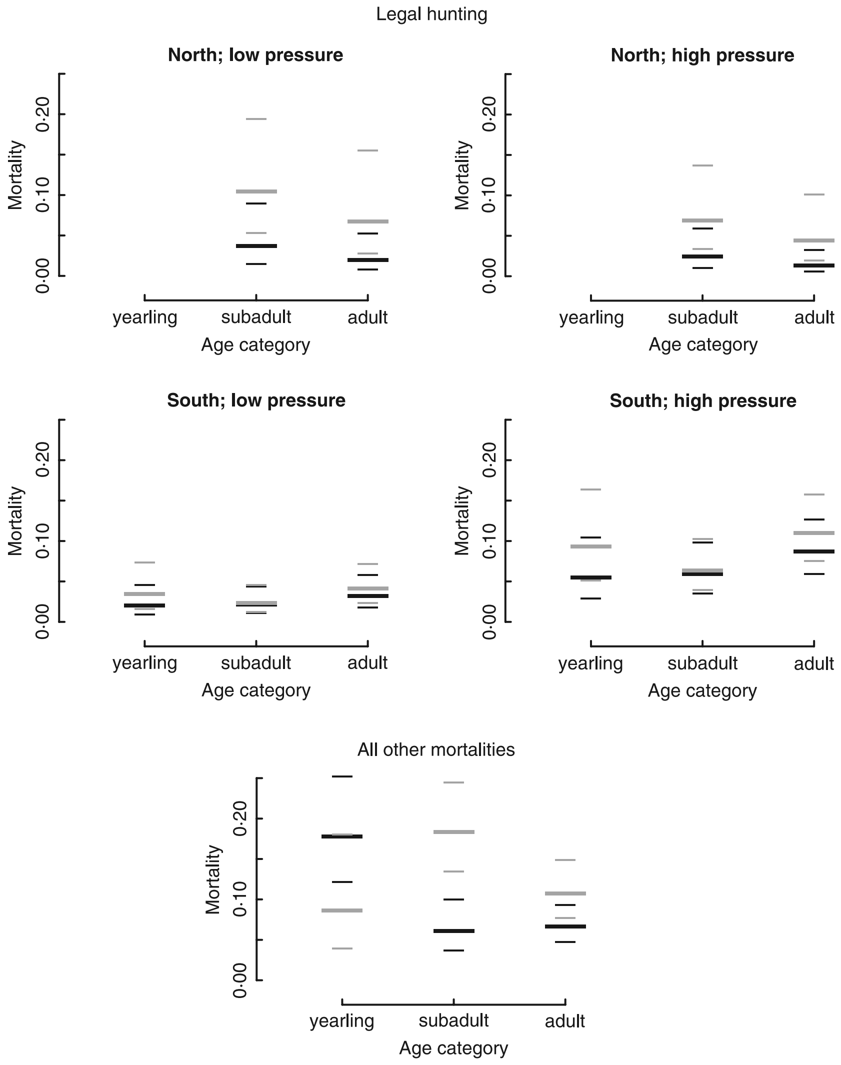

Fig. 2. Estimates of cause-specific mortality (thick bars) and 95% CI boundaries (thin bars) for female (black) and male (grey) brown bears monitored in Sweden between 1984 and 2006. Parameter estimates are from the best-fitting candidate multistate model, with the following effects on mortality transition probability in M-SURGE notation: $\Psi_{\text{from(12)to3(intensity subpop+subpop age+subpop sex)+from(12)to(4)(sex age)+others}}$. The vulnerability of yearling brown bears to legal hunting in the north was estimated to be 0 (not shown here), but no confidence interval could be constructed due to the small sample size and lack of hunting mortalities in that group. Nonetheless, legal hunting mortality for yearling bears in the north can be expected to be relatively small, for reasons outlined in the main text. The graph for mortalities other than legal hunting does not distinguish between subpopulations and periods of harvest intensity because these terms were not included in the top-performing multistate capture–recapture model.

The general pattern for vulnerability to causes other than legal hunting was one of greater risk for young individuals, particularly males (Fig. 2, Table 2). Subadult males and yearling females were most vulnerable. Subadult male bears were more vulnerable than subadult females and adults of both sexes, whereas among females, yearlings were the most vulnerable. Depending on population and age/sex group, individuals were between 1·6 and 9·1 times more vulnerable to the combination of other mortalities than to legal hunting. However, during the period of high harvest quotas, legal hunting mortality estimates in the south, with the exception of subadult males and yearling females, were similar to the mortality estimates associated with other causes (Fig. 2, Table 2).

In addition to the top model, two other candidate models received plausible support based on AIC_c (ΔAIC 0–2; Burnham & Anderson 2002); one included an effect of subpopulation on mortality due to causes other than legal hunting (slightly lower in the south), and the other did not include a subpopulation:sex interaction on legal hunting mortality. Aside from these differences, all top-performing candidate models showed similar results in terms of structure and effect sizes.

Recapture probability estimates (Fig. 3) were at or near 1 for instrumented bears alive inside the study area but were substantially lower for bears alive outside the study area. Recapture probabilities for live bears without radiotransmitters were at or near 0, regardless of location. The probability of detecting a newly dead bear due to mortality causes other than legal hunting was higher for instrumented bears than bears without transmitters and higher for animals in the south than the north (with yearling bears having the highest detection probability among the three age categories). The top-performing candidate models did not make a distinction between the sexes in terms of capture probability, regardless of the state (Table 3).

Discussion

Assessing the magnitude and selectivity of cause-specific mortality in managed populations is crucial for understanding their population dynamics and the evolutionary forces acting upon them. Legal hunting, in addition to being the most convenient to assess, is also the most easily managed component of mortality in many wild populations. Although it is the single-most

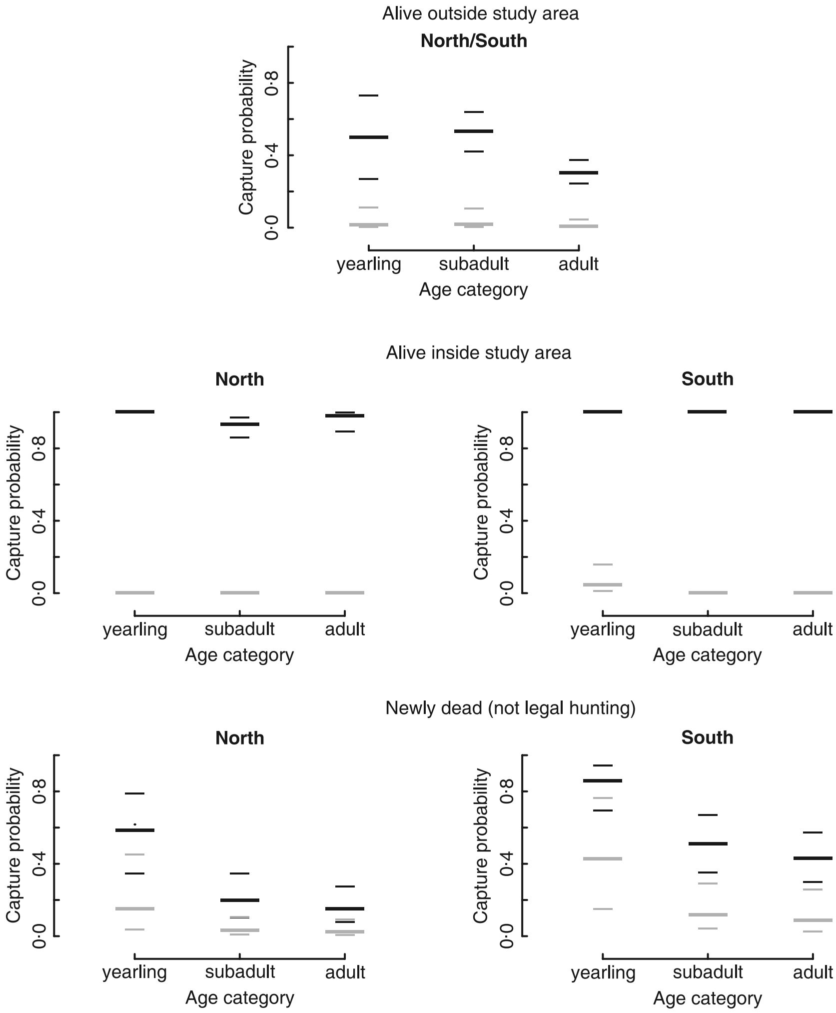

Fig. 3. Recapture probability estimates (large horizontal bars) for brown bears in Sweden with 95% CI boundaries from the top MCR model for states 1 (alive inside the study area), 2 (alive outside the study area), and 4 (newly dead due to causes other than legal hunting). Recapture probability for animals newly dead due to legal hunting was set to 1 (because of the reporting requirement of legally harvested bears) and is not shown. Black and grey bars represent estimates for instrumented and non-instrumented bears, respectively. Parameters without standard error boundaries indicate that all individuals in that group either had 0% or 100% recapture probability. The recapture probability component of the MCR model in M-SURGE notation is: $P_{\text{to}(1,4)\,(\text{age+radio+pop})+\text{to}(2)\,(\text{age+radio})+\text{others}}$.

Table 3. Comparison of model terms[a] and interactions with respect to state-specific capture probabilities and conditional movement in and out of the study areas in the full MCR model and those used in the best performing overall models (see also Table 1). Because of the reporting requirement of legally harvested bears, capture probability for animals newly dead due to legal hunting was set to 1.

Probability	State	Full model	Top ranking model (see table 1)
capture	alive inside	a + s + p + r	a + p + r
	alive outside	a + s + p + r	a + r
	newly dead: legal hunting	1	1
	newly dead: other	a + s + p + r	a + p + r
transition	alive inside -> alive outside	a + s + p + a.s	a + s
	alive outside -> alive inside	a + s + p + a.s	a + s + p + a.s

[a] Symbol interpretation: age (a), sex (s), subpopulation (p), radio-marked (r).

important cause of mortality for bears in Sweden (Sahlén *et al.*, 2006), we found that the combined mortality from other causes is as great, and for several demographic groups greater than legal hunting. In addition to being of considerable magnitude, mortalities other than legal hunting also show greater demographic selectivity than legal hunting. Interestingly, although only a fraction of the 'other' mortality category was natural mortality, these nonharvest mortalities still showed a general pattern of demographic selectivity that we would expect from a natural mortality regime in long-lived species, namely greater vulnerability of young animals. We cannot say whether this comparison also holds quantitatively, as no similar brown bear population has been studied under purely natural conditions. Nonetheless, it is clear that this combination of natural and human-caused mortalities is an equally important contributor to this brown bear population's dynamics and potentially evolution as is hunting. The low selectivity of harvesting mortality, on the other hand, contrasts clearly with results obtained in marine ecosystems (Olsen *et al.*, 2004) and trophy hunting cultures (Coltman *et al.*, 2003) with a very strict size-selective harvesting regime. Therefore, one should not underestimate the role of hunting traditions and management regimes for harvesting as a selective force.

Demographically selective harvesting is receiving growing attention from ecologists and evolutionary biologists, as it has the potential to affect population dynamics (Langvatn & Loison, 1999; Mysterud, Coulson & Stenseth, 2002; Milner, Nilsen & Reassen, 2006) and evolutionary processes (Coltman *et al.*, 2003; Garel *et al.*, 2007; Proaktor, Coulson & Milner-Gulland, 2007). Males have generally been found to be more vulnerable to hunting than females, with young males being the most vulnerable age/sex class, both in bears (Derocher *et al.*, 1997; Noyce & Garshelis, 1997; McLellan *et al.*, 1999) and in other large mammals, such as cervids (e.g. Langvatn & Loison, 1999). Such selectivity may arise due to direct management actions (e.g. selective quotas), active choice by the hunter (e.g. trophy hunting), or differential vulnerability caused by differences in individual characteristics (e.g. behaviour, morphology). We found an overall pattern of weak demographic selectivity of legal hunting, with a trend towards greater male vulnerability, at least in the north. Although only a trend, a difference in vulnerability between the sexes (at least among adults) could in part be due to the legal protection that females receive in Sweden during the time they are with dependent young. Another contributing factor may be passive selectivity as a result of behavioural differences between male and female bears, rather than active hunter selectivity (see also Bischof *et al.*, 2008a). With respect to the first argument, lower cub-of-the-year mortality (Swenson *et al.*, 2001) and higher average age at weaning (Dahle & Swenson, 2003a) in the north means that females spend a greater proportion of their time with dependent young than in the south, which could explain the trend towards a gender effect on legal hunting mortality in the north, but not in the south.

With the exception of yearling bears in the north, we found no clear indication of age-specific vulnerability to legal hunting among Swedish brown bears. The vulnerability of yearling bears to legal hunting in the north was estimated to be 0, but no confidence interval could be constructed due to the small sample size and lack of hunting mortalities in that group. Nonetheless, legal hunting mortality for yearling bears in the north can be expected to be relatively small, mainly for two reasons: (i) because in the north 46% of litters are weaned at 2·5, thus a smaller proportion of yearlings are available for legal harvest than in the south, where almost all litters are weaned at age 1·5 (Dahle & Swenson 2003a) and (ii) about one-third of the northern study area is made up of national parks, where bears are protected by law and most yearlings born in those areas have not yet dispersed to be available to hunters on the periphery of the protected areas (Støen *et al.*, 2006). Several studies on bears have found age-specific vulnerabilities to hunting (e.g., brown bears: McLellan & Shackleton, 1988; Bunnell & Tait, 1985; black bears, *Ursus americanus*: Noyce & Garshelis, 1997; Czetwertynski, Boyce & Schmiegelow, 2007; polar bears, *Ursus maritimus*: Derocher *et al.*, 1997). The lack of consistent and pronounced age effects on vulnerability to legal hunting in our study is therefore somewhat surprising. Analysis of the composition of the harvest revealed relatively little demographic bias between hunting methods in the Swedish harvest (Bischof *et al.*, 2008a), and we suggested that differences in the hunting system (no bag limit, few guided hunts, quota-limited season, etc.) are partially responsible for the limited effect of sex and age on relative vulnerability, compared with North American bear populations. It is worth stressing again that a quota-limited harvest without individual bag limits provides little incentive for a hunter to pass up a shot at a legal brown bear. We note that active hunter selectivity may increase in the future should the brown bear population continue to grow, thus increasing encounter probabilities and therefore harvesting opportunities for hunters. An increase in active selectivity, although not necessarily desirable, is more likely to be brought on by a change in the hunting system, for example, a shift from the current quota-limited hunt to one with a single bear tag assigned to individuals hunters.

Although biased harvest can cause demographic and evolutionary side effects, so can unbiased harvest. In an ungulate population model, Proaktor *et al.* (2007) noted that harvest pressure played a greater role in the selection for lighter weight at first reproduction than the degree of harvest selectivity. An increase in overall mortality can lead to a discounting of future reproduction, which may eventually result in the benefits of earlier reproduction outweighing its cost, such as lower offspring survival (Bischof, Mysterud & Swenson, 2008b). Thus, an elevated total mortality of Swedish brown bears as a consequence of growing harvest quotas may not only directly reduce the population growth rate in the long run, but cause additional indirect effects if a reduced age (and body mass) at primiparity is favoured.

Our results confirm that the increase in harvest pressure coincided with elevated vulnerability to hunting for individuals in the affected subpopulation. Whereas a positive effect of hunting pressure on vulnerability is intuitive, the quantitative effect of increased harvest pressure and how this may affect the level of compensation has rarely been evaluated. We found that the 3·4-fold increase in average annual quotas in the south was comparable to the estimated 2·8-fold increase in average vulnerability to hunting over the same time periods. The change in harvest pressure in conjunction with the availability of cause-specific mortality estimates presented an opportunity to evaluate the assumption of additivity in mortalities implemented in the matrix of transition probabilities (equation 1). This assumption was motivated by the precautionary principle and the following considerations: (i) hunting mortality occurs over a relatively short time frame (1–2 months), (ii) it takes place after much of the other mortalities have already been experienced (see below), and (iii) as Lebreton (2005) suggested, strong compensation can rarely be expected as a consequence of density dependence or heterogeneity in survival, and should be less likely in long-lived species than short-lived ones. The assumption of additivity was supported by the finding that vulnerability to natural mortality did not change as a result of increasing harvest pressure in the south. In the case of complete or partial compensation, we would have expected a depressing effect of increasing harvest intensity on the risk due to mortalities other than legal hunting. Nonetheless, overall population densities increased during the study period, so we concede that some caution is advised when interpreting changes in risk between periods of high and low harvest pressure.

Sex and age effects were most pronounced for mortality causes other than legal hunting and showed patterns of greater vulnerability of young animals and greater vulnerability of males than females, at least among subadults. These effects are similar to findings from brown bear populations in North America (McLellan *et al.*, 1999; Haroldson, Schwartz & White, 2006), with the exception that in our study population female yearlings were the most vulnerable female age class to mortality causes other than legal hunting, rivaling the vulnerability of male subadults. As mentioned earlier, the relatively high vulnerability of subadult males can be explained by increased mobility and dispersal behaviour of males, as well as their propensity to be less cautious (Blanchard & Knight, 1991; McLellan *et al.*, 1999). The causes of elevated vulnerability of yearling females, compared with the other two female age classes and even adult males, are less clear. Swenson *et al.* (2001) reported mortality rates due to intraspecific predation for female yearlings in Sweden that were several times higher than that of male yearlings, but the reason for this sex bias is unknown and warrants further investigation.

In addition to the differences in magnitude and selectivity, legal hunting and other mortalities also differ in the timing during the biological year. Whereas legal hunting is concentrated in a relatively short time period in late summer and early fall, the combined other mortalities are spread over the entire out-of-den period, albeit unevenly. The strong temporal focus of hunting mortality, compared with other mortalities, is likely to have consequences in terms of selectivity, for example if there is seasonal variation in the manifestation of life-history strategies (e.g. if some individuals were to wean their young after, rather than before the hunting season). This issue goes beyond the scope of our current analysis, but should be explored in future empirical and theoretical work.

An obvious information gap that remains for our study population is an assessment of the spatial and temporal patterns of harvest effort. Bischof *et al.* (2008a) explored and described harvest patterns and the demography of the harvest in the Swedish brown bear population. In the present study, we examined individual vulnerability to cause-specific risks in the same population, over roughly the same time frame. Estimates of cause-specific risk, harvest patterns, and harvest effort should be considered an essential information triage that can give ecologists and managers a comprehensive picture of the implications of harvest and other mortalities for wild populations.

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Article III

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Can compensatory culling offset undesirable evolutionary consequences of trophy hunting?

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Summary

1. There is growing concern about the evolutionary consequences of human harvesting on phenotypic trait quality in wild populations. Undesirable consequences are especially likely with trophy hunting because of its strong bias for specific phenotypic trait values, such as large antlers in cervids and horns in bovids. Selective hunting can cause a decline in a trophy trait over time if it is heritable, thereby reducing the long-term sustainability of the activity itself.

2. How can we build a sustainable trophy hunting tradition without the negative trait-altering effects? We used an individual-based model to explore whether selective compensatory culling of 'low quality' individuals at an early life stage can facilitate sustainability, as suggested by information from managed game populations in eastern and central Europe. Our model was rooted in empirical data on red deer, where heritability of sexual ornaments has been confirmed and phenotypic quality can be assessed by antler size in individuals as young as 1 year.

3. Simulations showed that targeted culling of low-quality yearlings could counter the selective effects of trophy hunting on the distribution of the affected trait (e.g. antler or horn size) in prime-aged individuals. Assumptions of trait heritability and young-to-adult correlation were essential for compensation, but the model proved robust to various other assumptions and changes to input parameters. The simulation approach allowed us to verify responses as evolutionary changes in trait values rather than short-term consequences of altered age structure, density and viability selection.

4. We conclude that evolutionarily enlightened management may accommodate trophy hunting. This has far reaching implications as income from trophy hunting is often channelled into local conservation efforts and rural economies. As an essential follow-up, we recommend an analysis of the effects of trophy hunting in conjunction with compensatory culling on the phenotypic and underlying genetic variance of the trophy trait.

Key-words: early conditions, evolutionarily enlightened management, large mammals, selective harvesting, sexual ornaments, sexually selected traits, ungulates

Introduction

Accounts of ecosystem change caused by selective human harvesting are accumulating (Allendorf & Hard 2009). In terrestrial ecosystems, traits targeted by trophy hunters are often sexually selected traits that evolved as signals of superior phenotypic quality. Antlers in cervids and horns in bovids are the most common targets of trophy hunters. The best supported evidence of evolutionary consequences of trophy hunting comes from wild sheep (Coltman *et al*. 2003; Garel *et al*. 2007), where trophy hunting decreased size and altered shape of horns. Long-term reduction in average trophy trait values undermines the sustainability of the activity itself.

How to manage populations that are evolving has become a key focus in fisheries (Jørgensen *et al*. 2007; Kuparinen & Merilä 2008) and to an increasing degree in terrestrial ecosystems (Allendorf *et al*. 2008; Coltman 2008). There are few viable suggestions on how trophy hunting can be made 'evolutionarily enlightened' (Ashley *et al*. 2003). Reducing offtake of trophy antlers will lower the chance or increase the time it takes to get an evolutionary response (Thelen 1991; Lindsey, Roulet & Romañach 2007). Allowing prime-aged individuals to breed for a few years before being shot may suffice to maintain their superiority as breeders. However, long delays may often be

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undesirable due to the cost of waiting and the risk that the animal will die before harvest; a risk that increases substantially after prime-age. One could argue that economic income from trophy hunting should not be an important motivator for accommodating high harvest quotas. Yet these activities may benefit the local economy by providing employment and using local services. Furthermore, trophy hunting income is sometimes channelled into conservation efforts (Lewis & Alpert 1997; Lindsey *et al.* 2006). Is it possible to counter the selection pressure induced by trophy hunting by means other than reducing the overall harvest?

One possible practice is the so-called 'Wahlabschuß' (i.e. selective shooting) commonly used in countries such as Germany, Poland and Hungary for sustainable management of red deer (*Cervus elaphus* L.) and other ungulate populations. This Germanic tradition, called compensatory culling from here on, entails the selective culling of individuals that show poor antler characteristics (e.g. based on tine length or volume) at an early age (Fig. 1, Lockow 1991; Drechsler 1992). Compensatory culling operates on the premise that early age antler sizes correlate with later age antler sizes (Bartos, Bahbouh & Vach 2007). The larger yearlings are allowed to mature to be available for trophy hunting at a later stage. The hunting of low-quality males is performed by local hunters (Mysterud, Tryjanowski & Panek 2006). The compensatory culling is their opportunity to hunt and acquire meat (S. Csanyi, pers. comm.). Compensatory culling does not have to be costly and is therefore a feasible management alternative. Similar approaches involving compensatory culling have also been suggested for ungulate management in Spain (Torres-Porras, Carranza & Pérez-González 2009) and the USA (Williams, Krueger & Harmel 1994), although certain assumptions that the strategy is based on are still debated (Koerth & Kroll 2008).

There is a noticeable absence of any theoretical evaluation of whether compensatory culling at an early life stage can counter the undesirable effects of trophy hunting (Fig. 1). It may seem intuitive that appropriately applied selective pressures can alter the fitness landscape in a way that may accommodate trophy hunting while at the same time minimizing the decline in trait quality in the population. However, there are a number of factors involved besides young–adult correlation in traits and heritability, including population dynamic responses to selective culling at different ontogenetic stages, the impact of age structure changes and density-dependent effects on individual trait values (Kruuk *et al.* 2002; Mysterud *et al.* 2005). These complexities demand a more elaborate approach than just intuition in order to generate valid predictions about the feasibility of compensatory culling. Here we develop an individual-based model of a male red deer population to explore the potential short- and intermediate-term effects (up to 100 years) of compensatory culling. The model was parameterized and validated using the extensive empirical knowledge available primarily from red deer populations in Norway and Scotland. This includes information of population dynamics and how trophy traits, age, density and breeding success are related.

Materials and methods

We used an individual-based simulation model of a male red deer population, where age and antler size were individual- and time-dependent attributes. We follow Grimm *et al.* (2006) guidelines for describing individual-based models. Assumptions and the model parameter space are listed in Table 1, while the validation is given in the Supporting Information. Our model allows trait values that were associated with greater fitness to emerge under a given selection regime, and is thus akin to optimization approaches (e.g. Cody 1974; Smith 1978; Rice 2004), albeit in our case non-deterministic. Although simplified, the model was based on a complex system with the following important challenges:

1. overlapping generations;
2. age-dependent survival and reproductive rates;
3. stochasticity in population dynamics and trait expression;

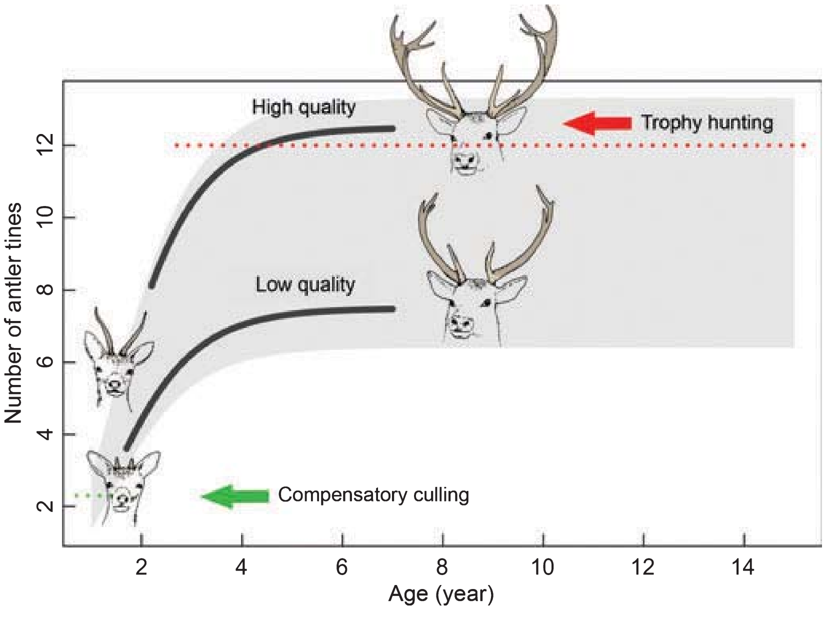

Fig. 1. Graphical representation of the concept to use compensatory culling at an early age (aimed at yearling males of low quality) to offset the undesirable effects of trophy hunting of prime-aged individuals (aimed at males with large antlers). Antler size is a trait indicative of phenotypic quality; it is highly variable and clearly visible from a distance already in yearlings, thus permitting selective harvesting of low quality individuals. The grey area signifies the range of trait values assumed during growth by individuals with different growth potentials. The dotted red line is drawn at the lower threshold for trophy hunting (12 antler tines), whereas the dotted green line marks the upper threshold for compensatory culling (variable).

Table 1. Overview of input parameters and assumptions of the individual-based model of male red deer population and antler size dynamics

Parameter, assumption	Symbol	Sources	Value(s) used
Demography			
Natural mortality	$S_{0,a}$	Catchpole *et al.* (2004); Coulson *et al.* (2004)	**Nonlinear function of age**
Density-dependent survival	S_a	Catchpole *et al.* (2004)	{**true**, false}
Reproductive rate (male calves born per female)	f	Coulson *et al.* (2004); Langvatn *et al.* (2004)	**0·32** (constant)
Male:female ratio at birth		Clutton-Brock *et al.* (2002)	**1**
Female population size	N_f		**400** (constant)
Male carrying capacity	K		**300**
Constant natural abiotic environment			**True**
Antler size ($x_{a,i}$)			
Heritability	h^2	Kruuk *et al.* (2002)	{0, 0·15, **0·329**, 0·7}
Permanent individual error	ε_p	Kruuk *et al.* (2002)	{0·1, 0·15, **0·3**}
Annual individual error	ε_a	Lockow (1991)	{**0·1**, 0·15, 0·2}
Density-dependent antler growth	$x_{a,i}(N/K)$	Kruuk *et al.* (2002); Mysterud *et al.* (2005)	{**true**, false}
Mutation rate	μ	Radwan (2008)	**0·01**
Antler growth curve parameters	P, B_2, B_3	Mysterud *et al.* (2005)	Nonlinear model fit to data **9·86, 4·44, 0·35**
Relative annual breeding success	ABS	Kruuk *et al.* (2002)	**Linear**
Management			
Overall hunting quota (proportion of male population size)	Q		**0·15**
Culling risk (proportion of poor quality individuals)	q_c	Predictor	0 to 0·9
Culling threshold	τ_c	Predictor	1·5 to 3
Trophy pressure (number of trophies)	h_t	Predictor	{0, 3, **5**, 8}
Trophy threshold	τ_t		**12**

Terms in '{}' represent alternative values for which simulations were run. Default values (i.e. those best supported by empirical evidence or conjecture) are shown in bold. Boolean responses (true/false) are used where appropriate.

4. different selection pressures (magnitude and direction) on an ontogenetically changing trait at various ages;
5. additional effects on the focal trait through density dependence.

OVERVIEW

Purpose

The purpose of the model was to explore whether compensatory culling at the yearling stage could compensate for the trait-depressing effects of trophy hunting at the adult stage.

State variables and scales

Four scales were considered in the model: (i) individual male red deer; (ii) birth cohort; (iii) the population; and (iv) the environment (defined by the management regime). Individuals were described by the following state variables: age, individual trait size potential, expressed and age-specific antler size. Individuals 5- to 8-years old were considered prime-aged. Cohorts were characterized by the average potential size of all individuals that had entered the cohort at the time of birth. The population was described by its size, i.e. the total number of males alive at a given time. The abiotic environment was assumed to be constant and the model was not spatially explicit. Only males were modelled explicitly. The female segment of the population was assumed to be of fixed size and total recruitment dependent only on female fecundity. Maternal effects on offspring trait values were ignored.

Process overview and scheduling

Simulations followed an annual schedule of events (Fig. 2), which began with calving, followed by antler growth of individuals 1 year and older, hunting mortality, mating (i.e. recruitment allocation to individual males) and finally natural mortality (i.e. winter and spring mortality). Although the rut and mating often coincide with the hunting season, for simplicity, we modelled hunting and mating sequentially. Similarly the winter/spring mortality overlaps with calving and early ontogeny of newborns, but these events were separated in the model. At the end of each model cycle, survivors aged 1 year and the cycle began anew with the calving season (Fig. 2).

DESIGN CONCEPTS

Population dynamics and dynamics of the focal trait in the population emerged as a result of individual characteristics. All interactions among individuals were modelled implicitly.

Survival and relative breeding success were interpreted as probabilities. Furthermore, stochastic elements were included in trait inheritance (as the error term in the sire-son regression) and trait expression (as the annual individual error).

Observation

For model testing, the distribution of sizes for each age class was observed annually. For model analysis, we recorded population-level variables (mean trait value, age distribution, population size, number

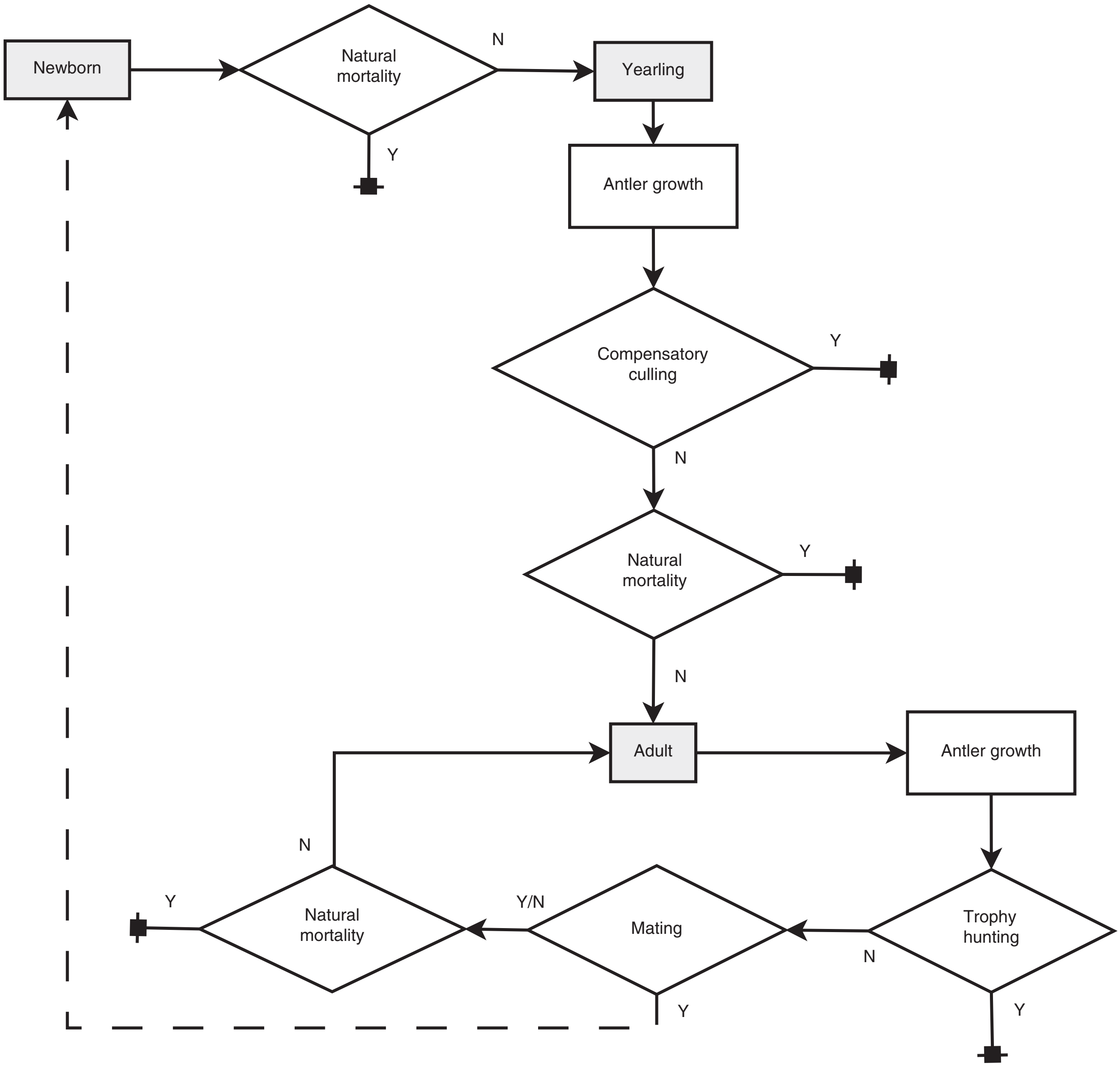

Fig. 2. Life history of male red deer in the individual-based model showing age classes (grey-shaded boxes), processes and survival transitions. The hashed line connecting reproducing adults with newborns indicates the contribution of adult males to next year's newborns. Deaths are marked with small black boxes with a strikethrough.

of trophy-sized individuals) over the entire simulation period (or at designated assessment times), and individual-level variables (all state variables) in the final year of the simulation.

DETAILS

Initialization

The initial population age structure was of limited importance. As long as there was a sufficient number of individuals that survived and reproduced during the first few years of the simulation, the population would go to an equilibrium age structure within a few years. Potential antler sizes in the initial population were drawn from a uniform distribution between 0 and 20 antler tines.

Input

We modelled three types of management regimes: (i) unbiased hunting mortality followed by natural mortality; (ii) trophy-biased hunting followed by natural mortality; and (iii) compensatory culling and trophy-biased hunting followed by natural mortality. The input parameters that guided the implementation of hunting, such as harvest pressures and selection thresholds, are summarized in Table 1.

Submodels

M1. Antler growth. The focal trait was antler size, measured in number of antler tines. We assumed that growth of antlers followed the Gompertz growth curve (Kruuk *et al*. 2002). The addition of a

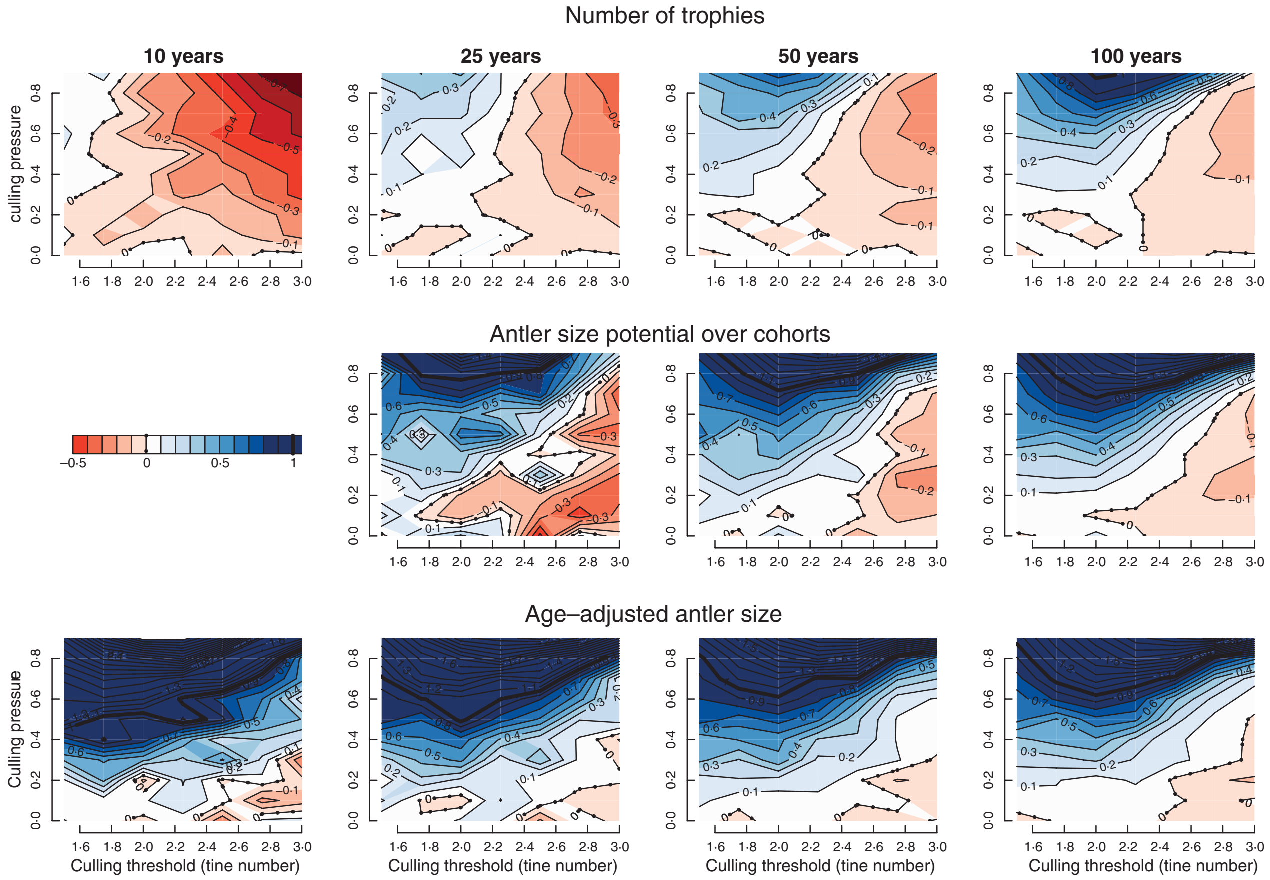

Fig. 3. Contour plots showing the simulated effects of culling pressure and culling threshold on compensation in (i) the number of trophy-sized individuals; (ii) the median antler size potential over cohorts (to monitor evolutionary change in trait values); and (iii) the age-adjusted antler size of red deer older than 2 years. Full compensation (solid thick black line) is achieved when compensatory culling leads to levels of the response equal to the level attained without trophy-biased hunting, whereas 0 compensation (hashed thick black line) is determined by the response level for trophy-biased hunting in the absence of compensatory culling. Shades of red indicate negative compensation, shades of blue positive compensation.

normally distributed annual error ε_a (Fig. S1; with SD expressed in per cent of size potential at age a) leads to:

$$x_a = P_i \exp(-B_2 B_3^a) + \varepsilon_a \qquad \text{eqn 1}$$

The parameters B_2 (4·4) and B_3 (0·4) were estimated by fitting the Gompertz growth curve to red deer antler tine and age (a) data from Norway (Mysterud *et al.* 2005) using nonlinear regression (Fig. S6). P_i is the individual growth potential (i.e. growth curve asymptote), with an average of 9·9 antler tines estimated from the Norwegian red deer data. We approximated density-dependent antler growth as a linear function of male population density (N/K, newborns excluded) with a slope of −1. Due to the small variation in the number of antler tines of yearlings (most individuals have 2), selection at age 1 was based on size (length) of the spikes. To enable use of the same unit for the trait under selection in both yearlings and adults, we assumed that spike length translates into (non-observable) tine number (used here as a continuous trait).

M2. Heritability. The asymptotic (potential adult) antler size of individuals entering the simulation as newborns was calculated based on their father's size potential by using the sire-offspring regression where the slope of the regression equals 1/2 heritability (h^2) and adding a normally distributed random error (Table 1), analogous to the permanent environment error described by Kruuk *et al.* (2002). To account for overlapping generations and age structure, the assigned asymptotic trait values of all individual's sired by the members of a cohort were regressed towards the mean trait value in their fathers' birth cohort at the time of that cohort's birth (i.e. before viability and fecundity selection acted on the fathers' cohort).

Heritability of antler mass in the most detailed study of red deer was 0·33 (Kruuk *et al.* 2002), and their review of other deer studies points to estimates usually in the same range though extremes include heritability estimates from 0·09 to 0·75. We assume a similar range for antler tines. Heritability of size of horns seems to be similar (0·24 in bighorn sheep *Ovis canadensis* Shaw; Poissant *et al.* 2008). We accounted for variation in empirical reports by testing model predictions under different heritability settings (Table 1, Fig. 4). The approach outlined above ignores genetic progress in the female part of the population. Although female preference for males with larger antlers was a basic tenant of the model, we assumed that mating was non-assortative, i.e. good males do not selectively mate with good females and vice versa.

Variation in the model was maintained through the permanent individual error introduced in each individual's potential size and subsequent regression of offspring trait value on the father's potential size.

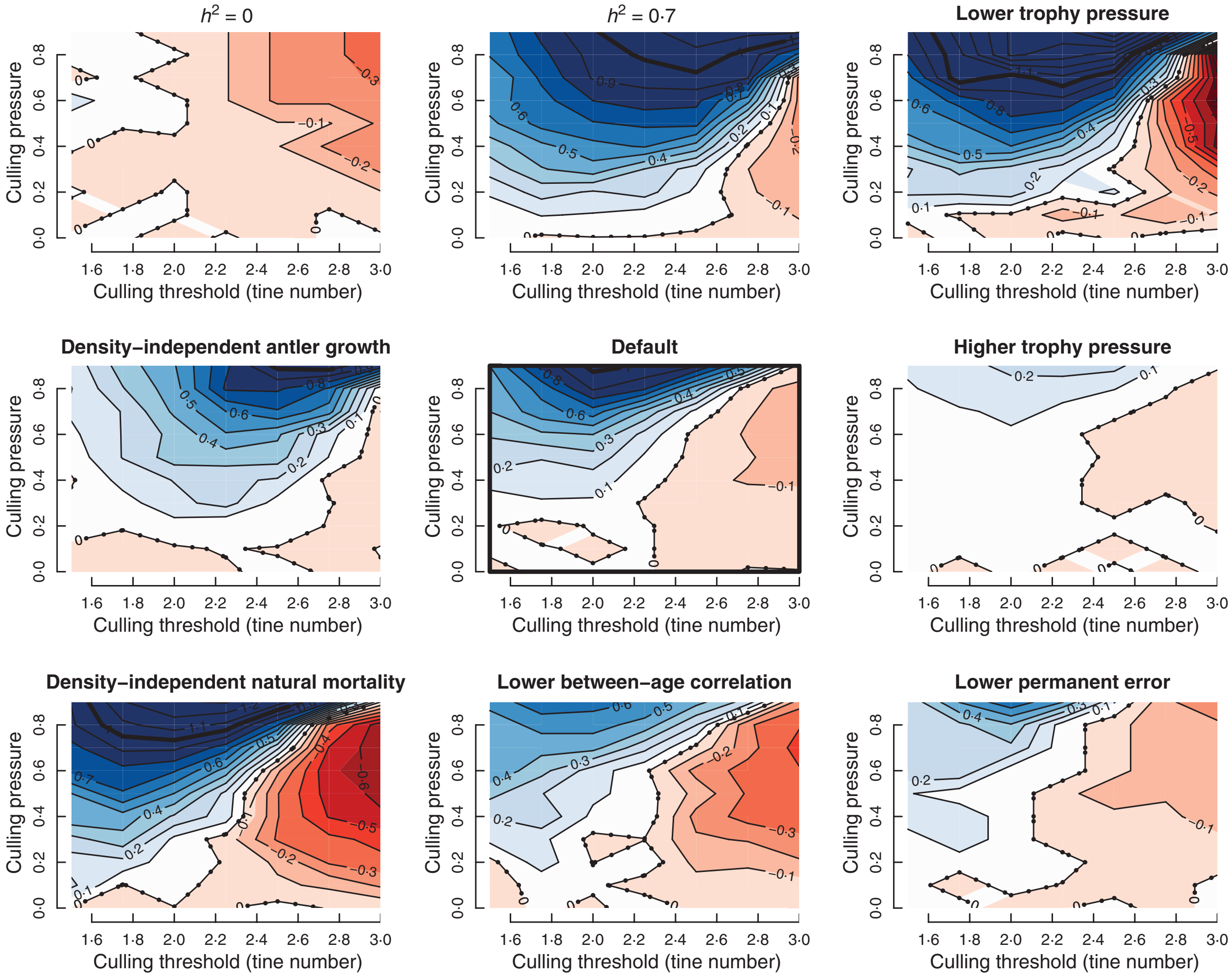

Fig. 4. Contour plots of compensation in the number of trophies as a function of culling threshold and culling pressure. The centre plot represents predictions resulting from default model settings (Table 1). The remaining panels illustrate the consequences of various violations of assumptions or deviations from default parameter values (clockwise starting top left corner): (i) no heritability of antler size; (ii) higher heritability ($h^2 = 0{\cdot}7$); (iii) reduced trophy pressure (3 trophy-specific tags per year); (iv) elevated trophy pressure (5 trophy tags per year); (v) reduced permanent error ($\varepsilon_p = 0{\cdot}15 \times 9{\cdot}9$ antler tines); (vi) increased annual error ($\varepsilon_a = 0{\cdot}2 \times$ current size potential); (vii) density-independent natural mortality; and (viii) density-independent antler growth.

This was an artificial way of maintaining genetic variation, but note that it was intended only as a proxy for the underlying true processes.

We allowed for a mutation rate of 0·01, termed a realistic mutation rate/genome/generation for sexual ornaments (Radwan 2008). Individuals affected by mutation received a trait value between 0 and 20, picked randomly from a uniform distribution. Mutations were not required to avoid trait fixation in our model, because variation was maintained through the sire/offspring regression as described above. Instead, mutations were permitted in order to facilitate the stochastic appearance (and disappearance) of extreme trait values, within the limits provided (0–20 in our model).

M3. Mating (and relative breeding) success. We assumed that an adult male's annual relative breeding success (ABS, interpreted here as its share in the number of 0-year-olds at the beginning of the next time step) was a function of its antler mass m and age a (no negative ABS values were allowed), such that:

$$\mathrm{ABS} = 4 + 1.276a - 0.0828a^2 + 0.00365m - 0.0002ma \qquad \text{eqn 2}$$

We adjusted the regression coefficient associated with the mass:age interaction to avoid eventual negative effects of mass on ABS at higher ages as arose if we used the coefficient provided by Kruuk *et al.* (2002). We also added an intercept to give ABS values similar to those reported in Kruuk *et al.* (2002). Because the coefficients estimated by Kruuk *et al.* (2002) were for antler size expressed in mass, we converted antler tine number into mass using a logistic function (Fig. S2) fit to data from Iberian red deer provided kindly by Y. Fierro and summarized in Fierro *et al.* (2002).

M4. Hunting mortality. Hunting mortality risk was implemented based on an annual harvest quota, calculated as a fixed proportion Q of current male population size (N). Depending on the current management regime, harvest was determined as follows:

1. Without trophy hunting, the entire annual harvest H was unbiased with respect to age and antler size, and constituted proportion Q of the male population.
2. With trophy hunting, a fixed number of trophy 'tags' h_t out of the total annual harvest quota were designated to be filled with

individuals with antler sizes above the trophy threshold τ_t, regardless of age. The remainder of the quota was filled without considering age and antler size. Thus, the number of individuals left for unbiased harvest (h_{ub}) was calculated as:

$$h_{ub} = NQ - h_t \qquad \text{eqn 3}$$

Adjustments to trophy pressure were accomplished by altering the number of designated trophy tags without changing the total number of animals harvested.

3. Compensatory culling followed a step function, affecting (with probability q_c) only individuals who were 1-year old and with antler sizes below the culling threshold τ_c.

Compensatory culling was not incorporated in the total harvest quota, hence its immediate effects in terms of survival were additive. Some compensation (not to be confused with compensatory culling) can be expected due to the density-dependent effects on natural mortality, but such compensation is likely weak (Lebreton 2005). Hunting and natural mortality were also assumed to be additive. We make the simplifying assumption of no effect of overall male quality on female fecundity (i.e. annual breeding success was relative), and we ignore other potential indirect effects of selective harvesting as they are usually weak (Mysterud, Coulson & Stenseth 2002) unless sex ratios are extreme (Milner-Gulland *et al.* 2003).

M5. Recruitment and population growth. Assuming an age structure similar to that reported for Norwegian red deer (Langvatn & Loison 1999), and annual age-specific female survival rates following a pattern and magnitude reported for red deer from the Isle of Rum, Scotland (Catchpole *et al.* 2004), we calculated the number of newborn males (assuming equal sex ratio at birth) produced each year as 0·32 times the number of females. The population was stable because the female population size and reproductive rate were fixed. In Norwegian red deer, there is weak density dependence in reproductive rates that affect only primiparous females (Langvatn *et al.* 2004), so we chose not to model this. Although we did not include density-dependent effects on fecundity in the model, recruitment of adults was density dependent due to density-dependent survival of newborns and yearlings.

M6. Natural mortality. We defined natural mortality risk experienced by individuals during simulation as a function of age (Fig. S4; Catchpole *et al.* 2004), with high mortality at the youngest ages, a rapid decrease in mortality as individuals approach prime age, low mortality throughout prime age and a senescent effect beginning around the age of 9 (Fig. S3) by using:

$$S_{0,a} = \left(1 - \frac{1}{1+e^{12-a}}\right)\left(1 - \frac{1}{1+e^{-0.5+a}}\right) \qquad \text{eqn 4}$$

We incorporated density-dependent effects on survival for newborns, yearlings and individuals older than 8 years (Fig. S4; Catchpole *et al.* 2004) by formulating their natural mortality function as (see also Collier & Krementz 2007):

$$S_a = 1 - \frac{1}{1+\exp\left(-\left(\ln\left(\frac{S_{0,a}}{1-S_{0,a}}\right) - 0.5\frac{N}{K}\right)\right)}, \text{ where } a \text{ was in } (0, 1, \geq 9) \qquad \text{eqn 5}$$

Because the evidence for a relationship between antler size and natural mortality in ungulates is inconclusive (Bonenfant *et al.* 2009), we did not account for it in the model.

SIMULATIONS AND ASSESSMENT OF UNCERTAINTY

We explored the behaviour of the model and made predictions by running 50 simulations over 150 years for each set of parameters. The first 50 years of each simulation were implemented without any hunting mortality, allowing population size and age structure to reach their respective equilibria. Because we incorporated a more biologically realistic mechanism for trait inheritance than typical optimization approaches, we used a fixed time limit instead of waiting for trait values to approach an asymptote. The rationale was that, under selection, heritability stays near its original level for a limited time only (5–10 generations, sometimes more, Falconer & Mackay 1996). We therefore provided forecasts only for the short and intermediate term (up to 100 years). Preliminary simulations indicated that stable age distribution and equilibrium population size were achieved within just a few years (see also Fig. 5).

The main responses measured were the effect of parameter changes on (i) the distribution of potential and expressed antler sizes and (ii) the number of trophy-sized (≥12 antler tines) individuals. We also assessed various other attributes of the population to monitor the population dynamic response to and impact on compensation. Responses were assessed in the 10th, 25th, 50th and 100th year of each simulation, approximately equivalent to 2, 5, 10 and 20 times red deer generation time (~5 years, Mysterud, Yoccoz & Langvatn 2009). We report median values of the response parameters from all simulations associated with a given parameter set. Upper and lower CI limits around each median were calculated as the 0·975 and 0·025 quantiles of the distribution of the response parameter, respectively. Growth model fitting, individual-based simulations and analysis were conducted in R 2.8.0 (R Development Core Team 2008).

Results

EFFECTS OF COMPENSATORY CULLING

Results of the assessment of model validity are detailed in the Supporting Information (Figs S5-S7). Simulations show that selective culling of poorer quality individuals at a young age can compensate for the detrimental effect of trophy hunting on both the mean value of the trait under selection and on the absolute number of prime-aged individuals that were trophy quality (i.e. ≥12 antler tines, Fig. 3). Numerical compensation was substantially weaker than the change in the mean trait value, because the latter was partially attained through reduction in overall population size. Both culling pressure and culling threshold were crucial for the outcome of compensatory culling in both the short and intermediate term. Reaching even moderate levels of compensation required high culling pressures. With certain parameter settings, compensatory culling can be counterproductive. Most or all yearlings fall below the culling threshold if it was set too high, decreasing the number of trophies instead of facilitating compensation. This was especially apparent during the early years of compensatory culling, when trait values in the population have not yet had sufficient time to respond to selection. In general, higher thresholds (but within the bulk of the yearling size distribution) and stronger pressures yielded greater compensation once trait values had responded to this form of selection.

ROLE OF TROPHY HUNTING PRESSURE

Selective culling of ‘poor quality’ yearlings increases the total number of trophy quality individuals in the population but full compensation was only achieved at relatively low trophy hunting pressure. Increasing trophy pressure quickly diminished the effectiveness of compensatory culling. With default parameter settings (Table 1), raising the number of annual trophy tags from 5 to 8 individuals reduced the maximum attainable level of compensation in the number of trophy quality individuals from just above 100% to between 20% and 30% (Fig. 4).

SHORT-TERM EFFECTS

Hunting affects population age structure and, as such, also the distribution of any trait that is age-dependent. We therefore compared observed antler sizes and age-corrected antler sizes among adult individuals (≥2 years), but found no obvious age structure effects in terms of the patterns of compensation in response to selective culling. Possible reasons for this were (i) as culling removes only yearlings, it does not change the relative size of the different age classes after the yearling age; and (ii) age structure was assessed before culling and trophy hunting, hence immediate selective effects (same year) were not detected.

To distinguish between viability selection and selection that results in an evolutionary shift in average trait values, we needed a measure of trait values in the population that was not sensitive to short-term effects of differential persistence of individuals with certain trait values. We obtained such a measure by first calculating the average antler size potential of each cohort at that cohort’s birth (i.e. before selection operated on that cohort). In any given year, the median antler size potential over cohorts is then calculated as the median of the average cohort-specific antler sizes of all cohorts still represented in the population.

We compared the effect of compensatory culling on the median antler size potential over cohorts (based on cohorts at birth), with that on the average age-adjusted number of antler tines (based on individuals). Changes in the former should represent an evolutionary response, although the latter would also include the short-term effect of differential longevity. However, we found little indication of a contribution of persistence effects to the observed patterns of compensation (Fig. 3).

VIOLATING ASSUMPTIONS AND CHANGING PARAMETERS

Heritability

Raising heritability from 0·329 to 0·7 increased the efficiency of compensatory culling due to a better link between selectivity and genetic response (Figs 4 and 5). At the same time, it increased the amount of compensation needed because the effect of trophy hunting on the trait distribution was also more severe (Fig. 5). When we assumed no heritability ($h^2 = 0$), the effects of compensatory culling on antler size were negative for most of the range of culling thresholds, and neutral at low culling thresholds, the latter presumably due to density-dependent effects on antler growth (Fig. 4). Heritability also influenced the demographics of the population (Fig. 5).

Yearling-to-adult correlation

As expected, the amount of annual variation in individual antler sizes affected the outcome of management. Increasing this variation led to a decrease in correlation between yearling and adult antler sizes, which in turn reduced the efficiency of compensatory culling with respect to the number of trophy-sized individuals available for hunting (Fig. 4).

Density-dependent antler growth

By definition, annual harvest quota (trophy hunt + unbiased harvest) remained unchanged, regardless of the amount of trophy pressure, and the removal of yearlings below the culling threshold appeared not to cause a gain in antler sizes due to further release from density dependence. However, density dependence caused a shift in optimal culling thresholds (a shift in the blue area from right to left in Fig. 4), because expressed trait values were naturally lower with than without density dependence.

Density-dependent survival

Removing the assumption of density-dependent natural survival amplifies the compensatory effect of selective culling, whereas the overall pattern remained unchanged qualitatively (Fig. 4). Negative density-dependent survival buffers population responses to management, as factors that increase population size also decrease natural survival, whereas factors that cause a decline in the population increase natural survival. Consequently, density-dependent natural survival buffers the effects of compensatory culling.

Permanent error in antler size

The error added to each individuals antler size potential was the source of both genetic variation (at least in part), as well as the permanent environmental error (equivalent to the one estimated by Kruuk *et al.* 2002). A more thorough explanation of its role and rationale is provided in the Supporting Information. We found that reducing this error from a standard deviation of $0{\cdot}3 \times P$ (P = average size asymptote in Norwegian red deer, not to be confused with individual antler size potential P_i) to $0{\cdot}15 \times P$ resulted in a diminished effectiveness of compensatory culling (Fig. 4). As the variation in the trait potential was reduced, selection had a smaller range of values to operate on, resulting in smaller responses to selection. This in turn caused a reduction in the speed of the trait changes, and consequently the change in the number of trophy-sized individuals.

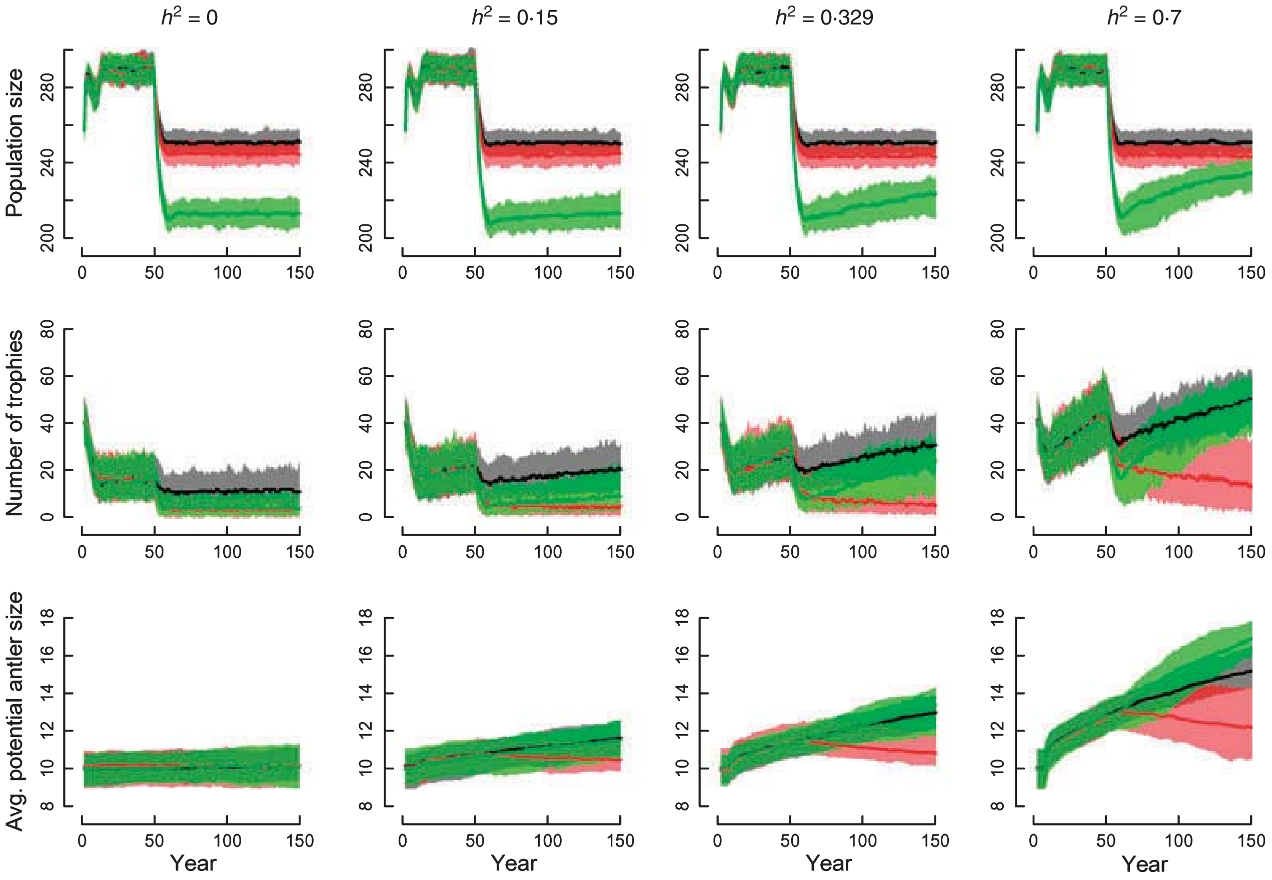

Fig. 5. Time series of population size, number of trophy-sized individuals and antler size potential over cohorts for three different settings of heritability (h^2). Solid lines represent point-wise median values from 100 simulations for each parameter setting and equivalently coloured semi-transparent areas show the associated 95% confidence bands (point-wise quantiles). Responses in the absence of trophy-biased hunting are shown in black, responses to trophy-biased hunting without compensation are shown in red, and responses to trophy-biased hunting with compensatory culling are shown in green. The first 50 years of each simulation proceeded without hunting.

Discussion

Our theoretical work showed that, within the bounds of a series of empirically well-supported assumptions, compensatory culling of poor-quality individuals at an early life stage had the potential to at least partially compensate for the trait-altering effects of trophy hunting in the short and intermediate term (up to 100 years).

COMPENSATION AND TROPHY HUNTING PRESSURE

Large males in natural populations sire a disproportionate number of offspring. Trophy hunting may in extreme cases cause a reversed relationship with smaller males siring more offspring, as reported in bighorn sheep (Coltman *et al.* 2003). This depends on the harvest pressure. The large-sized elephant (*Loxodonta africana* Blumenbach) bulls in Tarangire national park, Tanzania, retained a higher mating success even under poaching pressure (Ishengoma *et al.* 2008). Our model suggests compensatory culling might be enough to offset the likelihood for directional selection induced by trophy hunting. The average trait in the population responded readily to even mild compensatory culling in our simulations (Fig. 3). However, to achieve noticeable compensation in the number of trophy-sized individuals (≥12 tines) required substantial compensatory culling pressures. Achieving full compensation in terms of the number of trophies available may require average antler size among prime-aged individuals to be driven up substantially higher than it would be even under natural (non-hunting) conditions. Though empirical evidence for a cost of bearing antlers and horns is weak (Bonenfant *et al.* 2009), it is likely that fitness costs at very high antler sizes make such over-compensation in antler sizes difficult or perhaps impossible to achieve. It seems that the best results one can expect from compensatory culling will be achieved when trophy hunting pressures are relatively low (*c.* 10% in our model for the default parameter setting).

SHORT-TERM EFFECTS

Observed change in a focal trait may not necessarily be due to direct (fecundity) selection on the trait, but a result of changes to population structure and viability selection (Vaupel & Yashin 1985). Such effects are clearly less enduring than an actual change in the genetic make-up of the population. In the early stages of compensatory culling (< 25 years in our model), a temporary decline in the number of trophies appeared even with low trophy hunting pressures (Fig. 3). This was likely so because average trait values have to first increase in the population, before a sufficient number of high-quality yearlings fall above the threshold to form the next generations of prime adults.

The extent of the initial negative compensation was likely dependent on the culling threshold and on the strength of negative density dependence on antler growth. We expected a greater degree of compensation with negative density-dependent antler growth than with density-independent antler growth. However, changes to the age structure and short-term viability selection did not contribute noticeably to the observed changes in the trait distribution (Fig. 4). Though surprising, it could be explained if one considers that without density dependence, culling thresholds may be set higher, because yearling trait values will on average be higher than in the presence of density dependence. Consequently, gains in antler sizes through density-dependent effects may be offset by the decrease in overall effectiveness of selective culling due to lower optimal thresholds. This was consistent with the finding that the addition of density-dependent effects on antler growth shifts areas with positive compensation (blue area in Fig. 4) towards lower culling thresholds. We note that different assumptions about the hunting regime (e.g. a reduction in the overall harvest quota) may result in a positive effect of density-dependent antler growth on compensation through selective culling. Such short-term effects may be stronger in other systems depending on life histories or if vital rates and population size are assessed at different times during the year than in our model.

HERITABILITY

The most important assumptions for compensatory culling to work are heritability of the focal trait and young–adult correlation in trait values. Heritability of antler quality has received support not only from quantitative genetics studies (Kruuk *et al*. 2002), but also several alleles for antler growth in red deer have been identified (Hartl *et al*. 1995). Indeed, changes in allele frequency have been linked to selective trophy harvesting (Hartl *et al*. 1991; Hartl, Zachos & Nadlinger 2003). Greater heritability of the focal trait means that, in theory, a stronger and faster response can be expected to compensatory culling. However, greater heritability also means a stronger response to trophy hunting in the first place, requiring greater compensation. Indeed, increased heritability resulted in stronger effects of compensatory culling (Fig. 4). Heritability (for any given simulation run) was fixed in our model. Heritability may depend on environmental conditions (Lynch & Walsh 1998). As a consequence, we probably overestimated the speed with which antler size evolved in response to fecundity selection (breeding success) and viability selection (selective harvesting). Expected changes in heritability are generally not large and the response to selection can be maintained over many generations (Falconer & Mackay 1996).

To make our model tractable, fecundity selection acted on a single trait (in combination with age) and viability selection was purely age-specific. Natural selection may act on many different and often correlated characters simultaneously (Lande 1982; Law 1991). A lack of evolution in antler mass of red deer on Rum, Scotland, in the face of heritability and selection could be explained with environmental covariance between the focal trait (antler mass) and some unmeasured trait (e.g. body condition; Kruuk *et al*. 2002). These are important considerations, and the ability to detect and account for them is one of the benefits of quantitative genetics over optimization approaches traditionally used in ecological studies of evolution (Lande 1982; Lynch & Walsh 1998).

YOUNG–ADULT TRAIT CORRELATION

The concept of compensatory culling depends on the predictability of adult trait values from trait values at a young age. Although this has been shown to be the case in several field studies (e.g. Schmidt *et al*. 2001), there are also contradictory reports (Drechsler 1992; Koerth & Kroll 2008). However, sample sizes in these studies are rather low. The most thorough study followed 51 male red deer ageing (Bartos *et al*. 2007). The correlation between antler traits (mass, length, tine number) decreased with increasing distance between ages, but it remained relatively high for antler tine number even at age distances of 6 years. The correlation between individual antler tine numbers at age 3 and 8 years was 0·78, whereas the correlation between adjacent ages ranged between 0·68 and 0·84 (Bartos *et al*. 2007). In red deer on Rum, Scotland, antler length in yearlings and the number of antler points as 2-year-olds were also well correlated (r = 0·67, Schmidt *et al*. 2001). Antler composition and development are strongly dependent on early conditions and feeding (Landete-Castillejos, García & Gallego 2007), and the gene:environment interaction may prove important to determine the correlation between antler trait at young and old age. Only further empirical research can determine under which conditions this critical assumption holds.

MODEL LIMITATIONS

Trait evolution in real ungulate populations is complicated by the existence of alternate mating strategies (Hogg 1984), which we did not consider in our model. Yearling and subadult males allocate very little in antlers relative to body weight compared to at the prime-age stage (Vanpé *et al*. 2007). During the senescent stage, there is evidence of alternative antler growth tactics. Larger males continue to allocate heavily to antlers, whereas smaller males lower allocations (Vanpé *et al*. 2007). It was assumed that the best males were able to continue defending a mating territory or a harem, whereas the smaller males were forced to alternative mating tactics with little benefit of antlers. Similarly, we made only the asymptote of the Gompertz model individual-dependent; the other growth curve parameters were constant. However, it is possible that not only the size potential but also the speed with which it is attained varies (e.g. Lockow 1991). Violating this assumption could have important consequences, for example if selection would favour individuals with a lower asymptote but faster growth. This strategy would protect an individual from compensatory culling as a yearling, and subsequently protect it from trophy hunting as an adult.

Because we calculated offspring phenotype based on a regression on sire trait values instead of modelling genes, our model does not properly account for the loss in genetic variation due to strong directional or stabilizing selection as a result of selective hunting. Whereas traits under sexual selection generally have high amounts of additive genetic variation (review in Radwan 2008), the addition of strong viability selection through biased harvesting is bound to reduce not only expressed variability in trait values but also variability in their genetic basis (Bulmer 1971; Shnol & Kondrashov 1993). A more mechanistic and realistic approach to trait inheritance is required to evaluate the effects of selective harvesting on genetic variation in antler sizes in red deer and other ungulates. For now, our model assumes that, regardless of the selectivity path taken, there remains sufficient variation in the trait for selection to operate on. An important requirement for sustainability of trophy hunting with the help of compensatory culling in the long-run is the maintenance of variation in the trait and its genetic basis in the face of increased levels of stabilizing selection. We therefore consider the investigation of the dynamics of additional moments of the trait distribution following the implementation of a more mechanistic genetic model an essential and logical next step.

Several other important aspects of trophy hunting and compensatory culling remained unexplored, including (i) the effects of environmental stochasticity in recruitment; (ii) the possibility that the relationship between antler size and reproductive success may not be linear; and (iii) alternate hunting systems and different temporal patterns of harvest and culling. It also remains an open question whether compensatory culling can work with other sexually selected traits desired by trophy hunters such as mane size and colour in male lions (Whitman *et al*. 2004). Also, for large carnivores, one may run into conservation issues if implementing compensatory culling that is increasing overall mortality and thus reducing markedly population size (Fig. 5).

Conclusion

Although heritability and young–adult correlation in the focal trait were required for compensatory culling to work, shifting parameters and violating several assumptions revealed model resilience in terms of qualitative predictions. So far, there has been no formal statistical analysis of antler size trends in the cultures practising compensatory culling. However, one piece of empirical evidence for the utility of the approach comes from red deer trophy collections preserved in the castle of Detmold in Lippe, North Rhine-Westfalia, Germany. Specimens in the collection date from the end of the 17th to the beginning of the 19th century. Despite the fact that red deer antlers have been the most sought-after trophies for centuries in this culture, comparisons with red deer data in the same area today give no indication that trophy sizes have decreased notably over time (Ueckermann 1990). Although this evidence is somewhat anecdotal and awaiting more thorough analysis, it is contrasted by cases of hunter-caused trophy trait regressions in Africa (von Brandis & Reilly 2008), North America (Coltman *et al*. 2003) and in western Europe (Garel *et al*. 2007) without a tradition of compensatory culling. We conclude that evolutionarily enlightened harvesting (Ashley *et al*. 2003; Gordon, Hester & Festa-Bianchet 2004) and trophy hunting may not be incompatible, and that compensatory culling has the potential to make trophy hunting sustainable.

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Supporting Information

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

Fig. S1. Simulated antler sizes for individuals with three different antler size potentials (grey: 12 antler tines, red: average size asymptote in Norwegian red deer, blue: 8 antler tines) and two different levels of the annual errors in growth: (a) SD = 10% of potential size at a given age, (b) SD = 20% of potential size at a given age.

Fig. S2. Logistic function fit (solid black line) to antler mass and tine number data from Iberian red deer, kindly provided by Y. Fierro and summarized in Fierro *et al.* (2002).

Fig. S3. Survival probability (natural) plotted as a function of age as used in the simulation model of male red deer.

Fig. S4. Different levels of simulated age-specific survival probability (natural) of male red deer.

Fig. S5. Twenty-five-year dynamics of a simulated population of male red deer without hunting.

Fig. S6. Boxplots showing the distribution of antler sizes over all ages in Norwegian red deer (left) and a simulated population from the individual-based model. Both the real and the simulated population were hunted.

Fig. S7. Distribution of correlation estimates between simulated antler tine numbers of yearling and 6-year-old red deer, when the annual error (ε) in antler growth was set to 0·1 (thin hashed line), 0·15 (thick solid line) and 0·2 (thin solid line).

Supporting Information for "Can compensatory culling offset undesirable evolutionary consequences of trophy hunting?" by Mysterud and Bischof

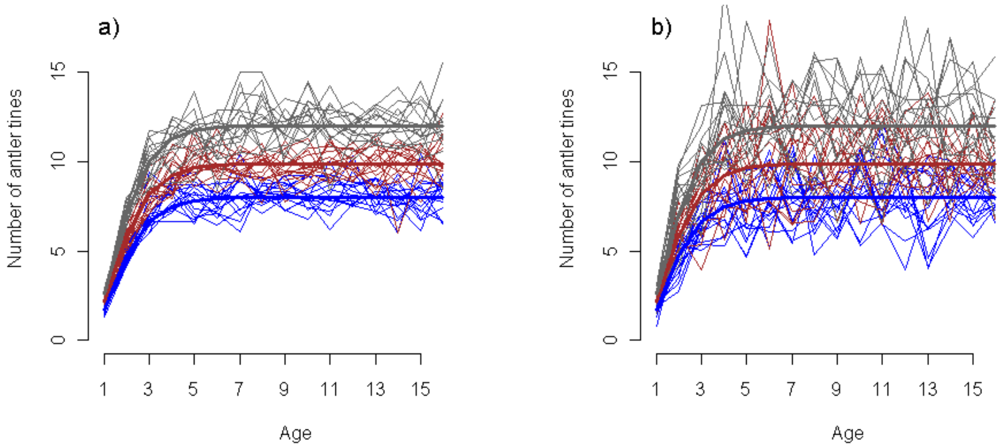

Fig. S1. Simulated antler sizes for individuals with 3 different antler size potentials (grey: 12 antler tines, red: average size asymptote in Norwegian red deer, blue: 8 antler tines) and 2 different levels of the annual errors in growth; a) SD = 10% of potential size at a given age, b) SD = 20% of potential size at a given age. Patterns of antler growth and variation therein correspond well with the development of red deer antlers on the international point scale (see figure 1 in Lockow 1991).

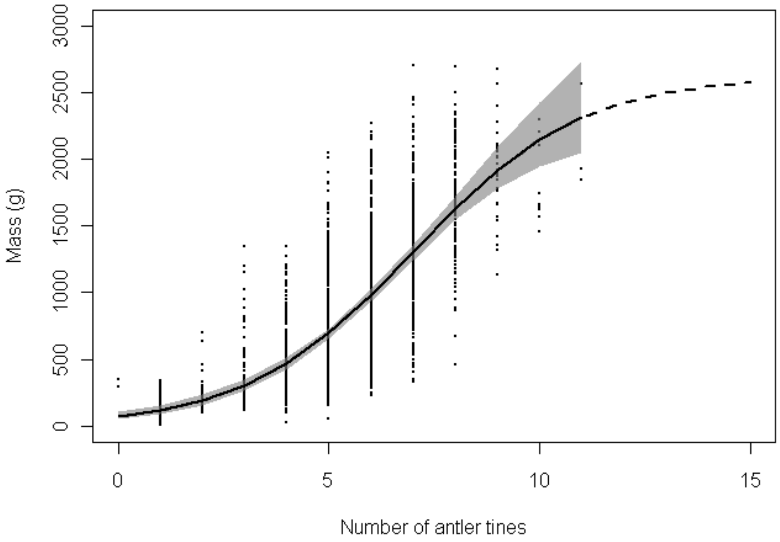

Fig. S2. Logistic function fit (solid black line) to antler mass and tine number data from Iberian red deer, kindly provided by Y. Fierro and summarized in Fierro et al. (2002). The hashed segment was the predicted antler mass associated with antler tine numbers ranging beyond the data. The grey area represents the 95% confidence band associated with the fit (not the data) and was based on the point-wise 0.025 and 0.975 quantiles of the predicted mass from 1000 bootstrap model fits (i.e., logistic function fitted to 1000 data sets re-sampled from the original data with replacement).

Fig. S3. Survival probability (natural) plotted as a function of age as used in the simulation model of male red deer. The function describing the curve (see main text) has been selected and parameterized to closely match age-specific survival probabilities reported for male red deer on the Isle of Rum by Catchpole *et al.* (2004). The thick black line represents age-specific survival in the absence of density dependent effects; thinner grey lines indicate density-dependent effects for young and senescent individuals (following empirical results from Catchpole *et al.* 2004), with density increasing from top to bottom: 0.5K, 1K, 1.5K (K =carrying capacity). Note that Catchpole *et al.* (2004) did not report values for calves (age = 0), while we included this.

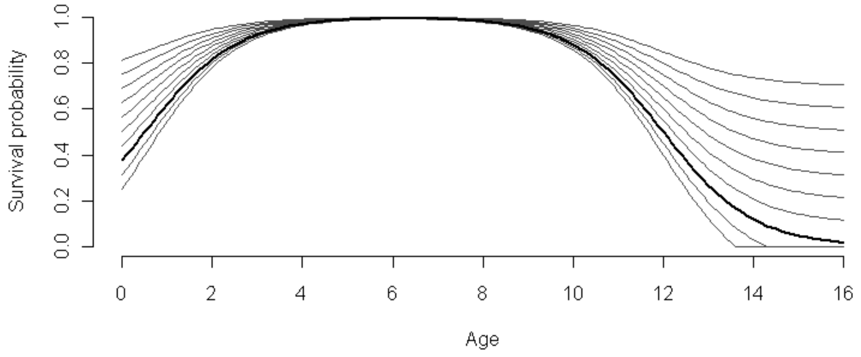

Fig. S4. Different levels of simulated age-specific survival probability (natural) of male red deer. The thick black line represents a risk multiplier of 1 (i.e. mortality magnitudes closely approximate those reported by Catchpole *et al.* (2004); thinner grey lines show the effect of multipliers ranging from 0.3 to 1.2 (from top to bottom in increments of 0.1).

VALIDATION

We found good correspondence between the dynamic behaviour of the simulated population and empirical reports of dynamic patterns. Heritability and correlation estimates from data simulated with the model were within the ranges reported for red deer in the literature. Additionally, model predicted distribution of antler size over ages under representative conditions, closely mimicked current age-size-distribution for Norwegian red deer. These and other evidence of correspondence with empirical results encourage confidence in model predictions, as does the fact that we limited forecast to the short- and intermediate-term (< 100 years). We add that a relatively small number of iterations (50) yielded clear response patterns, with mostly intuitive interpretations. Here we outline in more detail the validation of the individual-based simulation model.

V1. Age structure
V2. Antler growth and size distribution
V3. Correlation between yearling and adult trait value

V1. Age structure

Our model resulted in a similar age structure and distribution of cohorts (Fig. S5) as has been documented empirically for red deer (figure 1c in Coulson *et al*. 2004), although with a somewhat higher average age (5 instead of 4 years) for individuals older than 12 months.

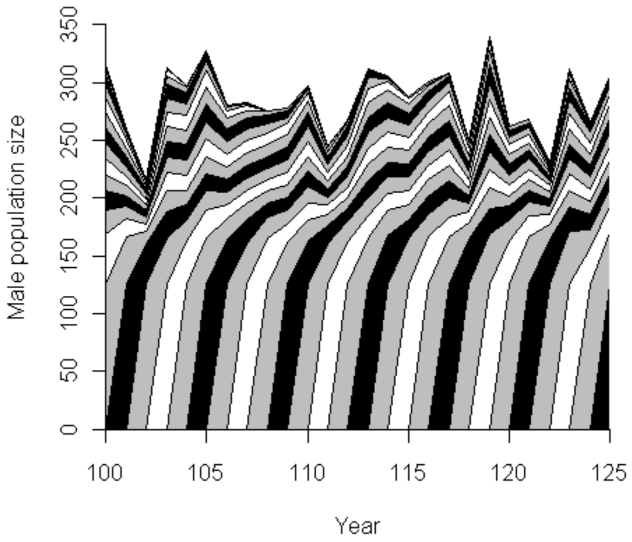

Fig. S5. Twenty-five year dynamics of a simulated population of male red deer without hunting. Each band (alternating black, grey, and white) represents a cohort. Individual cohort bands stack up to the total size of the population. The figure shows model-predicted patterns consistent with dynamics reported for red deer on the Isle of Rum (see Figure 1c in Coulson *et al.* 2004). Evenly spaced lower portions of the bands were indicative of the steady birth rate from a fixed female population assumed in the model for simplicity.

V2. Antler growth and size distribution

The pattern of antler growth resulting from our simulations (Fig. S1) was very similar to the development of red deer antlers on the international point scale (see figure 1 in Lockow 1991). This includes annual antler scores which (i) can decline from one year to the next and (ii) have an error that was smaller for individuals that were on a lower or delayed growth trajectory, supporting our use of an error structure implemented as a percentage of age-specific potential size. The close approximation of the simulated distribution of sizes in the hunted population to Norwegian red deer data from a hunted population (Mysterud et al. 2005) was further indication of reasonable model fit with respect to antler development and size distribution (Fig. S6).

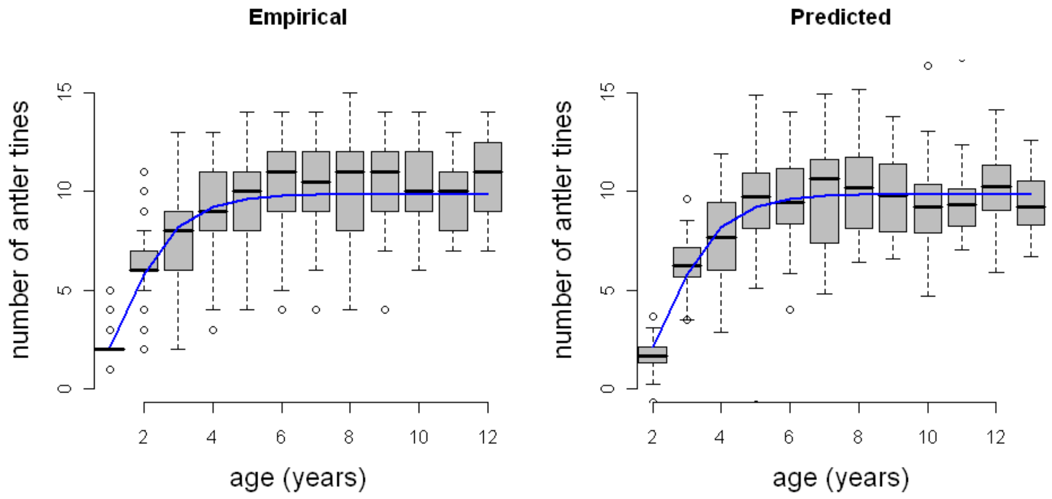

Fig. S6. Boxplots showing the distribution of antler sizes over all ages in Norwegian red deer (left) and a simulated population from the individual-based model. Both the real and the simulated population were hunted. The blue line represents the Gompertz growth curve, fitted to the Norwegian population.

V3. Correlation between yearling and adult trait value

We found that an annual individual error from a normal distribution with mean 0 and a standard deviation between 10% -15% of potential age-specific size (ε_a in equation 1) resulted in correlation (Fig. S7) in simulated antler tine number in individuals at the yearling and 6-year-old stage that corresponds well with correlation estimates in empirical studies (r between 0.68-0.84; Schmidt *et al.* 2001; Bartos, Bahbouh & Vach 2007). Through the size of the annual error, we could conveniently manipulate yearling-to-adult correlation in antler size and explore model sensitivity to changes in this parameter.

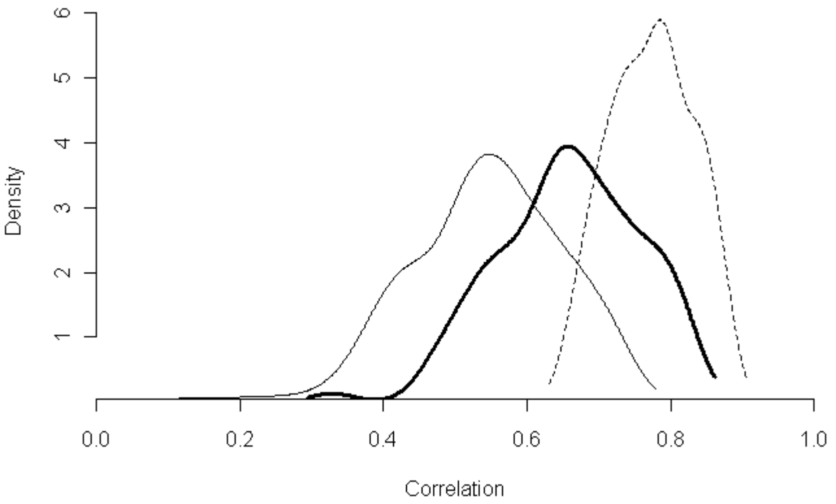

Fig. S7. Distribution of correlation estimates between simulated antler tine numbers of yearling and 6-year old red deer, when the annual error (ε) in antler growth was set to 0.1 (thin hashed line), 0.15 (thick solid line), and 0.2 (thin solid line). Estimates were calculated over the last 200 years of a 300-year simulation for each of the settings of ε_a and with all other parameters at their default values.

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Article IV

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The educated prey: consequences for exploitation and control

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There is convincing evidence that, in addition to improving their responses to natural predators, animals can also learn from their experience with human exploiters or man-made kill and capture devices. Despite its potential importance, the effect of improved defences to general exploitation (including human harvest) has received little attention so far. To address this void, and to link with practical considerations for management of exploited populations, we develop a general exploitation model with separate states for naive and educated individuals. We then evaluate and illustrate the relevance of acquired/improved defences for the dynamics of exploited populations and their management by applying the modeling framework to 2 management spheres with global scope, harvesting of wildlife populations, and control of invasive species. The strength of the predicted influence of educating prey on population and exploitation dynamics was positively affected by the intensity of exploitation and initial survival of naive individuals and negatively by the speed of life history of the target populations. We also demonstrate that the potential for response loss can lead to counterintuitive results with respect to effort and yield. Our model provides a framework for exploring adaptive behavior in the context of exploitation and for making both qualitative and quantitative predictions.
Key words: experience, hunting, improved defences, invasive species, learning, naive, survival. *[Behav Ecol 20:1228–1235 (2009)]*

Predator–prey interactions are of considerable importance in ecology (Begon et al. 1990), and it is apparent that their outcome is influenced by the participants' behavior. Although many behaviors involved in predator–prey interactions are acquired on an evolutionary timescale and are believed to be "hard wired," there is persuasive evidence for individual learning by both predator (e.g., Morse 2000; Gibbons et al. 2005) and prey (reviewed by Griffin et al. 2000). Prey, for example, can learn to recognize predators (Chivers et al. 1996; Mirza and Chivers 2000; Berger et al. 2001) and/or acquire avoidance or evasion responses (Griffin et al. 2000; Kelley and Magurran 2003). At least in models, such adaptive behaviors can lead to stabilization of predator–prey systems (Ives and Dobson 1987). The attention that trained antipredator responses have received in reintroduction projects (Griffin et al. 2000) and the growing interest in learned predator recognition when releasing hatchery-reared individuals in commercial fisheries (Mirza and Chivers 2000) attest to the practical importance of learned antipredator behavior in wildlife management and conservation.

In addition to learning to improve their responses to predators, prey can also become educated with respect to human exploitation. This aspect of adaptive behavior is less well documented but nonetheless prevalent. For example, first-generation toxicants for the control of pest and invasive species have been replaced by newer drugs and delivery systems, partially because of concerns over learned taste aversion after the ingestion of sublethal doses (Towns and Broome 2003). Hunters and trappers perceive an increased difficulty with which some animals are harvested once they have been educated to hunters or a certain trap type. Finally, although different in terms of its outcome for the individuals targeted, capture responses (trap happiness or shyness) in capture-mark-recapture (CMR) studies are acquired as a consequence of previous experience with a capture method or tool (Pradel 1993).

There is some theoretical work on the subject of learned predator avoidance (e.g., Dill 1973), but despite the intuitive feedback between nonlethal effects of exploitation and exploitation rate, there is currently no treatment of the management effects of improved defences to general exploitation, including human harvest. To address this void, we incorporate improved defensive responses to exploitation into a basic harvest model. We then expand this model to a more mechanistic state-dependent population exploitation model, which provides the needed balance of realism and flexibility for wider application.

Finally, in order to evaluate and illustrate the relevance of improved defensive responses for the dynamics and management of exploited populations, we apply the modeling framework to 2 management spheres with global scope: harvesting of wildlife populations and control of invasive species. Hereafter, we use the term "defences" or "defensive responses" in a broad sense to include avoidance and evasion responses toward human and nonhuman predators, as well as inanimate capture and kill devices such as traps and poison bait. We use "improved defences" to signify a change in response through learning that increases the survival of the affected individual with respect to the threat at which the response is targeted. Additionally, we use the term "exploiters," referring to both human and nonhuman predators.

MATERIALS AND METHODS

Model

We begin with a system of 2 equations, one for the change in the number of naive prey N_i and one for educated (experienced) prey N_e,

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$$\partial N_i/\partial t = (fL - h_i - d - g)N_i + fLN_e \quad \text{and} \qquad (1)$$

$$\partial N_e/\partial t = -(h_e + d)N_e + gN_i. \qquad (2)$$

The total number of prey alive at any given time is the sum of the number of living naive and educated prey. Both naive and educated prey contribute to population growth via a constant fecundity f; all new recruits are naive, regardless of their parents' status. L represents the density-dependent effect on fecundity, with carrying capacity K, so that $L = 1 - (N_i + N_e)/K$ (e.g., Williams et al. 2002). Individuals can be killed with probability h by an exploiter or die due to other causes with probability d (Williams et al. 2002). Naive and educated prey have separate exploitation mortality rates h_i and h_e, respectively. We assume that h is a function of exploitation pressure (e.g., number of active hunters, traps, or predators) and that $h_i > h_e$, which signifies the positive effect of improved defences on survival. Naive prey may become educated at a rate g, also a function of exploitation pressure, which we will define later. For simplicity, we assume instantaneous learning of a response that decreases mortality during subsequent encounters. This is not unrealistic; Maloney and McLean (1995) found that naive New Zealand robins (*Petroica australis*) learned to recognize invasive stoats as potential predators after just one training event. These authors pointed out the greater extinction risk posed by invasive predators that do not elicit learning of predator avoidance responses from a single encounter. Nonetheless, our model can be adjusted to account for a more gradual improvement in the response as a result of learning over multiple encounters.

Depending on the context, exploitation effort (e.g., the number of active hunters or traps) can be defined in various ways, such as

1. a constant (unchanging effort over time);
2. a time-dependent (and potentially prey dependent) variable; and
3. a Lotka–Volterra style transition equation for predators (Volterra 1926; Lotka 1932; Figure 1).

To increase the model's utility, we need an explicit formulation of the link between exploitation effort and increased

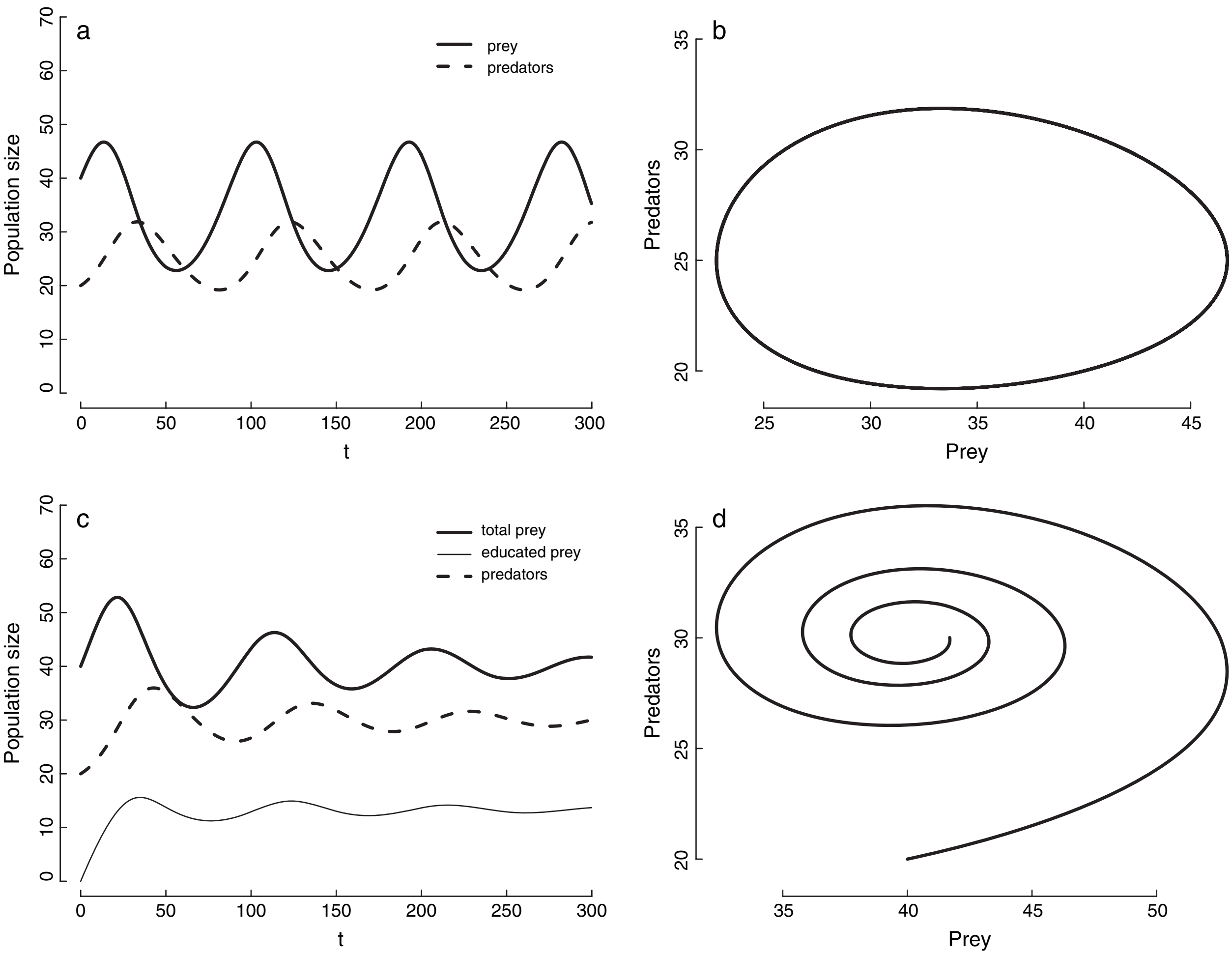

Figure 1
Dynamics of a Lotka–Volterra predator–prey system (a), with associated phase plane diagram (b). Dynamics for the predator–prey model with the potential for improved defences in the prey are shown in the lower panels (c and d). Changes in the predator population in the system with improved defences are defined as $\partial N_{\text{pred}}/\partial t = (b_iN_i + b_eN_e - d_{\text{pred}})N_{\text{pred}}$. N_{pred} represents the number of predators alive, d_{pred} is the mortality rate of the predator, and $b_iN_i + b_eN_e$ is the birth rate of the predator, a linear function of the number of prey. As in the traditional Lotka–Volterra predator–prey model, prey contribute positively to predator numbers but educated prey to a lesser degree than inexperienced prey ($b_e < b_i$), which reflects that the former are harder to prey on. Whereas equilibrium conditions in the basic continuous time Lotka–Volterra model lead to stable oscillations, the modified model incorporating learned antipredator behavior shows damped oscillations approaching a stable equilibrium.

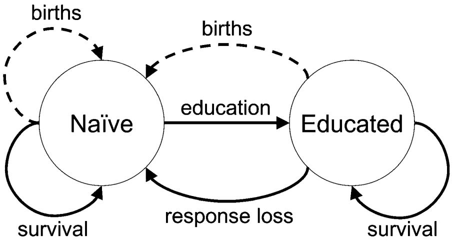

Figure 2
Life cycle diagram for a simple system with the potential for response improvement based on previous experience with an exploiter. Fecundity is represented by hashed arrows and survival transitions are indicated by solid arrows. Several of the transitions shown imply joined probabilities, for example, education and memory loss are conditional on survival and on encountering or not encountering an exploiter, respectively. Similarly, naive individuals have to survive natural mortality and not have an encounter with a hunter in order to remain naive.

survival due to experience. First, we decompose the prey mortality rate h into an encounter and a survival component so that

$$h = E(1 - S), \tag{3}$$

with E being the probability of encountering at least one exploiter and S the probability of surviving that encounter. Next, we define E as

$$E = 1 - (1 - P)^H. \tag{4}$$

The term $(1 - P)^H$ is based on the probability density function of the binomial distribution (reduced after the number of successes is set to 0) and represents the probability of encountering no exploiters when H exploiters are in the population (i.e., 0 successes out of H Bernoulli trials) and any individual exploiter is encountered with probability P. This approach assumes that the probability of encountering a predator increases with increasing number of predators in the system, but it does not differentiate between encountering 1 or more predators in a given time step. For small values of P, this is a reasonable approximation of the encounter probability as a function of the number of exploiters. Similarly, Luttbeg and Schmitz (2000) decomposed the probability of falling victim to predation into an encounter probability and conditional survival in one of their predator–prey models, but these authors modeled encounter probability as a step function of the number of predators. Our approach to linking encounter probability with exploitation pressure provides a more realistic, yet simple alternative, which should be equally useful for modeling inducible, not only improved defences. A further simplifying assumption is that prey do not "compete" for exploiters, that is, an exploiter remains dangerous to other prey regardless of whether it has already captured a prey in the current time step or not.

Incorporating Equation 3 into Equations 1 and 2 leads to

$$\partial N_i/\partial t = (fL - d - E)N_i + fLN_e \quad \text{and} \tag{5}$$

$$\partial N_e/\partial t = -[d + E(1 - S_e)]N_e + ES_iN_i. \tag{6}$$

We note here that antipredator behavior can be divided into 2 main categories (Lima and Dill 1990), namely, predator avoidance, which reduces the probability of encountering a predator, and response behaviors implemented when a predator has been encountered or detected. For our model, we chose to make the improvement of defensive response conditional on having survived an encounter with an exploiter. We also chose to have the improved defence increase the probability of surviving subsequent encounters. Although not an essential distinction for our purposes, it would have been

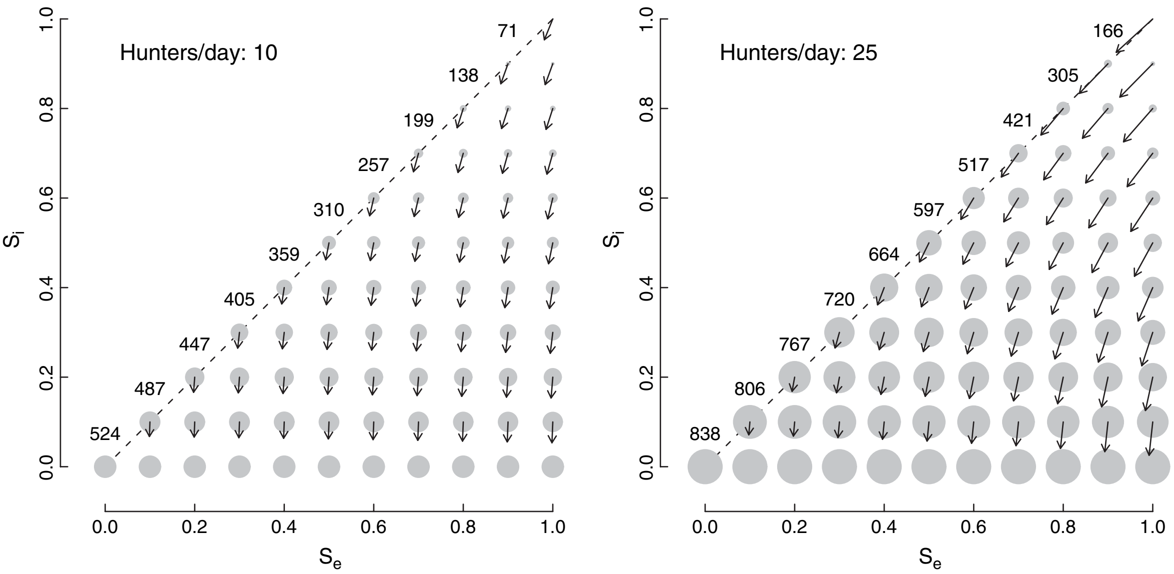

Figure 3
The effect of survival of naive (S_i) and educated (S_e) prey on total harvest after seasons of fixed length and different levels of harvest effort (active hunters per day). The size of the bubbles corresponds to total harvest yield (a subset of values is provided along the diagonal, referencing points directly beneath) for a given combination of S_i and S_e. Data are only shown for the range of S_i and S_e values, where $S_e \geq S_i$; the diagonal ($S_e = S_i$) represents populations where experience does not result in an improved response. Initial population size was set at 1000, and the probability of encountering an individual hunter was 0.002. Vectors show the direction and relative strength of change from low to high harvest yield at each point in the matrix of S_i/S_e pairs. Harvest is assumed to take place outside of the recruitment period ($f = 0$) and is short enough for nonhunting deaths to be negligible ($d = 0$).

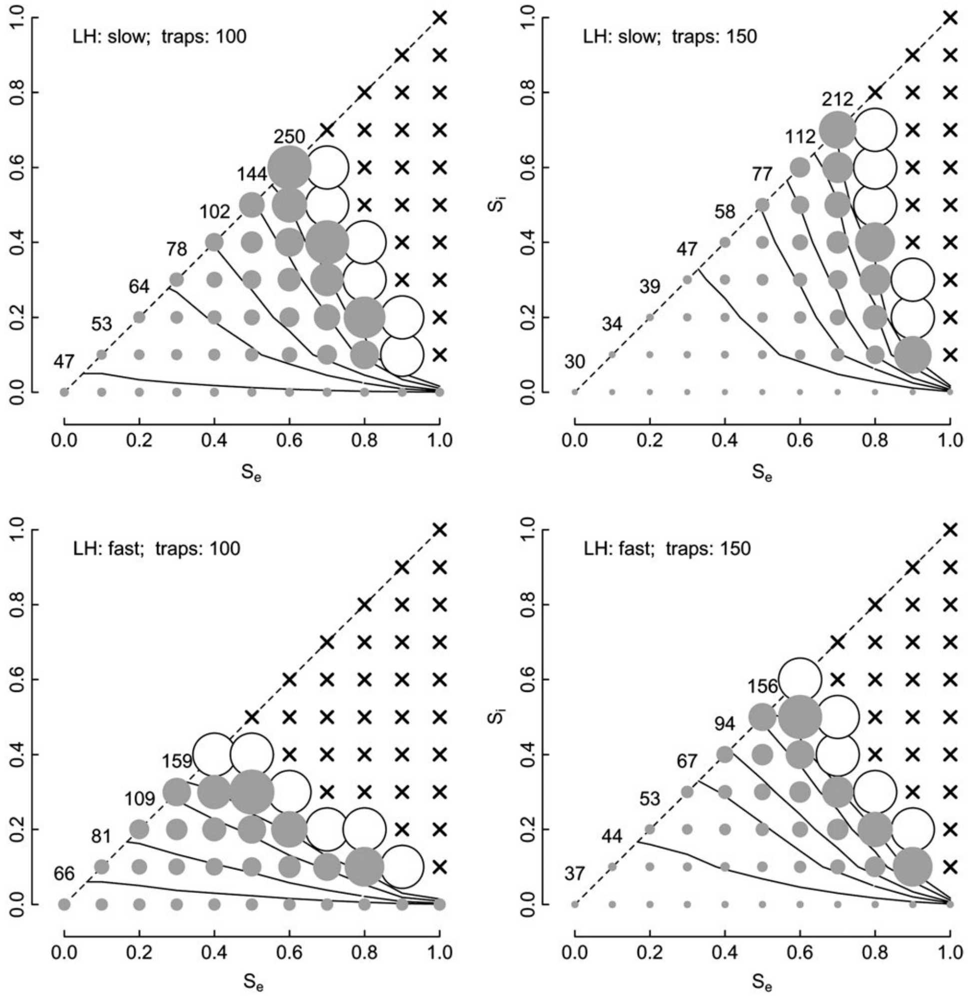

Figure 4
The effect of survival of naive (S_i) and educated (S_e) prey on invasive species control for 2 levels of control effort (number of active control devices) and for populations with slower (f = 0.07, d = 0.005) and faster life history (f = 0.13, d = 0.02). The size of the gray bubbles corresponds to the number of days of continuous control required to achieve complete eradication (a subset of values is provided along the diagonal, referencing points directly beneath) for a given combination of S_i and S_e (empty bubbles $\geq$ 300 days and $<$ 1000 days). Crosses indicate parameter settings at which the target can either not be achieved or requires $\geq$1000 days of continuous control. Data are only shown for the range of S_i and S_e values, where $S_e \geq S_i$; the diagonal ($S_e = S_i$) represents populations where experience does not result in an improved response. Contour lines have been added for required control duration of 50, 75, 100, 150, and 200 days (from bottom up) to help visually discern the relative strength of the effect of changes in S_e and S_i on the time required to achieve eradication.

equally plausible to have the improved response affect the probability of encountering exploiters in the first place (i.e., avoidance) or to have a combined effect on the probability of encountering an exploiter and on the probability of surviving an encounter once it has occurred.

Equations 5 and 6 assume that once an individual has obtained or improved a defensive behavior as a result of a previous encounter, the response (and associated elevated survival probability) remains unchanged over time. Nonetheless, there is empirical evidence that an individual can lose an acquired response over time (McLean et al. 1996; Brown and Smith 1998; Berejikian et al. 1999). We can model response loss by incorporating the probability m that an educated individual will lose the improvement in its defences if it does not encounter an exploiter (see also Figure 2):

$$\partial N_i/\partial t = (fL - d - E)N_i + [fL + m(1-E)]N_e \quad \text{and} \qquad (7)$$

$$\partial N_e/\partial t = -[d + E(1-S_e) + m(1-E)]N_e + ES_iN_i, \qquad (8)$$

where $m(1 - E)N_e$ represents educated individuals that have lost the improvement in their response. Similarly, Luttbeg and Schmitz (2000) incorporated a "rate of forgetting" into their predator–prey model with flexible prey behavior.

Example scenarios

Next, we apply the model developed above to situations routinely faced by wildlife managers in order to illustrate the potential relevance of educated prey to the outcome of management actions. We use representative sets of population parameters and show model responses over a broad range of exploitation parameters (exploitation effort and encounter probability) and associated survival (S_i and S_e) in order to allow for generalization of model predictions. Coding for model implementation was done in R 2.8.0 (R Development Core Team 2008). Differential equations were solved with the function lsoda in the odesolve package in R (Ellner and Guckenheimer 2008; Setzer 2008).

Harvesting

Exploitation of wildlife populations for commercial gain, subsistence, and recreation has important consequences for wildlife and human populations alike and is one of the driving forces behind wildlife management. Consumptive use of wildlife is often limited by seasons or quotas or both, and it is within this framework of a managed harvest that we first explore the role of improved defences in exploited populations.

We assume a game population which at the beginning of the hunting season consists entirely of naive individuals. As the hunting season progresses, some individuals are harvested, whereas others escape attempted harvest and become educated in the process. This dynamic can be expressed by Equations 5 and 6. We assume that harvest occurs outside the reproductive season (f = 0) and is short enough for nonhunting deaths to be negligible (d = 0). We explore the behavior of the model for different levels of exploitation effort over the full range of S_i and S_e values (where $S_i \leq S_e$) with

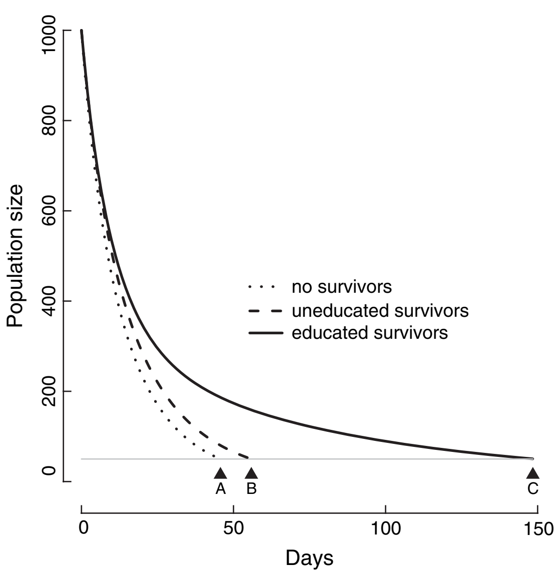

Figure 5
Population size over time of a hypothetical invasive species subjected to a control campaign with poison bait stations. Black arrows mark the times required to reach the target population level (5% of the original population) given (A) all individuals that encounter a poison bait station die, (B) 10% of individuals that encounter a bait station and ingest poison bait survive but do not develop a taste aversion, and (C) individuals that survive an encounter develop a taste aversion and have a probability of 0.2 of ingesting a lethal dose of poison in subsequent encounters. Initial population size is set at 1000, daily per-capita recruitment is 0.07, and the daily death rate due to causes other than control is 0.005. The probability of encountering an individual bait station on a given day is 0.005, and there are 50 bait stations active throughout the control period.

respect to the total harvest yield, given a fixed season length and constant effort over time.

Invasive species control

With increased globalization and associated anthropogenic introduction of nonnative and potentially invasive species, managers are now frequently faced with the task of devising and implementing control and eradication programs (Rodda et al. 1999; Towns and Broome 2003). We explore the consequences of improved defences for invasive species control using as an example the common problem of introduced rodent populations on islands (Towns and Broome 2003; Howald et al. 2007).

Because *r*-selected species are generally believed to be better invaders, we selected sets of vital rates representative of populations at the "fast"-end of the "fast-slow" continuum of life-history strategies (Gaillard et al. 1989). For purposes of illustration, we assume 2 different populations with sets of vital rates representative for tropical rodents with slower ($f = 0.07$, $d = 0.005$) and faster ($f = 0.13$, $d = 0.02$) life-history speed, although both can be considered r selected. The parameters used are within the range of values reported by Wirtz (1972), Adler (1998), and Stenseth et al. (2001) for tropical rodents (Central American spiny rat, *Proechimys semispinosus*; Polynesian rat, *Rattus exulans*; and multimammate rat, *Mastomys natalensis*; respectively). Because our model is not age or stage structured, we calculated f (interpreted here as the per-capita rate of recruitment of adults) as the product of reported adult fecundity and juvenile survival over the total number of days required to reach adulthood. We use daily rates for aforementioned parameters instead of more common monthly or annual ones in order to keep the probability of encountering a single capture device low, consistent with the requirements for Equation 4. To keep the focus on the role of differential survival of educated prey, we make several simplifying assumptions including geographic closure, lack of seasonality in fecundity and viability, and a female-only population. We assume that management wants to eradicate the population, which is to be achieved through poison bait stations (e.g., Thomas and Taylor 2002) set randomly throughout the island. We then use Equations 5 and 6 to determine the time required to achieve eradication given the parameter sets associated with the 2 life-history speeds mentioned above and different levels of control effort.

RESULTS

Harvesting

Not surprisingly, increasing survival of educated individuals results in reduced overall mortality. In the case of a hunting system regulated solely by season length (and assuming constant harvest effort), improved defences decrease the total harvest (Figure 3). Correspondingly, in systems regulated by quotas, improved defences increase the number of days required to fill the quota. This effect is modified by survival of inexperienced individuals: as survival of inexperienced individuals increases so does the negative effect of S_e on mortality due to the growing number of individuals that survive an encounter, become educated, and consequently enjoy greater survival during subsequent encounters. Greater effort (e.g., number of active hunters per day) results in greater yield but also in an increase in the proportion of individuals that are educated; thus, there is a positive relationship between harvest effort and the effect of changes in S_e on harvest yield. Overall, the effects of educated prey are mild for most of the parameter space and given harvest rates that are intended to be sustainable.

Invasive species control

Elevated survival due to experience with a control tool has the potential to dramatically increase the time required to extirpate or substantially reduce a population of invasives and can even prevent extinction (Figure 4). Effects of educating the population are strong even when the probability with which individuals survive an initial encounter is relatively low (Figures 4 and 5). In our example (Figure 5), it will take 46 days to reduce the population to 5% of its original size in the absence of improved defences and 100% effectiveness of the control tool (0% chance of surviving an encounter). If individuals have an average probability of 0.1 of surviving an encounter with a bait station, but do not learn from their past experience (e.g., if microencapsulation of the poison leads to delayed symptoms of poisoning which prevents the formation of learned aversion; Cowan et al. 1994), it would take 56 days to reach the target population level. If, however, individuals that survived an encounter with the poison develop a taste aversion to the bait and have a probability of only 0.2 of ingesting a lethal dose of poison when encountering traps in the future, the time to reach the target population size increases to 148 days. For the parameter space explored, the negative effect of S_e (relative to the effect of S_i) on the time required to reach a desired population reduction increases with 1) increasing survival of naive individuals, 2) increasing effort (i.e., number of active control devices), and 3) with a shift toward slower life histories (Figure 4).

By definition, response loss facilitates a reduction in educated prey and consequently increases average vulnerability.

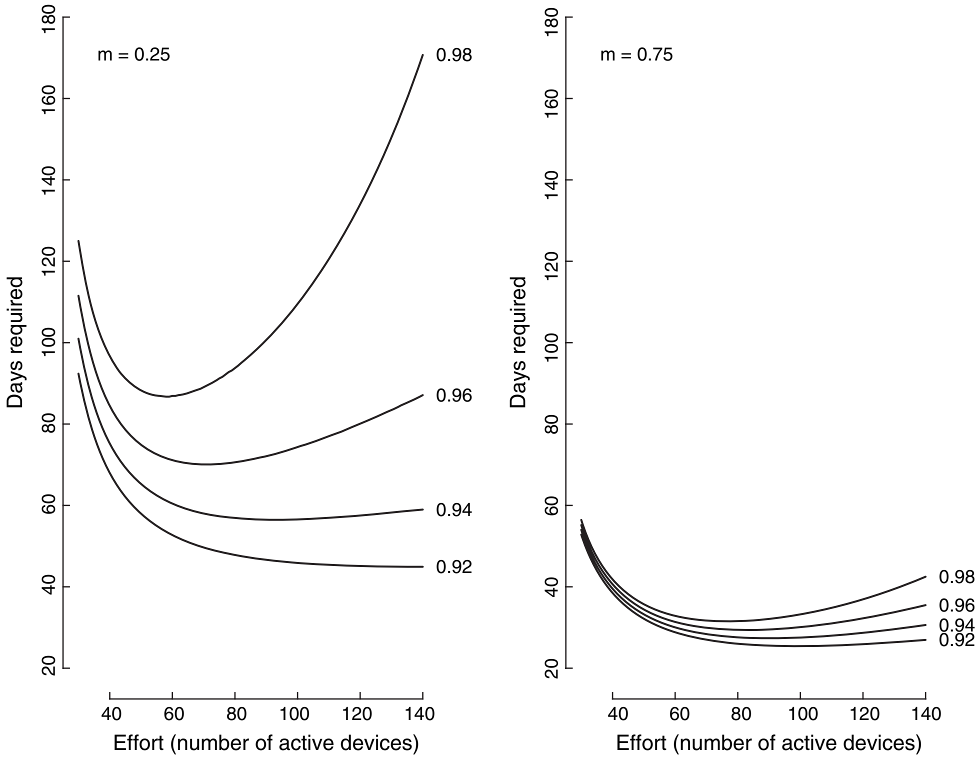

Figure 6
Graph demonstrating that at high survival (S_e) of educated individuals in a population of invasives (with the potential for response loss), increasing control effort can have the counterintuitive effect of increasing the time required to reach a desired population reduction. The effect of changing effort is shown for 2 levels (0.25 and 0.75) of the probability *m* that a response is lost if no control device is encountered. Target population size is set at 5% of the original population size (1000). The probability of encountering a single bait station is 0.01; inexperienced individuals survive an encounter with probability 0.5. Educated individuals have a reduced probability of ingesting a lethal dose of poison bait; 4 different S_e values are shown to the right of the lines that they correspond to. Fecundity and the death rate due to causes other than poison control are set to 0.07 and 0.005, respectively.

Increasing exploitation pressure results not only in greater encounter rates with the potential for a kill/capture but also in 1) greater number of naive individuals that become educated and 2) lower number of educated individuals that lose their response. It is conceivable that this dynamic can lead to a reduction in total captures over a given time frame as capture effort increases if the benefits of higher encounter rates are outweighed by the cost of maintaining a higher proportion of educated prey in the population. We found that at high survival of educated individuals, exceeding a certain threshold of effort can indeed result in an increase in the time required to reach target population size (Figure 6).

DISCUSSION

It is apparent that in addition to the typical factors influencing population dynamics, systems with improved defences have an added level of complexity, at the core of which lies the triangular relationship between 1) capture effort (e.g., exploiter density or exploiter activity), 2) the rate at which individuals in the population become educated (e.g., reflecting exploiter activity and efficiency), and 3) differential prey survival. With typical harvest rates, that is, rates that are not intended to cause the quick extinction or severe reduction of the population, the effects of improved defences on yield or the time required to reach a quota are relatively mild, although they increase with the proportion of individuals that survive an initial encounter and become educated. The pattern that emerges is one of greater importance of changes in survival of naive individuals than educated individuals. This is intuitive, given that individuals first have to become educated before they can enjoy the benefits of an improved response. More complex dynamics may be expected over multiple hunting seasons and with long-lived species, which could be the subject of future studies.

At high harvest rates, such as those intended for invasive species control or eradication, the effects of educated prey become more noticeable and from a practical standpoint more relevant. Even with a relatively low rate of education to a control tool, the effect on the time it takes to reach a target population size can be dramatic. As mentioned earlier, the importance of educated prey for invasive species control (i.e., acquired taste aversion) has long been recognized and was one of the motivators behind the replacement of first-generation toxicants with newer toxicant and application systems (Towns and Broome 2003). However, to our knowledge, the model described here is the first theoretical treatment of the subject and will allow others to explore the dynamics involved and, given real-life parameter estimates, predict the extent of the effect for specific systems.

An important prediction was that the effect of educating prey (relative to changes in survival of naive individuals) on the time required to reach a certain reduction in the target species was greater in populations with slower life histories. This is not surprising; with greater longevity, individuals will benefit longer from having been educated with respect to a type of exploiter, whereas educated individuals in population with fast-paced life histories have shorter average life span but higher output of (naive) recruits. In other words, populations with slow life histories have a longer population-level "memory" of learned responses to exploitation.

All else being equal, because of the reduced vulnerability of educated individuals, time to extinction can be expected to be greater in populations with the potential for defence improvement than in populations without. Interestingly, optimal control effort (e.g., bait station density)—in terms of the time required until the population has been reduced to a desired level—may not always be the highest affordable capture effort but rather a capture effort that is somewhat lower. We demonstrated this seemingly counterintuitive effect in theoretical systems where response loss is possible because for certain parameter values, the benefits of increased control effort are outweighed by the cost of turning naive individuals into educated ones and meanwhile continuously reeducating (i.e., preventing response loss in) educated individuals. It remains to be seen whether this is of practical importance, but, as Brown et al. (1999) argued in their description of a model of fear-driven predator–prey dynamics, a reduction in the number of predators "engenders less vigilant and more catchable prey."

Given the potential for learned responses in invasive or pest species, one should strive to keep the proportion of the target population that is educated to a minimum by 1) ensuring the highest probability of success at the first encounter and 2) minimizing the possibility of formation of learned aversion, for example, by delaying the symptoms of poisoning. Increasing the reliability of a control tool is not only desirable from the perspective of efficiency; minimizing the escape/survival rate conditional on encountering a control device is essential in situations where it can lead to improved defensive responses. In the worst-case scenario, educating individuals can create and maintain an uncatchable segment in the population with respect to a given control tool (e.g., if $S_e \sim 1$). Additionally, alterations of the temporal pattern of captures (e.g., punctuated vs. uniform effort to allow for response loss) and variation in the control tools applied may help offset the effects of educating the target species. Similarly, although in the context of evolved/induced responses rather than individual learning, Gardner et al. (1999) recommended control schedules of alternating high and low dosage to delay the onset of pesticide resistance in plants.

Our theoretical treatment of the potential role experience plays in the dynamics of exploited population was by no means exhaustive. We ignored many interesting aspects with potentially important implications, such as age-dependent ability to learn and produce an improved response (Mateo 1996; Hollen et al. 2008), the possibility of social learning (Galef and Laland 2005), and stochasticity in population dynamics, exploitation pressure, and individual vulnerability. Although our presentation focused on exploitation, the importance of acquired responses has also been recognized in CMR studies (Pradel 1993). An interesting aspect of CMR studies is the potential not only for learned avoidance but also learned affinity to capture. Capture responses require consideration during the modeling of CMR data (Pradel 1993), and they may also have consequences for efficiency and economy of CMR studies.

Fitness trade-offs are a major component of the theory on inducible defences, which generally postulates that without costs, defensive traits will be fixed (Tollrian and Harvell 1999). A focus on gains through individual learning and the assumption of no or negligible fitness costs sets our treatment of improved responses apart from that of inducible defences, as does the fact that the former may include learning to recognize and respond to novel stimuli (e.g., exotic predators). Nonetheless, fitness trade-offs can easily be incorporated into our model by using different vital rates (f and/or d in Equations 7 and 8) for naive and educated individuals. A reduction in fecundity or increase in natural mortality due to the implementation of a learned response to human exploitation may buffer population-level effects of educating prey.

Although more theoretical work remains to be done, most needed is empirical illumination of the role of educated prey in the dynamics of exploited populations to provide context and real-life parameter estimates. Such investigations should estimate the strength of the effect in natural populations and ultimately shed light on the inner workings of the relationship between exploitation pressure, prey "education," and corresponding changes in the pattern of survival on the individual and population levels.

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Article V

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Population ecology

Should hunting mortality mimic the patterns of natural mortality?

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With growing concerns about the impact of selective harvesting on natural populations, researchers encourage managers to implement harvest regimes that avoid or minimize the potential for demographic and evolutionary side effects. A seemingly intuitive recommendation is to implement harvest regimes that mimic natural mortality patterns. Using stochastic simulations based on a model of risk as a logistic function of a normally distributed biological trait variable, we evaluate the validity of this recommendation when the objective is to minimize the altering effect of harvest on the immediate post-mortality distribution of the trait. We show that, in the absence of compensatory mortality, harvest mimicking natural mortality leads to amplification of the biasing effect expected after natural mortality, whereas an unbiased harvest does not alter the post-mortality trait distribution that would be expected in the absence of harvest. Although our approach focuses only on a subset of many possible objectives for harvest management, it illustrates that a single strategy, such as hunting mimicking natural mortality, may be insufficient to address the complexities of different management objectives with potentially conflicting solutions.

Keywords: demography; life history; simulation; management; selection; vulnerability

1. INTRODUCTION

There is growing concern regarding potential demographic side effects and evolutionary consequences of selective harvesting on wildlife populations (Harris *et al.* 2002; Coltman *et al.* 2003). Perturbations of a population's demographic structure (Mysterud *et al.* 2002; Milner *et al.* 2006) and short- and long-term changes of morphological traits or life-history strategies due to artificial selective pressures (Festa-Bianchet & Apollonio 2003) are some of the processes through which selective hunting may affect populations beyond more obvious, direct effects on population size and growth rate through the removal of individuals. In search of management strategies that minimize the demographic side effects and are 'evolutionarily enlightened' (Gordon *et al.* 2004), it has been suggested that harvesting regimes should mimic natural mortality patterns (e.g. Milner *et al.* 2006; Loehr *et al.* 2007; Bergeron *et al.* 2008). Surprisingly, the general applicability of this recommendation has received little theoretical or empirical evaluation. Recently, Proaktor *et al.* (2007) presented model-based evidence that selection for lighter weight at first reproduction in ungulates could be a consequence of harvest and that harvest pressure is more important in driving this adaptive response than the degree of harvest selectivity. It seems plausible that this would apply to other situations in which the benefits of more and earlier reproduction eventually outweigh its costs (e.g. lower quality offspring), possibly due to higher overall mortality and consequently a greater chance of not reproducing later. To our knowledge, this is the only strong argument thus far in support of the statement that harvest selectivity patterns should mimic natural mortality, because a harvest biased towards younger (and lighter) individuals could minimize the aforementioned adaptive response. Even in such a case, simply targeting small (i.e. young) individuals may lead to further decreases in the size at, and time to, maturation as recent literature on fisheries-induced evolution suggests (Kuparinen & Merilä 2007 and references therein).

In this article, we are specifically concerned about the lack of scrutiny of the statement with regard to the immediate disruption caused due to demographic or other changes as a result of biased harvest. To avoid ambiguity, we identify a clear objective for harvest management with respect to selectivity, namely that harvesting and natural mortality acting on a population should result in a post-mortality population structure (or biological trait distribution) that is identical or at least very similar to the structure that would be expected in the absence of harvest (see also Harris *et al.* 2002). With this objective in mind, we ask the question: should hunting mortality mimic natural mortality in order to limit the potential for disruptions caused by demographic or trait-distribution changes?

The effects of selection on trait distributions are now relatively well understood (e.g. Lynch & Walsh 1998). Particularly relevant to our work is a paper by Vaupel *et al.* (1979), which explores the effects of viability selection on the distribution of a trait over time and age cohorts. The authors termed this trait 'frailty' to highlight the fact that it is related to an individual's risk of mortality, and assumed that the probability density function of frailty follows a gamma distribution. Vaupel *et al.* (1979) further assumed that the force of mortality (a measure of an individual's risk) is a function of time, age and frailty. Although our basic approach is similar, we develop a slightly different model and explore the outcome through the simulations. We also extend Vaupel *et al.* (1979) by discriminating between two mortality causes and by investigating how altering the shape of the viability selection function affects the post-mortality trait distribution.

2. MATERIAL AND METHODS

(a) *Model*

For model construction, we assume a normally distributed random variable x (with mean μ and variance σ) that represents a certain trait of individuals in the population, with associated probability density function

$$f(x)=\frac{1}{\sigma\sqrt{2\pi}}\exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right). \tag{2.1}$$

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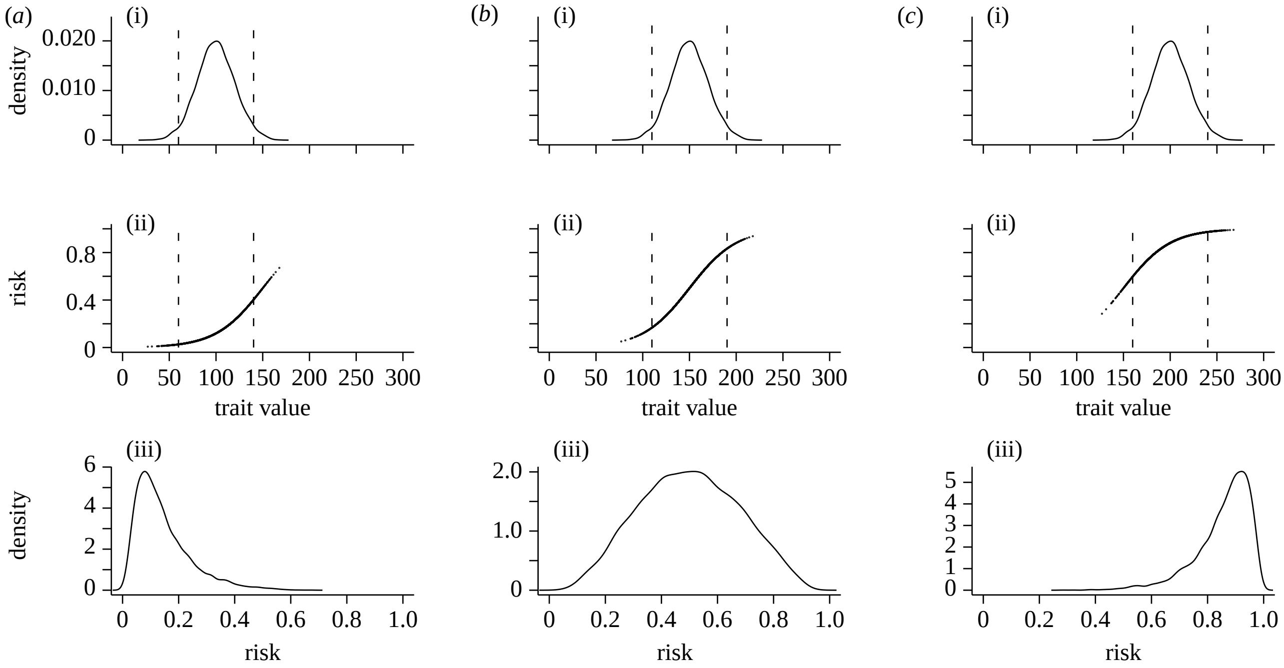

Figure 1. Illustration of the link between the density distribution of risk and a normally distributed biological trait x (s.d. = 20; hashed lines: 2×s.d. boundaries, arbitrary unit), with risk being a logistic function of x. Shifts in the mean trait value ((*a*(i)–(iii)) 100, (*b*(i)–(iii)) 150 and (*c*(i)–(iii)) 200) of a hypothetical population ($n = 5000$) change the density distribution of risk in the population.

We then assume that risk p is a logistic function of trait x (figure 1), where the relationship between p and x can be expressed as

$$p_x = \frac{1}{1 + e^{-(a+bx)}}. \qquad (2.2)$$

Here, a and b are the intercept and slope of the linear regression (with the logit link), respectively. Although the assumptions behind equations (2.1) and (2.2) oversimplify a world where risk probably is a complex function of multiple variables (morphology, age, experience, behaviour, space use, etc.), the approximation is sufficient for our purposes. The above approach centres on a logistic relationship between risk and a normally distributed continuous feature of the population, but this representation also allows the incorporation of discrete or factor variables, as well as other distributions. Following the precautionary principle and because strong compensation can be expected to occur only rarely (Lebreton 2005), we assume that mortality is additive. Furthermore, we ignore potential density-dependent effects that in real populations may, for example, positively affect the growth rate of individuals exhibiting trait values that are selectively targeted.

An interesting finding of Vaupel *et al.* (1979) was that, as individuals age, their force of mortality increases more rapidly than the average force of mortality of the age cohort they belong to, because the removal of frail individuals decreases the average frailty of the surviving cohort. The mechanism underlying this phenomenon applies also to our model, although for simplicity we did not include an age term. While surviving individuals retain their original trait value as they move from pre- to post-mortality, the average trait value shifts towards the less vulnerable end of the trait spectrum (assuming no recruitment within that time step).

(b) *Simulations*

We investigated changes in the probability density distributions of trait x (e.g. size) in a heterogeneous hypothetical population with two groups with different mean trait values (e.g. females and males) resulting from exposure to harvest followed by natural mortality. We evaluated the effect of different shapes of the logistic function linking harvest risk and trait value on both the post-mortality trait distribution and the ratio of the two groups in the population. We used three main expressions of the logistic function based on its shape (‘mimic’, ‘inverse’ and ‘unbiased’; figure 2) relative to the risk associated with natural mortality, by altering the intercept and slope in the logistic function (equation (2.2)).

We conducted stochastic simulations using R v. 2.5.0 (R Development Core Team 2007). We repeated simulations with the same settings 100 times and calculated bias and 95% CI limits from 1000 bootstrapped replicas of the mean parameter values. We note that, although we chose to illustrate the effect of viability selection using simulations, the effects of multiplying a distribution with a function can also be evaluated analytically, e.g. through the use of conjugate priors within a Bayesian framework (Fink 1997).

3. RESULTS

For the case of harvest preceding natural mortality, simulation results (figure 2, table 1) indicate that (i) inverse harvest risk prior to natural mortality diminishes and in extreme cases reverses the biasing effect of natural mortality on the density distribution of the biological trait, (ii) unbiased harvest risk keeps the biasing effect of natural mortality unchanged, and (iii) mimicking harvest risk amplifies the biasing effect of natural mortality on the density distribution of the biological trait. Biased natural mortality alters the ratio of the two groups in the population, with additional changes in the ratio due to mimic and inverse harvest mortalities, but no further alterations if harvest is unbiased. The altering effect of biased harvest on the trait distribution and the ratio of the two groups in the population increases with increasing harvest rate (table 1). Because we assume no density-dependent effects and, if harvest mortality is limited by a quota, the above patterns, at least qualitatively, also hold true for harvest following natural mortality.

4. DISCUSSION

The general statement that harvest mortality should mimic natural mortality in order to avoid demographic disturbance or evolutionary consequences is not yet sufficiently supported, and needs to be qualified. We found that, for the specific objective of maintaining

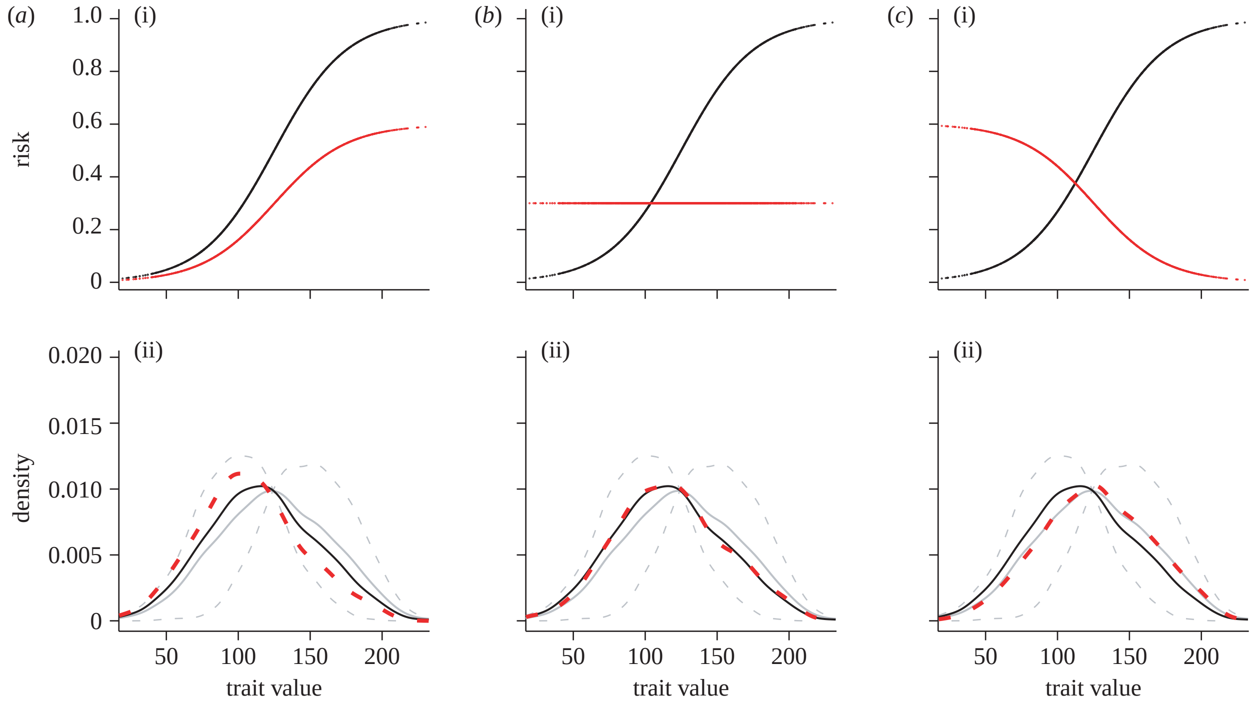

Figure 2. Changes in trait distributions as a result of various patterns of hunting mortality relative to biased natural mortality for a simulated heterogeneous population (two cohorts with $n=1000$ each, s.d.$=30$, 100 and 150). (*a*–*c*(i)) show natural and hunting risks as a logistic function of the normally distributed biological trait x (arbitrary unit; lines: red, hunting; black, natural). (*a*–*c*(ii)) show distributions of the biological trait before and after mortality (lines: grey dashed, before mortality (groups separate); grey solid, before mortality (joint); black, after natural mortality without hunting; red dashed, after hunting and natural mortality). Risk associated with hunting mortality either (*a*) mimics natural mortality, is (*b*) unbiased (slope and intercept of the logistic function set to 0), or is (*c*) inverse to natural mortality. Harvest rate was set at 30% of the initial population size.

Table 1. Bootstrapped estimates of the mean trait value (μ, arbitrary unit) and ratio (r) of groups (group 1 : group 2) of surviving individuals in a hypothetical population after hunting followed by natural mortality and after natural mortality in the absence of hunting mortality (μ_0, r_0) from 100 simulation runs for each of the three shapes of the risk function (see text and figure 2) and two different harvest rates. (The initial population consisted of two groups ($n=1000$ each) with mean trait value $\mu=100$ and 150, respectively, and s.d.$=30$. Natural mortality was modelled as a logistic function of x (see text), with intercept $a=-5$ and slope $b=0.04$.)

harvest risk shape	harvest rate	μ	CIL[a] (μ)	μ_0	CIL(μ_0)	r	CIL(r)	r_0	CIL(r_0)
mimic	0.25	103.95	103.82, 104.09	109.12	108.99, 109.25	2.10	2.08, 2.12	1.74	1.72, 1.75
	0.5	96.65	96.52, 96.78	109.05	108.90, 109.20	2.82	2.78, 2.86	1.77	1.75, 1.78
unbiased	0.25	108.92	108.72, 109.12	109.10	108.96, 109.24	1.77	1.75, 1.79	1.75	1.73, 1.77
	0.5	109.14	108.88, 109.38	109.14	109.01, 109.27	1.76	1.73, 1.78	1.74	1.73, 1.76
inverse	0.25	114.47	114.25, 114.70	109.01	108.87, 109.17	1.45	1.43, 1.47	1.77	1.75, 1.78
	0.5	123.97	123.67, 124.25	109.01	108.86, 109.17	1.05	1.04, 1.07	1.75	1.73, 1.77

[a] Ninety-five per cent CI limits from 1000 bootstrapped estimates.

unchanged post-mortality distributions of a trait (or demographic feature), hunting mortality should be unbiased. This holds true regardless of whether hunting occurs prior to or after natural mortality. Therefore, in the absence of strong compensation in mortalities and until further supporting evidence emerges, we would limit recommending that hunting mortality should mimic natural mortality patterns to the following cases.

(i) Natural mortality regimes have been altered, e.g. as a result of extermination of natural predators.
(ii) The objective is to minimize selective pressure for earlier reproduction driven by increased overall mortality as a result of adding harvest.
(iii) An amplification of the biased outcome of natural mortality is desired.
(iv) The main objective is to minimize the negative direct impact of harvest on population growth by targeting those demographic groups whose survival has the lowest elasticity/sensitivity.
(v) Natural mortality is unbiased.

In our example, increasing overall mortality (whether the latter is biased or not) by a constant (e.g. adding unbiased harvest) does not alter the selective pressure on traits directly linked to risk. We emphasize that different objectives, such as (i) minimizing the effects of harvest on the distribution of traits or demographic features or (ii) limiting the selective pressure for lower age and size at first reproduction, may have conflicting solutions, as well as different temporal scopes (see also Law 2001).

We focused on the potential of selective harvest to alter the post-mortality distribution of a single trait from the distribution that would be expected if natural mortality occurred in the absence of harvesting. A wider scope is required to evaluate all important ecological and evolutionary consequences of harvesting and to answer the questions about optimal harvesting strategies comprehensively. Such models may include age effects on trait values and risk, density-dependent effects, and environmental and demographic stochasticity. Furthermore, empirical exploration into how various harvesting strategies in concert with biased natural mortality affect trait distributions of natural populations are required to validate what theory suggests.

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