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Factors that determine whether commercial exploitation of introduced mammals in New Zealand provides a useful method for reducing their densities and therefore their impacts on native biota are examined. The history of commercial harvesting of three introduced species, red deer *Cervus elaphus*, Himalayan thar *Hemitragus jemlahicus* and possums *Trichosurus vulpecula* is described. It is then assessed why the conservation outcomes of this harvesting have differed for these three species and an attempt is made to define some general rules about where and when commercial exploitation is a useful pest control tool. Commercial harvesters of red deer for game meat and by-products have harvested over 2 million deer since 1960 and reduced the national population from over 1 million to a current population size of ca 250,000 deer, a 75% reduction overall. Current annual harvests average ca 20,000 deer, with annual variations explained largely ($r^2 = 0.89$) by the price of venison. Commercial harvesting of thar for game meat between 1971 and 1982 killed at least 39,000 thar and reduced the population by over 90% to <5,000 animals. After the peak harvests before 1976, low annual harvests of only a few hundred animals were able to be sustained as thar were killed as bycatch of the deer industry - but the harvest was stopped between 1983 and 1994 because of pressure from recreational hunters. Commercial exploitation of possums for fur began in 1921, with over 56 million skins being exported. The annual harvest is correlated with the price of furs. Compared with deer or thar, the prices paid per possum are low, and possums are much more abundant (ca 60 million) and ubiquitous pests. The annual harvests of possums have therefore been variable and never sufficient to have more than locally significant effects on population densities.

Key words: red deer, Himalayan thar, possum, commercial harvest, market price, conservation, pest impacts

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Commercial harvesting of wildlife has often resulted in the collapse of the exploited population (e.g. Clark 1990, May 1977). Such population crashes are usually undesirable, but where the animals harvested are pests, a crash might be beneficial if it can be sustained (e.g. Challies 1990, Ramsay 1994). Whether such harvesting contributes significantly to pest control depends on whether the harvest is both large enough and sustained or repeated frequently enough to keep the target population below densities acceptable to pest managers, whether it can be integrated into a wider pest control regime, or whether it can reduce the population to a low density and leave the sustained control to others.

New Zealand terrestrial ecosystems evolved in the absence of mammals (apart from three species of bat), but since Polynesian and European settlers arrived (ca 1,000 and 200 years ago, respectively), 31 mammal species have established wild populations (King 1990). Most are legally defined as pests, and the general official attitude is that if they were not already present, Government would not allow their introduction. On this basis, Government would eradicate them if it could (Department of Conservation 1993). It is unlikely that any of the 31 species will be removed completely from New Zealand in the foreseeable future because the general pre-conditions (no immigration, a kill-rate higher than the rate of increase at all densities, and all pests at risk) for successful eradication cannot be met (Parkes 1990, Bomford & O'Brien 1995). Land managers are therefore often faced with doing nothing or implementing some form of sustained con-

trol, either using their own resources or by encouraging commercial or recreational hunters.

In New Zealand, pests that affect conservation values are generally the responsibility of the Department of Conservation (DoC), which manages 80,000 km^2 or 30% of New Zealand. This Department currently allocates NZD 20 million annually to pest control, focusing mainly on possums *Trichosurus vulpecula* and feral goats *Capra hircus*, and is now applying control to ca 10% of the land it manages with possums and 30% of that with goats. However, these efforts do not adequately address all the threats to indigenous biodiversity posed by possums or goats, or by other pest species. It is therefore crucial that the limited resources available to DoC for pest control are not wasted by killing pests that could be adequately controlled by commercial hunters at no cost to the Department. In this paper, we assess the sustainability of commercial harvesting of three species with similar intrinsic rates of increase, red deer *Cervus elaphus*, Himalayan thar *Hemitragus jemlahicus*, and possums, and discuss whether these harvests contribute to protecting conservation values.

Methods

Information on historical trends in the size of commercial harvests was obtained from the scientific literature, and is complemented by information about the number of harvested deer and thar obtained from two sources. The number of deer harvested by commercial hunters each month between 1988 and 1994 was obtained from the Game Industry Board, an agency established to manage the production and marketing of farmed venison. Because the actual prices paid for wild deer are not easily standardised between processing companies, we have used the price of a grade of farmed deer (60-kg stags quoted in The Deer Farmer Nos 43 to 119) as an index of the value of wild venison on the international market. The annual harvest of thar between 1971 and 1977 is taken from estimates given in Tustin (1980), between 1978 and 1982 from those in Parkes & Tustin (1985), and in 1995 from figures provided by Mair Venison Ltd, the company responsible for processing thar meat. The quantity and FOB value of possum skins exported annually between 1962 and 1994 was taken from the New Zealand Department of Statistics. All prices are given in 1994 NZD (NZD 1 = USD 0.68).

Results

Red deer

Red deer were first introduced to New Zealand in 1851 as game or trophy animals and were subsequently further released at over 50 other sites (Challies 1990). Red deer occupied ca 140,000 km^2 (52%) of the country by the 1950s, living in a wide range of habitats from sea level to alpine areas. Before commercial harvesting began, the population size must have been over 1 million to be sufficient for the known harvests. Before commercial deer hunting became established, various Government agencies had attempted to reduce deer densities using ground-based hunters. Between 1931 and 1961, the agencies killed-to-waste an average of 28,000 deer per year (Howard 1965). These control efforts were largely abandoned once commercial hunting became widespread, and DoC now kills <200 deer per year in a few key conservation areas. Recreational hunters have shot deer for meat, sport, or trophies since their introduction, but the only estimate available for their national harvest is for 1988 when ca 37,000 recreational hunters shot ca 54,000 deer, 76% of them red deer (Nugent 1992).

History of commercial harvesting

A market for New Zealand wild venison was developed in Europe in the late 1950s and by the late 1960s most deer shot for game meat export were obtained by shooting and recovering carcasses from helicopters (Challies 1990). Annual harvests peaked in the late 1960s - early 1970s, when over 100,000 animals were shot each year, and have totalled nearly 2 million to date (Fig. 1A). Between 1978 and 1987, deer were also captured alive to stock deer farms, but live capture virtually ceased after 1987 once the demand could be met from farm-bred deer. Helicopter-based hunters require both a licence to operate, issued by DoC, and the permission of the landowner over whose land they wish to hunt (generally also DoC). Carcasses are purchased from hunters by game meat processors. Prices are determined largely by the supply and demand for game meats on the international market, particularly in Germany.

Effect of commercial harvesting on density and distribution

Ground-based recreational and official control hunting has had little effect on the distribution of deer other than to remove them from the most developed and most accessible areas. However, once helicopter-based hunting began, deer were quickly removed from unforested habitats (mainly alpine grasslands) where the lack of protective cover meant harvesting costs were low even in the most remote areas (Nugent et al. 1987, Challies 1990). Once the easily hunted deer had been removed, the heli-

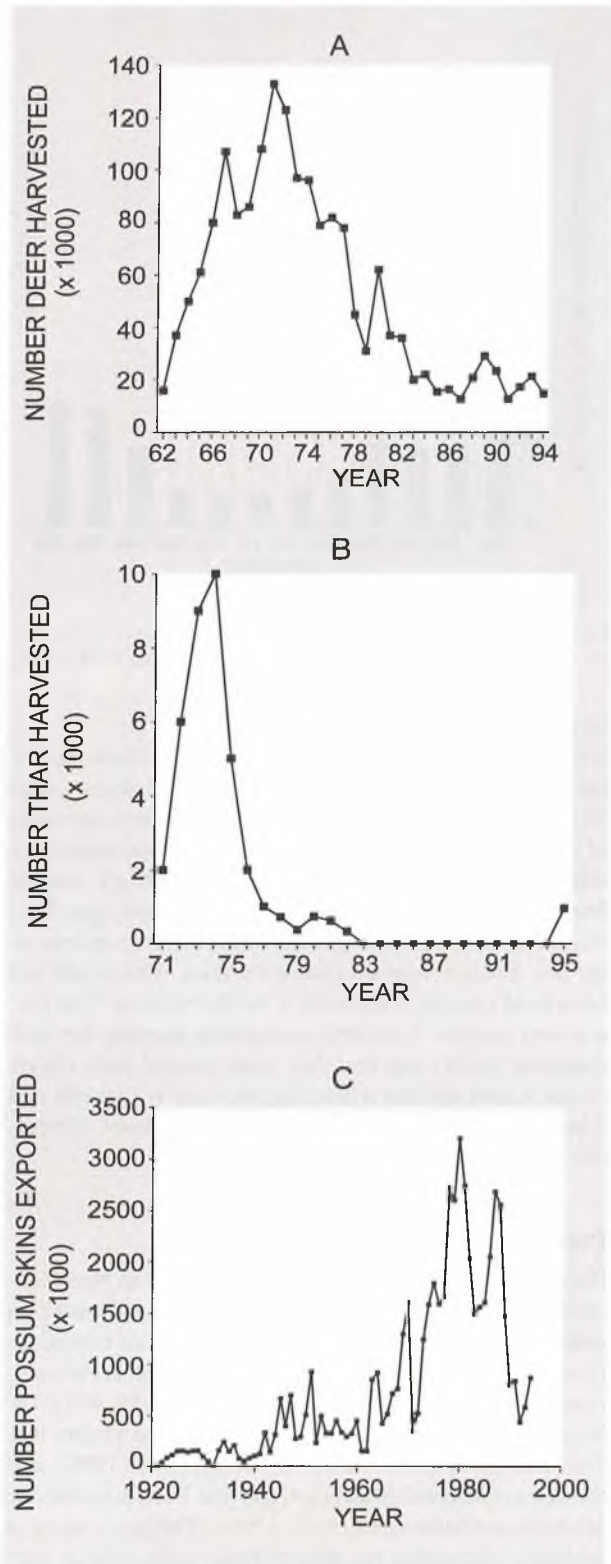

Figure 1. Annual harvests by commercial hunters of red deer (A) between 1962 and 1994, Himalayan thar (B) between 1971 and 1995, and possums (C) between 1921 and 1994.

copter-based hunters began taking deer from forested areas where deer were less accessible and hunting costs were higher. These forested habitats cover about 60,000 km^2, and hold an estimated 250,000 deer (Nugent & Fraser 1993). Densities remain highest in forests with the most complete canopy cover and the greatest distance from grasslands (Nugent et al. 1987, Nugent & Sweetapple 1989).

Sustainability of harvests

Since 1988, the annual harvests of deer by commercial hunters have varied between 12,800 and 29,200 with no trend with time (Fig. 1A), the variation being almost entirely explained ($r^2 = 0.89$) by the price of venison (Fig. 2). Assuming linearity at lower prices, commercial harvests would fall to zero if the indicator price fell below NZD 91/carcass. However, this assumption is almost certainly unwarranted. The companies that purchase and process wild venison need a minimum number of carcasses annually to remain viable, so it is likely that the price at which commercial hunting would cease is above the modelled NZD 91. We think it is close to the minimum observed value of NZD 272, because in that year (1991) one of the processing factories closed until prices recovered.

The strong relationship between harvest size and price suggests interest in commercial hunting should be highest in years when prices are high. However, there has been no relationship between the number of applicants for licences and prices since 1989 ($r^2 = 0.15$). Rather, the number of applicants has increased from 54 in 1989 to 70 in 1994 and 1995, probably simply reflecting the increasing number of helicopters in New Zealand. Despite this in-

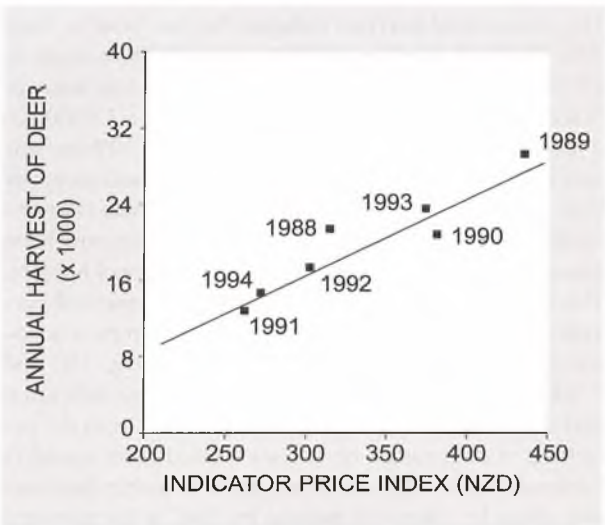

Figure 2. Effect of price of venison on the number of red deer harvested annually by commercial hunters during 1988 - 1994; ($y = -7482 + 82x$; $r^2 = 0.89$).

creased interest, DoC has chosen to allocate a relatively constant number of licences, between 49 and 56, each year since 1989, i.e. DoC has not reacted to the market.

Himalayan thar

Thar (or tahr), a caprid native to the Himalayas, were introduced in the South Island in 1904 as game animals (Tustin 1990), and have dispersed to currently occupy a breeding range of about 7,000 km² of the South Island. Like deer, thar were also controlled by Government agencies between 1937 and 1970, with an average of 750 thar being shot each year (Tustin 1990), and also like that for deer, this control effort was virtually abandoned once commercial hunting began. The limited official control being conducted now aims at halting dispersal at the edges of the species' breeding range and accounts for <100 animals per year. An estimated 752 thar were shot by 1,255 recreational hunters in 1988 (Nugent 1992), and harvests have probably increased since then as the thar population increased.

History of commercial harvesting

A commercial market for thar meat was developed in Europe in 1971. Animals were shot from helicopters during winters when snow restricted their movements and made them easy to find. About 39,000 animals were recovered between 1971 and 1982 (see Fig. 1B), and annual harvests peaked in 1974. All commercial hunting was banned between 1983 and 1994 because of pressure from recreational hunters.

Effect of commercial harvesting on density and distribution

The commercial harvests reduced the thar herd by over 90% (Tustin & Challies 1978) from ca 50,000 animals to <5,000 in 1983, when commercial hunting was banned. Since then the population has increased to ca 13,000 animals, despite the recreational harvest of ca 10% per annum (Parkes 1993). A national control plan sets an upper limit for the thar population of 10,000 animals (Department of Conservation 1993), but this limit has now been exceeded despite the best efforts of recreational hunters. The Department therefore permitted a commercial harvest in 1995, when ca 2,900 thar were shot from helicopters - 900 being recovered for meat (see Fig. 1B) and 2,000 shot but not recovered. There was some indication that the harvests of the 1970s removed thar from the periphery of their range, or at least slowed their spread (-Parkes & Tustin 1985), and they are held within their current range by intensive hunting by DoC at the northern and southern boundaries.

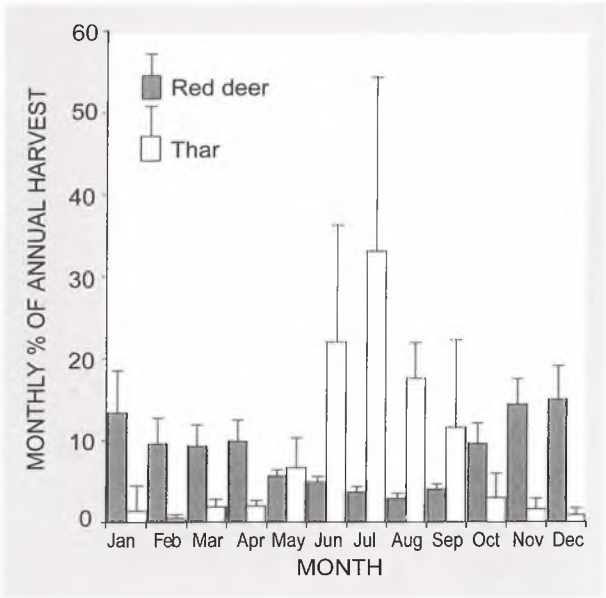

Figure 3. Mean (+S.E.) monthly distribution of harvests of red deer (N = 101,674) and Himalayan thar (N = 2,742) during 1978 - 1982.

Sustainability of harvests

We have no data on the price paid for thar meat during the period 1971-1982, but the small annual harvests after 1976 will have produced little revenue relative to the costs of operating a helicopter. Prices paid for thar meat were similar to those paid for venison (ca NZD 3/kg), and the dressed carcasses of thar weigh ca 25 kg on average (Tustin 1990). Helicopters cost over NZD 600/h to operate so the few hundred thar shot annually after 1980 would not have been enough to maintain a viable business. One reason why hunters were able to continue hunting for such marginal returns was that they concentrated their efforts on the winter months when thar are most vulnerable and when the hunters' main prey (red deer) are least vulnerable (Fig. 3).

Possums

Possums were first successfully established in New Zealand in 1858, and were reliberated within the country on numerous occasions (Cowan 1990). They currently occupy ca 257,000 km² (95%) of the country and are ubiquitous in all habitats, urban and rural, indigenous and exotic, and from sea level to the limit of alpine vegetation. Possums can reach densities of 24/ha (Cowan 1990), and the current national population size has been estimated at 60 million (Sutherland et al. 1996). The population is probably decreasing because of large-scale official control operations which routinely kill 80% plus of the target populations.

Between 1951 and 1961, ca 8.2 million possums were

killed under a bounty scheme that paid NZD 3.15 per token returned. The token was a strip of fur from the ears down the back of each possum sufficient to ruin the skin as a commercial product. After 1961, Government controlled some populations using aerial poisoning, but few of these operations were sustained. Since 1993, Government has allocated increasing budgets (NZD 30 million in 1995) to control possums as vectors of bovine tuberculosis and as pests of conservation values. Many millions have been killed in large-scale aerial poisoning and ground hunting campaigns over ca 10% of the country.

History of commercial harvesting

Commercial harvesting of possums for their fur began in 1921, since when ca 56 million skins have been exported (see Fig. 1C). The price of possum furs was until 1990 set at auctions held in New Zealand, where the price was determined entirely by demand. Since 1990, however, no auctions have been held in New Zealand and trappers deal directly with buyers or send furs to European auctions. Since 1983, a growing proportion of skins are tanned in New Zealand before export.

Effect of commercial harvesting on density and distribution

Before 1940, commercial fur hunters were responsible for liberating possums in many possum-free areas, including 17 islands, but are restrained from doing so now mainly by lack of financial incentive and by the lack of areas without possums. Commercial harvesting has not removed possums from any areas, but when prices were high (e.g. 1980 - 1981) densities in places easily accessible to hunters were reduced by over 50% compared with those in unhunted areas (Brockie 1982).

Sustainability of harvests

The number of possums killed each year since 1962 (when the bounty scheme ended) is directly related to the price of skins within two periods - before and after value was added to skins by extra processing (Fig. 4A and B). The relationship after 1983 was more sensitive to price than that before value was added.

The effect of commercial harvesting on possum numbers can be modelled by assuming the harvest/price relationship remains linear, logistic growth, an intrinsic rate of increase (r_m) of 0.29, and that the estimated population of 60 million is near carrying capacity (K). A mean annual sustained harvest of 1.5 million (i.e. the harvest since 1983) would results in an equilibrium population of 54.3 million possums. From Figure 4B, the price per skin would have to exceed NZD 22 to attain the sustained annual harvest of 4.35 million possums ($MSY = r_mK/4$) required to attain an equilibrium population of K/2 - the bare minimum reduction needed to protect conservation values and insufficient to eradicate bovine tuberculosis (Cowan 1990, Barlow 1991).

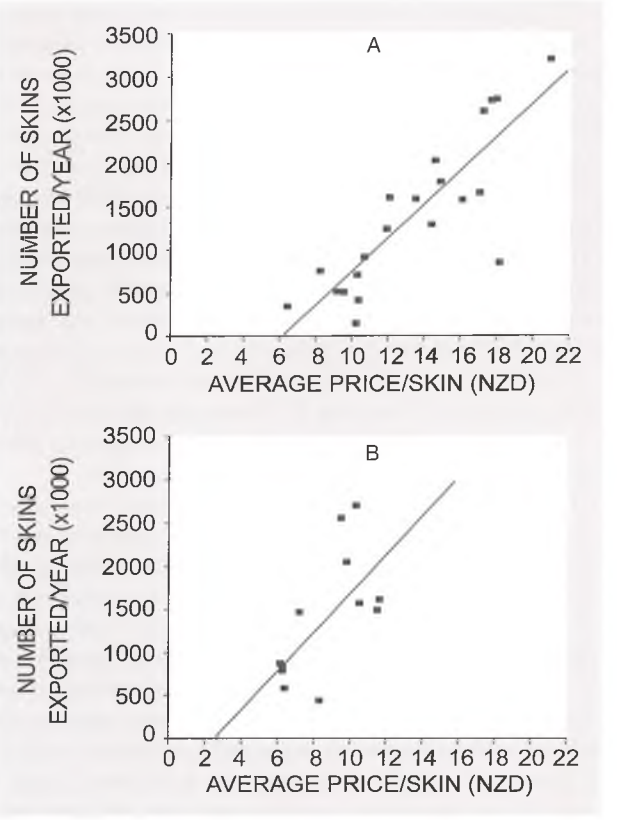

Figure 4. Effect of average annual skin price on the number of possum skins exported during 1962 - 1982 before some skins were tanned (A; $y = -1148880 + 189371x$; $r^2 = 0.71$); and during 1983 - 1994 (B; $y = -547126 + 225888x$; $r^2 = 0.42$).

Discussion

Commercial harvesting can provide effective pest control when the demand for the product is ongoing and when the price paid is above the costs of harvesting at the animal densities required to protect the conservation resources affected by the pest. The effectiveness of the commercial hunting regimes for the three species discussed in this paper has varied widely in terms of its ability to reduce the populations and maintain them at low levels. The different outcomes reflect differences in the prices paid per animal, in the relationships between pest densities and harvest costs, and the accessibility of the populations. Commercial hunting should have its greatest impact when the price per animal is high, the costs of harvests low and independent of animal densities, and the hunters do not rely solely on that species for their livelihood.

The conservation benefits of commercial harvesting of red deer has been substantial in grasslands (Rose & Platt

1987) but more variable in forests. In forests with sparse canopies, many canopy gaps, or with substantial adjacent grasslands, deer have been reduced to low densities and all but the most vulnerable plant species have made some recovery (Stewart et al. 1987). However, in forests without these characteristics, deer densities are higher and few palatable plant species are able to regenerate (Nugent & Fraser 1993). The inaccessibility of most deer in forests to helicopter-based hunters means that the forests provide an ongoing breeding stock of deer, a proportion of which move to areas where the commercial harvesters can shoot them. This proportion increases in the spring as yearling animals disperse and is reflected in the seasonal distribution of the harvest (see Fig. 3). So long as the index price remains above ca NZD 272 per animal commercial harvesting of red deer therefore appears sustainable.

Commercial exploitation of Himalayan thar also achieved population reductions sufficient to protect many of the conservation resources in their alpine habitats, all of which are accessible to aerial hunters. The evidence for this protection consists of photographs taken before and after the 90% reduction of thar numbers (e.g. Department of Conservation 1993). However, unlike red deer, thar had no refuge from the helicopters and the commercial harvest soon collapsed to marginally economic levels - although we suggest the harvest may have been sustainable as a bycatch of the larger red deer industry with thar being in a predator pit. Because the commercial harvest was stopped between 1983 and 1994, its current viability remains unclear.

Commercial exploitation of possums has been sustained but is insufficient to afford any significant protection to conservation resources. Managers of possums as pests require reductions in density of at least 60% of carrying capacity to ensure the elimination of bovine tuberculosis (Barlow 1991) and an unknown but larger reduction to protect conservation values. Commercial harvests of possums have been too small to achieve these reductions at national scales, and too ephemeral to maintain benefits at local scales. The effectiveness of the bounty scheme was also limited by the small annual kill. With less than 1 million possums being taken on average each year the equilibrium density would again be too high to achieve the goals. Control agencies are therefore obliged to use large-scale poisoning to achieve their goals, despite the costs and biological and social risks (Sutherland et al. 1996).

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