

Does sport hunting benefit conservation?

Andrew J. Loveridge, Jonathan C. Reynolds
and E. J. Milner-Gulland

There is a passion for hunting deeply implanted within the human breast

(Charles Dickens, *Oliver Twist*, 1837–8)

Introduction

When a wildlife population is threatened, deliberately killing individuals from it may seem perverse. Yet some argue that, paradoxically, well-regulated sport hunting benefits wildlife populations, and may sometimes be the only way to ensure their persistence. In this essay we consider whether this assertion is supported by experience.

When poorly regulated, hunting can be – and historically often has been – damaging to the target population, with dramatic examples of extinction and population decline (Roth & Merz 1996). Even in the 1980s, hunting contributed to drastic reductions in populations of the dorcas gazelle (*Gazella dorcas*) and to extermination of the Nubian bustard (*Neotis nuba*) from Sahelian Africa (Newby 1990). The tally of millions of migratory birds shot and trapped annually by Mediterranean hunters has alarmed observers and caused them to question its sustainability (Lindell & Wirdheim 2001). However, the impact of hunting on population dynamics can be complex and difficult to quantify. For example, although there has been much concern about the

impact of hunting on migratory turtle doves (*Streptopelia turtur*), Browne & Aebischer (2004) found that the observed decline in UK breeding turtle doves could be entirely explained by changed UK farming practices with no direct evidence for a damaging impact of hunting. There are many examples all over the world where hunting has been regulated successfully (Tapper & Reynolds 1996). The wild turkey (*Meleagris gallopavo*; Dickson 1992), white-tailed deer (*Odocoileus virginianus*; Woolf & Roseberry 1998) and beaver (*Castor canadensis*; Novak 1987) in North America are all species whose fortunes have been dramatically improved by a programme of conservation measures that includes substantial regulated harvests.

Sport hunting and nature conservation have both been part of human culture from the earliest times. For example, Ancient Egypt had a strong tradition of sport hunting (Osborn & Osbornova 1998). Bogd Khan Mountain Reserve, Mongolia, was formally protected in 1778, but informal prohibitions on hunting and logging on this sacred site date from the thirteenth century (United Nations Mongolia Office 2004). Other similar examples include the Royal Chitwan National Park in Nepal and the New Forest in the UK. However, the roots

of contemporary conservation are usually traced back to nineteenth century colonial sport hunting (Adams 2004). Pressure from hunters, alarmed at unregulated destruction of game habitats and populations, led to the establishment of parks and reserves in the British colonies and the USA (Fitter & Scott 1978; Adams 2004). Many of these were initially set aside as hunting grounds, and many national parks services and government conservation departments have origins in agencies established to defend hunting reserves and suppress poaching (Adams & Hulme 2001). This purely preservationist view of conservation has given way to a perspective that is more inclusive of humans (Duffy 2000; Hutton & Leader-Williams 2003; Jones & Murphree 2004). Modern conservation is about reducing extinction risks, maintaining essential ecological processes, preserving genetic diversity and ensuring that the

use of species and ecosystems is sustainable (Convention on Biological Diversity 2003). Although this definition does not positively promote use as a conservation tool, the explicit inclusion of sustainable use is a recognition that human use of wildlife happens, and that the appropriate role of conservation is to ensure that it is sustainable, rather than to prohibit it.

Sport hunting is a multifaceted activity, occurring in many ecological and socio-political landscapes, variously motivated and generating a range of revenues. A single characterization of its impact on conservation is necessarily simplistic. We begin by clarifying what we mean by sport hunting, and discussing the ethical issues that bedevil the debate on its role in conservation. We then address the key issues summarized in Fig. 15.1.

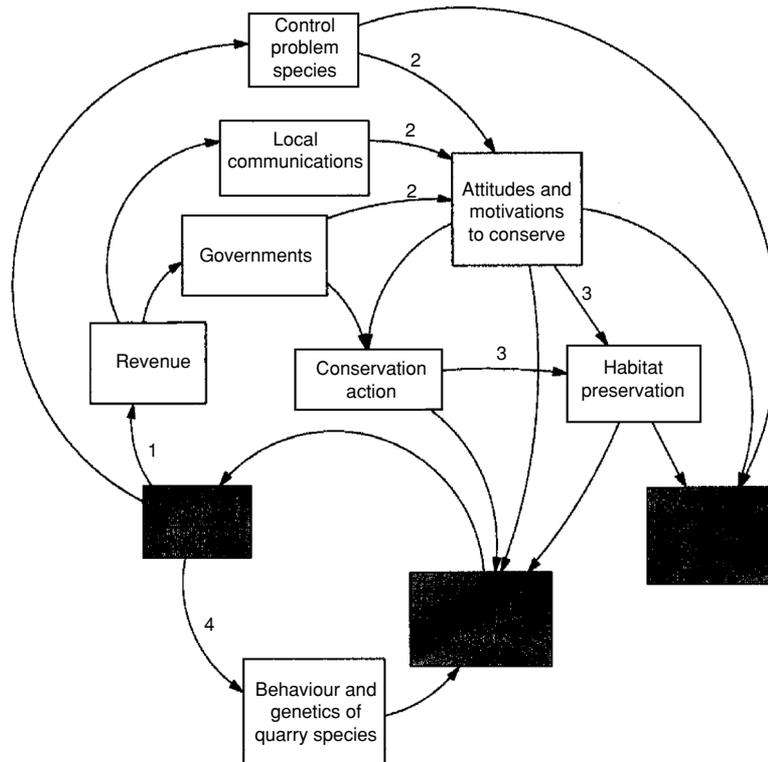


Fig. 15.1 Illustrating the relationship between sport-hunting and conservation discussed in this essay. The numbering corresponds to the key questions addressed in the main text.

- 1 We ask whether or not hunting raises revenue, and if so whether this revenue can be used to benefit conservation?
- 2 One important issue is whether or not revenue earned from hunting offsets the opportunity costs of not engaging in other activities, especially in the case of poor communities living in areas of rich biodiversity.
- 3 We explore whether hunting affects the conservation of habitat and biodiversity.
- 4 We explore whether there are any subtle side-effects affecting hunted populations.

What is sport hunting?

Hunting is often categorized into subsistence hunting, market (or commercial) hunting and sport (or leisure or recreational) hunting, the differences being primarily motivational. Whereas subsistence hunting provides food for hunters and their dependents, market hunting supplies food to a consumer community for cash. Sport hunting is undertaken primarily for leisure, motivated by 'the thrill of the chase'. However, complexities of motivation blur distinctions between these various kinds of hunting. For instance, there is a commercial element to sport hunting, because hunters are prepared to pay for it, and many components of the activity are saleable commodities. Neither is the distinction between subsistence and sport hunting clear-cut. Although some sport hunters do not link their hunting with personal consumption, others choose not to kill more than they can eat. It is also not just sport hunters who enjoy the experience of hunting.

Beyond subsistence, profit or recreation, hunting has profound cultural and spiritual importance for some peoples. As Canadian citizens with access to the welfare state, the Inuit no longer need to hunt for subsistence. But hunting remains intertwined with self-esteem, history and cultural identity (Canadian Arctic Profiles 2004). For this reason, hunting of threatened Arctic species (e.g. polar bears *Ursus maritimus*, walrus *Odobenus rosmarus*) is permitted, albeit

under quotas. A seeming inconsistency is that traditional hunting methods have been largely replaced by exogenous technology such as snow-mobiles, motor boats and high-powered rifles (Stewart & Fay 2001; Stirling 2001). Even industrial societies have deeply rooted hunting traditions. European colonists in North America relied on hunting wildlife for subsistence up until the mid-nineteenth century, when the need to supplement protein requirements was reduced in an increasingly urban and wealthy society, and hunting became more recreational (Organ & Fritzell 2000). As a result, the right of citizens to hunt is still enshrined in law in many states within the USA (Muth & Jamison 2000; Grandy et al. 2003).

For some sport hunters, even killing the quarry may be unnecessary. For example, the hunting of foxes (*Vulpes vulpes*) with dogs in the UK, outlawed in 2004, evolved out of the wish to control foxes as a livestock/poultry pest, but became a ritualized socio-cultural activity in which the original aim of killing foxes was overshadowed or replaced by the thrill of the chase. Although hunting with dogs could – and in some situations did – control fox numbers (Heydon & Reynolds 2000), most hunts promoted a deliberately restrained strategy, resulting in a density of foxes that was acceptable to farmers yet ensured abundant hunting opportunities (Macdonald *et al.* 2000). At the extreme, 'green hunters' pay merely to immobilize wild animals, under the supervision of a veterinarian and usually as part of a management or research activity. Clients in South Africa pay up to US\$25,000 to immobilize a trophy bull elephant, which is then fitted with a radio-collar as part of ongoing research. The revenue contributes to the research and management of the game reserve, and the hunter takes home moulded fibre-glass copies of the animal's tusks (Save the Elephants 2002).

Ethical considerations, inescapable elements of every conservation issue, are especially prominent in evaluations of sport hunting, polarizing debates on this topic. The acceptability

of hunting as a component of conservation action is influenced by two central issues: the motivation of the hunter, and the extent to which the hunted animal suffers. Sport hunting is by definition pleasurable to the hunter. To others, killing living creatures is fundamentally wrong and therefore not to be enjoyed. Conservation is laden with non-utilitarian values (e.g. aesthetic, spiritual and bequest values), which are particularly strongly felt on both sides of the hunting debate. Our relationship with nature, simultaneously worshipped and exploited, has always been complex (Serpell 1986). Cultural and ethical issues do play a part in conservation success; for example, Oates (1999) argues that India has had more success than West Africa because its Government's conservation policy is based on recognizing the intrinsic value of nature rather than its utilitarian value. However, the ethical standpoint from which sport hunting is viewed is not easily subjected to rational analysis. We shall therefore lay aside motivational issues and take a utilitarian viewpoint in this essay, assuming that sport hunting is as valid as any other human relationship with nature.

The second issue is the distress and suffering caused to individual animals by hunting. Hunted animals may show measurable indications of stress (Macdonald *et al.* 2000), starting at first awareness of the natural (Chabot *et al.* 1996) or human (Jeppesen 1987) predator. At some point during a successful hunt, the hunted animal fails to cope with events, and stress becomes distress. In red deer (*Cervus elaphus*) hunted by hounds, Bateson & Harris (2000) found severe glycogen depletion, elevated cortisol levels and muscle damage. Although these symptoms are ambiguously associated with exercise whether voluntary or forced, it was clear that deer were attempting to cope with pursuit in unusual and costly ways. Equivalent indicators were not found in deer cleanly shot by deer stalkers (Bateson & Harris 2000), demonstrating that for such animals any period of distress was brief. So the probability, duration and magnitude of distress caused by

hunting depend on the method used. The welfare of animals at an individual level often conflicts with conservation of the species at a population level (Home Office 2000; Reynolds 2004). Furthermore, even non-hunting human activities can involve stress to wild animals. For example, translocation and release of animals for conservation purposes can be stressful for individuals (Mathews *et al.* 2005). So too can tourist viewing of endangered species (Sorice *et al.* 2003), and a supposedly neutral human activity such as orienteering also can cause significant stress (Jeppesen 1987). In this essay we try to deal dispassionately with the question of whether hunting can aid wildlife conservation at the population level, and not with the important, but different, question of whether hunting has welfare implications for individual animals.

Sport hunting as an economic driver

Sport hunting can generate substantial revenue. Some hunters spend extravagantly and travel extensively (PACEC 2000), and may pay high fees for syndicate membership, logistical support and guides. They may pay extremely high prices to shoot spectacular species (e.g. Table 15.1). Although the travel component of such hunting varies widely, even local hunters may bear large operating costs. Fox-hunters in the UK had operating costs (maintenance of hound packs, horses and associated equipment, hunt staff) of roughly £2600 per hunter per year (PACEC 2000).

Revenue from hunting affects economies at national and regional levels. Expenditure on field sports in the UK exceeded £1.4 billion in 1992 (Cobham Resource Consultants 1997). In 2000, red grouse (*Lagopus lagopus scoticus*) shooting in Scotland supported the equivalent of 940 full-time jobs, and £17 million worth of GDP in Scotland (FAIRSC, 2001). Employment related to fox-hunting in the UK is estimated at 6000 to 8000 full-time equivalent jobs (PACEC 2000).

Table 15.1 Trophy fees paid per animal shot in Botswana, illustrating the large fees that are charged to sport hunters for various species (Sources: <http://www.gondala.co.za>; Botswana Wildlife Management Association 2001; <http://allafrica.com/stories/printable/200402050156.html>)

Species	Trophy fee per animals (\$US)
Warthog	200–300
Spotted hyaena	500–930
Zebra	900–1070
Giraffe	1800–3000
Crocodile	1850–2000
Buffalo	2500–10,800
Leopard	2800–6550
Cheetah	3000
Hippo	3000–6150
Lion	3000–30,000
Sable antelope	3100–10,000
Elephant	19,000–40,000
White rhinoceros	25,000–60,000

Jackson (1996) estimates that the monetary benefit of hunting to the USA economy in 1991 was US\$35 billion, of which US\$2 billion was spent annually on conservation and acquiring habitat. Hunters may also voluntarily contribute to conservation. For example Ducks Unlimited, a USA wildfowling charity, raised and spent \$140 million in 2003, 79% of which was spent on conservation in the USA. Hunters pay up to US\$160,000 for a single trophy big-horn sheep (*Ovis canadensis*, Marty 2002). Although trophy prices in North America are unequalled elsewhere, sport hunting in developing countries can be economically significant. South African game farms earned US\$44 million in 2001 (Van der Merwe & Saayman 2003). In the year following the Botswana Government's moratorium on lion hunting in 2000, the hunting industry experienced US\$1.26 million of lost revenue (BWMA 2001).

Hunting revenue can also accrue locally. The Botswana Wildlife Management Association estimates that 49.5% of hunting expenditure, totalling US\$9.5 million per annum, remains in individual hunting districts; a further 25.7% remains in the country (BWMA 2001). Similarly, Humavindu & Barnes (2003) show that 24% of hunting revenue earned in Namibia

(totalling US\$19.6 million) accrues to the poorer segments of society in the form of wages, rentals and royalties. In Zambia, the ADMADE programme (Administrative Design for Game Management Areas) receives around 67% of all revenue generated by sport hunting activities in Zambia's Game Management Areas. Fifty-three per cent of ADMADE revenue is allocated directly to local wildlife management, the remainder to community development (Lewis & Alpert 1997). See Jones & Murphree (2004) for more examples.

Hunting revenue can in some instances be directly used by Government for conservation purposes. For instance, hunting revenue contributes to conservation throughout the USA via taxation: all sport hunting equipment sold in the USA is subject to an 11% tax under the Federal Aid in Wildlife Restoration Act (1937), which contributes directly to acquisition of habitat, research, conservation training and education and provision of access to hunting and recreational facilities (US Fish and Wildlife Service 1999). In the UK, angling licences generate substantial funds, which are spent on management of aquatic ecosystems by the relevant agency (Environment Agency). By contrast, the UK Game Licence, administered

by central Government, is currently under review because it is widely evaded and does not generate significant funds. Virtually all game hunting in the UK takes place on land that is privately owned and managed. Although Government does influence conservation on privately owned land through agri-environment schemes, centrally raised taxes may not be 'ear-marked' for specific uses such as conservation. Nevertheless, game hunting in the UK is an economically significant land-use (Cobham Resource Consultants 1997), which influences both policy at a national scale and the implementation of conservation measures at a local scale.

Linking conservation benefits with attitudes to wildlife

There is both a practical and a moral imperative for conservationists to engage with local people, particularly in poor countries where people's livelihoods may be compromised by conservation actions (Adams & Hulme 2001; Hulme & Murphree 2001). Where people live alongside, and thus potentially in conflict with wildlife, their tolerance may be proportional to any financial benefits received from wildlife. Elephants (*Loxodonta africana*) raid crops, and lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) kill domestic stock (e.g. Butler 2000). Jones (1999) and Duffy (2000) propose that these burdens might be compensated if problem animals can be sold to sport hunters. However, as Taylor (1994) notes, trophy hunting does not always target problem animals. For instance, crop raiding by elephants in Omay Communal land, Zimbabwe, occurs largely in the wet season (November to April), but the majority of sport hunting takes place during the dry season (May to October), so elephants shot as trophies are not necessarily the animals involved in crop raiding, nor does removal of these animals alleviate the problems of crop loss at other times of the year. However, hunt-

ing revenue and activity can contribute to local infrastructure (clinics, schools, roads), further enhancing its value. Some safari hunting companies have worked hard to ensure that local communities benefit from their activities, and are motivated to collaborate to protect hunted wildlife (e.g. Cullman and Hurt Community Wildlife Project 2004). The Bar Valley project in Pakistan, based on trophy hunting for ibex, is another example of successful community-based conservation using sport hunting as its main income generator (Garson et al. 2002).

Benefits derived from hunting affect attitudes, in ways that may further conservation goals. In 1982, Shangaan people in the Mahenye area, adjacent to Gonarezhou National Park, Zimbabwe, were allowed after protracted negotiation to sell two trophy elephant hunts to foreign hunters. They received both the financial profit and the meat from the elephants sport-hunted in their tribal area. In response to this relaxation of wildlife laws by the Department of National Parks the local community voluntarily relocated 100 people from Ngwachumene Island, an important wildlife habitat on the border of the National Park. The local community not only gained benefit from the hunting activity, but more importantly felt that they had reclaimed part of their ancestral ownership and rights to use local wildlife resources – an important factor in ameliorating ongoing enmity with wildlife authorities in the area (Murphree 2001). Based on experiences such as this, Jones & Murphree (2004) argue that revenue from hunting is not the only benefit to local communities: local institutions and management can be enhanced through participation in community-based natural resource management (CBNRM), strengthening traditional hierarchies and rights to common property and enabling interactions with external institutions.

The CAMPFIRE (Communal Areas Management Plan For Indigenous Resources) scheme in Mahenye, Zimbabwe is a widely-known CBNRM initiative. It attempts to alter people's perceptions of natural resources, from either a

nuisance or a food source to a viable and sustainable revenue source (Murphree 2001). Trophy hunting is a key component of income generation for CAMPFIRE; Bond (2001) shows that in 1989–1996 Zimbabwean rural district councils earned US\$ 8.5 million (93% of their income) from leasing out sport hunting concessions through CAMPFIRE. However, benefits were not always equally shared by all members of the community and individual households accrued significant benefits only in areas where there was low human population density and high abundance of trophy species. Similarly, Murombedzi (1999) suggests that corruption, poor representation and political marginalization prevented disbursement of revenue to individual households.

Sport hunting is just one way by which CBNRMs can obtain revenues from wildlife. It is a highly lucrative form of use, usually generating higher revenues per animal than, for instance, subsistence hunting. However, some question the value of CBNRM as a conservation strategy, suggesting that its underlying assumptions are flawed (Kiss 2004; du Toit et al. 2004). Local communities are not necessarily willing to bear the opportunity costs of conservation and may not be willing to reinvest gains derived from CBNRMs in conservation. In some cases earnings from CBNRMs have been reinvested in agricultural expansion, which is ultimately damaging to biodiversity (Murombedzi 1999). The CBNRMs require heavy investment with an uncertain outcome. Given this, there is a growing belief that the more cost-effective way to conserve biodiversity in poor countries is for wealthy states simply to compensate local people for not damaging sensitive sites or species (James et al. 1999; Nicholls 2004; Kiss 2004; du Toit et al. 2004). However, there is as yet no global commitment to financing the costs of conservation, nor the institutional capacity to distribute such payments. Until there is, encouraging local sustainable use of natural resources through high return, arguably low impact activities, such as sport hunting, may be preferable to more destructive alternatives, such as

agriculture, subsistence hunting or logging, which tend to extirpate wildlife populations and destroy habitat.

However, sport hunting faces all the difficulties that other forms of enterprise-based conservation have. These include getting the incentive structures and resource ownership correct, and ensuring effective and robust institutions for resource management and disbursement of benefits (James et al. 1999; Milner-Gulland & Mace 1998; Salafsky et al. 2001). Many countries also suffer from broader problems of corruption and poor governance, institutional failure, social and economic upheaval, which reduce the likelihood of long-term success for any conservation or development activity (Smith 2003).

Direct ecological effects of sport hunting

Sport hunting acts directly and indirectly on the ecology of the target species and other species. For example, where population management is thought desirable (e.g. red fox or roe deer *Capreolus capreolus*), hunters may take on the role of extirpated natural predators. Population management is often necessary when species have been reintroduced for conservation reasons (e.g. beaver (*Castor fiber*), lynx (*Felis lynx*) and wolf (*Canis lupus*) in several European countries), and revenue generated by sport hunting could potentially offset some of the losses caused by these species. This can in turn improve public acceptance of such reintroductions (Ericsson et al. 2004). One of the most important potential benefits is habitat preservation, which acts to conserve both the target species and associated species. Any kind of hunting affects the demographic structure of the target species, and this can have knock-on effects, including evolutionary change. Sport hunting may be particularly detrimental in this regard because it is often highly selective, targeting trophy individuals. We discuss these two issues in more detail below.

Habitat protection

Hunters are frequently instrumental in protecting habitats for hunted species. Oldfield *et al.* (2003) showed that landowners in the UK who allow shooting and fox (*Vulpes vulpes*) hunting on their property apportion a greater part of their farmland to woodland than average and take up government subsidies to plant woods or hedges as habitats for game species. In Norway, European beavers are hunted on centrally administered quotas. Revenues are distributed to landowners based on the amount of beaver habitat they maintain, encouraging habitat protection (Parker & Rosell 2003). It is difficult to distinguish causation from correlation in these examples; to what extent is hunting the cause of conservation behaviour by landowners? It could be argued that conservation-minded landowners would continue to protect habitats regardless of whether they are able to hunt on their land (Macdonald & Johnson 2000). However, experience within the UK game management sector (Game Conservancy Ltd advisory service, Reynolds personal observation) confirms that hunting is very often the motivation for investment in habitat management of wide conservation benefit, and for taking up agri-environment grants to assist with this.

In Africa, areas set aside for sport hunting and sustainable wildlife-use greatly increase the amount of habitat available to wild species. Without revenue from hunting, political pressure might be exerted to turn these areas over to domestic livestock production, which could irreversibly damage these ecosystems (e.g. Barnes 2001). Twenty per cent (140,000 km²) of Zambia's land area is made up of Game Management Areas, whereas only half as much land is designated for National Parks (Lewis & Alpert 1997). The Zimbabwean rural district councils participating in the CAMPFIRE scheme set aside substantial areas for wildlife, estimated at 36,000 km² (Taylor 1998), whereas safari areas and private hunting land administered by National Parks make up another 50,000 km²

(Cumming 2004). In South Africa from the late 1990s to 2002, land was converted from cattle ranching to extensive game ranching, largely for hunting, at a rate of 500,000 ha yr⁻¹. By 2002, 13% of the country's agricultural land was being used as game ranches (Van der Merwe & Saayman 2003).

In the USA, Ducks Unlimited conserves 10 million acres of waterfowl habitat across North America (Ducks Unlimited 2004). Proponents of hunting claim some remarkable recoveries of waterfowl species have occurred as a result (Jackson 1996). However, others claim that, despite reclamation of habitat, there is little evidence for population increases and some species (e.g. black duck, *Anas rubripes*) may have declined in number (Grandy 2003). In this case sport hunting may well contribute to habitat protection, but evidence is equivocal whether it has improved the fortunes of the species that it claims to protect. However, the net benefit of habitat protection and its associated biodiversity might outweigh this doubt.

Advocates of hunting often claim that hunters are effective custodians of wildlife habitat (Jackson 1996), providing support for anti-poaching teams and preventing poaching by operating in an area (Pasanisi 1996). Additionally although hunters are often instrumental in protecting species that they wish to hunt, this can sometimes be detrimental to habitats. In the USA some hunters put maintenance of artificially high quarry populations (e.g. white-tailed deer) ahead of ecosystem health and biodiversity and may be averse to or impede efforts to restore native wildlife and protect biodiversity (Holsman 2000; Peyton 2000). In another example, red deer (*Cervus elaphus*) are maintained in high numbers on some upland shooting estates in Scotland and also in New Zealand (where they are an alien species), with consequent damage to native habitat (Caughley 1983; Grandy *et al.* 2003). Sport hunting in these cases exacerbates the conservation problem. However, it could also be part of the solution, if it were structured to provide conservation revenues while keeping deer numbers low.

Direct impacts of hunting on the quarry population

Hunting is a selective force and must have consequences for demography and population genetics. Some hunters like to retain trophies, especially exceptionally fine, large or old specimens. Species with sexually selected features that are easy to preserve (such as antlers in deer, or tusks in elephants) may generate a particular demand among trophy hunters. This can lead to genetic change within populations due to highly selective removal or sometimes management of a population specifically to produce trophy animals. We discuss these issues in more detail below.

Species with harem breeding structures appear to be robust against quite intensive selective hunting, and trophy males have even been considered to be surplus to the population (Fairall 1985). Caro *et al.* (1998) found no consistent impact of sport hunting on ungulate population sizes in southern Tanzania. Nevertheless, intensive selective hunting pressure targeting adult males can cause sudden population collapse (Ginsburg & Milner-Gulland 1994). In saiga antelopes (*Saiga tatarica*), a harem-breeding species, conception rates remained normal (near 100%) when the sex ratio was highly distorted by commercial hunting (2.5% adult males in the population). However, when the sex ratio of adults fell below 1% males, only 20% of females conceived (Milner-Gulland *et al.* 2003). Fergusson (1990) describes intensive trophy hunting of male sable antelope (*Hippotragus niger*) in Zimbabwe, disturbing territorial and mating behaviour, leading to reduced calving rates and a protracted parturition period, which resulted in high calf mortality. However, there are many instances in which effects of trophy hunting are ambiguous. In Dall sheep (*Ovis dalli*), Heimer (1980) found reduced lamb production in a sport-hunted population, but Murphy *et al.* (1990) were unable to detect demographic differences between hunted and unhunted popu-

lations. In moose (*Alces alces*), Laurian *et al.* (2000) found no differences in mating behaviour or reproductive success between two populations, of which one had selective hunting of adult males and the other was unhunted; whereas Solberg *et al.* (2002) found that hunting-induced female-biased sex ratios reduced fecundity in primiparous moose.

Social disruption has also been observed in highly skewed populations. If older bulls are removed from elephant populations, young bulls can show aberrant or delinquent behaviour. In Pilanesburg Game Reserve, South Africa, young bull elephants killed 40 white rhinoceros (*Ceratotherium simum*) over a period of 5 years, but this behaviour ceased when mature bulls were introduced to the population (Slotow *et al.* 2000). The disturbance caused by sport hunting can have an impact on movement behaviour. Ruth *et al.* (2003) showed that in hunting areas adjacent to Yellowstone National Park, cougars (*Puma concolor*) and elk (*Cervus elaphus*) avoided areas where hunting occurred, although grizzly bears (*Ursus arctos*) used hunting areas more frequently due to increased scavenging opportunities. In southern Quebec, snow goose (*Anser caerulescens atlanticus*) spring migrations were disturbed by introduction of a spring hunting season. Disturbance reduced feeding opportunities and pre-nuptial fattening prior to the 3000 km Arctic migration. Reduced body condition resulted in reduced breeding effort, lower clutch size and delayed laying. Hunting disturbance also caused geese to migrate westwards into sensitive agricultural land, causing a tenfold increase in damage compensation paid to farmers in these areas (Béchet *et al.* 2003). Loveridge & Macdonald (2001) found that sport hunting in safari concessions surrounding Hwange National Park, Zimbabwe, removed around 67% of mature male lions from a study population covering 6000 km² of the National Park and reduced the proportion of males in the adult population from around 30% to 13%. Reduction in male lion density resulted in males expanding their ranges to include multiple

prides of females. Furthermore, inflation of male home-range size increased the probability that males would leave the protection of the park and themselves become vulnerable to sport-hunting. In a similar situation in Savuti, Botswana, where male lions were also rare because of sport-hunting, female groups did not benefit from the protection of males and were exposed to high levels of kleptoparasitism by spotted hyaenas (Cooper 1991). However, notwithstanding high offtakes of male lions in some areas, well regulated sport-hunting does not appear to affect the viability of large healthy populations of this species (Whitman *et al.* 2004).

In social species, especially carnivores, killing one individual can have knock-on effects that result in unanticipated disturbance or death of other individuals in the population (Tuytens & Macdonald 2000). Male felids and ursids enhance their reproductive success by killing a rival male's offspring. This brings newly acquired females into oestrus earlier than if they had successfully raised their offspring to maturation. In African lions and brown bears (*Ursus arctos*) removal of territorial males by sport hunters may result in the deaths of their offspring, killed by new males filling the newly opened space in the territorial hierarchy. If this occurs frequently it lowers population growth rates (Swenson *et al.* 1997; Greene *et al.* 1998; Whitman *et al.* 2004). Similarly in a brown bear population in Alberta, removal of mature males by hunters and the resulting immigration of subadult males caused poor cub survival and population decline (Weilgus & Bunnell 1994). The mechanisms involved were infanticide and the use of suboptimal habitat by females with cubs to avoid the new males.

The highly selective nature of most sport hunting may also have genetic consequences. A priori, it is likely that hunting regimes that closely resemble mortality patterns in natural populations will have fewer long term evolutionary consequences than those with highly artificial or biased mortality patterns (Harris

et al. 2002). This might suggest that alteration of mortality patterns by highly selective hunting could affect the gene pool of a hunted population, although it is not obvious that these alterations always have serious consequences for biodiversity. For example, hunting can cause increased gene flow and heterozygosity (e.g. for grey-winged francolin (*Francolinus africanus*); Little *et al.* 1993). Increased gene flow is problematic only if locally adapted gene complexes are threatened (Harris *et al.* 2002). It is even a moot point to what extent particular types of sport hunting actually lead to artificial patterns of mortality. Frati *et al.* (2000) showed that sport hunting of red foxes resembles predation by larger locally extinct predators such as wolves, leopards (*Panthera pardus*) and lynx.

Phenotypic changes caused by hunting have been linked to reductions in population performance. For example, Coltman *et al.* (2003) showed that body weight and horn size decreased significantly in a hunted population of big-horn sheep in response to hunter selection of large-horned rams (Fig. 15.2). Horn and body size are heritable traits closely linked to fitness, with larger-horned and -bodied rams able to defend and inseminate more ewes than smaller individuals. Likewise Shea & Vanderhoof (1999) found alteration of allele frequencies in white-tailed deer due to hunter selectivity. Larger-antlered bucks are those born earlier in the year and have fast growing antlers and high reproductive success. However, it is the large antlered animals that are chosen by hunters, leading to increased survival of late-born animals with slower growing antlers and lower reproductive potential.

In some instances, sport hunters select targets with the specific intention of "improving" the genetic stock of a population. There is a long-established tradition of attempting to improve the antler quality of red deer (*Cervus elaphus*) populations by selection as well as nurture (Thelen 1991). However, Kruuk *et al.* (2002) found no association between antler size and fitness, despite antler size being heritable, because of the large environmental influ-

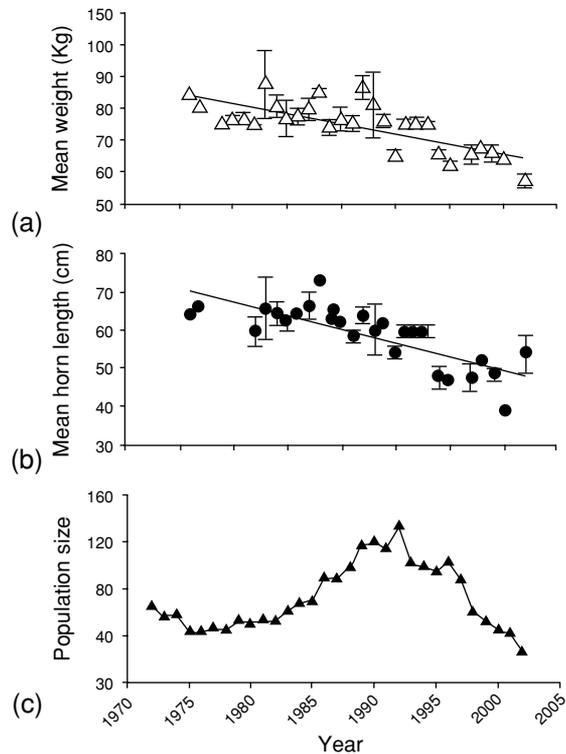


Fig. 15.2 Observed changes in mean weight and horn length and in the population size in big horn sheep from 1972 to 2002. (a) Relationship between weight (mean \pm s.e.m.) of 4-year-old rams and year ($N = 133$ rams). (b) Relationship between horn length (mean \pm s.e.m.) of 4-year-old rams and year ($N = 119$ rams). (c) Changes in population size (taken as the number of ewes aged at least 2 years plus yearlings) over time. (From Coltman et al. 2003; Copyright Nature Publishing Group.)

ence on each. This suggests that attempts to manipulate antler quality through selective shooting are unlikely to lead to an evolutionary response in antler size.

What role should sport hunting play in contemporary conservation?

In many parts of the world conservation had its roots in an era where wild species were preserved to be hunted by a small, wealthy elite. However, in contemporary conservation, there are many more interest groups with claims on wildlife and its habitats. Thus we need to evaluate sport hunting against viable alternative ac-

tivities. We take it as read that, from a conservation perspective, sustainable use of natural resources is preferable to extirpation of a population, either through overhunting or through conversion of habitat to alternative uses. Hence we compare sport hunting with other activities that contribute to conservation, rather than with economic activities that might be more lucrative, but which are ecologically damaging.

Sport hunting can clearly generate economic activity, but how does the magnitude and pattern of that activity compare with other conservation options? Sport hunting competes to varying extents with other land-uses (e.g. agriculture, subsistence hunting, logging, other tourism). Its significance as a conservation tool

depends on each activity's relative contribution to human livelihoods and habitat degradation. Most commonly, sport hunting serves to preserve a mosaic of wildlife habitat within an agricultural landscape, and to mitigate the damaging effects of competing land-uses. Examples range from sport hunting in an agricultural landscape of communally owned land in Zimbabwe as part of CBNRM initiative (e.g. Bond 2001), to the conservation of grey partridges (*Perdix perdix*) within an agricultural landscape in the UK (Potts 1986).

Hunting is commonly compared with photographic tourism in its contrasting impact on wildlife populations and ecological systems (e.g. Leader-Williams 2002, Leader-Williams & Hutton 2005). An example from Zimbabwe indicates that photographic tourism can out-compete hunting as a revenue generator. In one CBNRM area a tourist lodge was established in 1994; by 1997, lodge revenue exceeded that from hunting by 100% (Murphree 2001). However, mass market tourism is also extremely volatile. When countries experience political instability, mass tourism rapidly disappears, but sport hunters often continue to travel (Bond *et al.* 2004; Muir & Bojo 1994). During the civil war in Zimbabwe in the late 1970s there was virtually no photographic tourism, but foreign hunters continued to come to the country (Martin 1996). In addition photographic tourism is not viable in some areas, even though wildlife is present (e.g. agricultural areas, areas where charismatic species are difficult to see or landscapes are unremarkable). Photographic tourists need to be accommodated in larger numbers than hunters for the same level of profit, and this causes greater incidental environmental damage (e.g. waste from tourist accommodation and collection of firewood can pollute or destroy wildlife habitat; Goodwin *et al.* 1998).

It is often assumed that demonstrating tangible economic benefits is the way to generate support for conservation (Goodwin *et al.* 1998). The degree to which any externally imposed revenue-generating activity genuinely influ-

ences public attitudes towards conservation depends on the incentive structure in place. African CBNRMs can contribute to livelihoods and, although small in global terms, incomes from CBNRM activities can make a significant difference to households. In some CAMPFIRE areas dividends from sport hunting exceeded income from agriculture (Bond 2001), but this does not necessarily mean that people are willing to abandon established activities. The fewer the competing activities, the lower human population levels and the more abundant the wildlife populations, the more likely it is that hunting can actually or potentially contribute to livelihoods and regional economic success. However, land use is dynamic. Currently protected areas have the potential to support other livelihood activities such as hunting or even agriculture and settlement (e.g. Murphree 2004). Likewise, agricultural land can be converted into wildlife sanctuaries (Goodwin *et al.* 1997), where sustainable sport hunting and wildlife conservation may become a primary economic activity. The actual or perceived value, at governmental or local levels, of conservation activities (including sport hunting) may be an important determinant of this change.

Conclusion

Sport hunting can benefit conservation in a number of ways, with acquisition and protection of habitat being a major benefit. Generation of substantial revenue is also possible, and there are cases where this revenue is used in conservation of biodiversity. There are also many cases where it is less clear that hunting revenue is reinvested in conservation. Genetic, behavioural and population impacts may need to be guarded against, although there are few clear-cut cases where these have had significant impacts on the viability of populations. On balance it appears that the benefits of sport hunting can outweigh any disadvantage if responsibly managed and monitored. However, an institutional

structure that is able to implement regulations effectively is a necessary precondition for success. All conservation and resource use requires that managers can monitor wildlife populations and ecosystems, set and enforce limits, and ensure that benefits are disbursed wisely so that conservation is competitive with alternative land-uses. Such a regulatory infrastructure can be expensive. Compared with other, non-consumptive uses of wildlife, sport hunting has the potential to generate large profits, and sport hunters often collectively demonstrate a

responsibility and passionate concern to see their quarry species conserved. This makes sport hunting a potentially attractive option for conservationists.

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If a bird's nest chance to be before thee in the way in any tree, or on the ground, whether they be young ones, or eggs, and the dam sitting upon the young, or upon the eggs, thou shalt not take the dam with the young; But thou shalt in any wise let the dam go, and take the young to thee; that it may be well with thee and that thou mayest prolong thy days.

(Deuteronomy 22: 6–7, written c.560 BC and attributed to Moses c.1300 BC on the fundamental tenets of moral law. King James translation.)

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