Is culling of grey squirrels a viable tactic to conserve red squirrel populations?

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SUMMARY

- Red squirrels populations have historically undergone large population fluctuations. Causes include habitat loss and disease. At various times in the 19th and 20th century, red squirrels from Europe have been introduced to re-establish or augment populations. Genetically, red squirrels in Britain are not distinct from those in Europe.

- Grey squirrels have been introduced to various localities in Britain. Despite culling, these populations have now spread over most of England and Wales, and into many parts of Scotland.

- Red squirrel populations are declining for two reasons: ecological displacement by grey squirrels, which may take many years, and squirrel poxvirus (SQPV). Grey squirrels act as vectors for SQPV and aid the spread of this disease into novel red squirrel populations. Grey squirrels quickly fill the vacant ecological niche when red squirrel populations die out from SQPV.

- It is widely argued that controlling grey squirrel numbers is the best way of conserving red squirrels. However, there is little evidence to support this belief. Most squirrel control is carried out with warfarin, but only live trapping and/or shooting can be carried out in areas with reds. Attempts to create an immunocontraceptive for grey squirrels have failed and no biological control methods are currently available.

- Most control is done within the context of protecting commercial woodlands from squirrel damage. There is mixed evidence that grey or red squirrel control worked; bounties schemes in the past have proved unsuccessful at lowering population numbers. Success has been limited to isolated populations such as islands; grey squirrels can colonize areas quickly, so most grey squirrel control is ineffective.

- Grey squirrels can damage commercial forestry and are cited as having a negative impact on woodland birds. Whilst the evidence with regard to commercial forestry is unequivocal, controlling squirrel numbers is not always effective and current silviculture techniques may exacerbate the problem. There is at best limited data to suggest the minor role of grey squirrel's impact on two species of woodland bird. These arguments ignore damage to forestry and predation on woodland birds that historically were attributed to red squirrels when they were more abundant. In addition, no consideration is given to the benefits that grey squirrels may have, including the formation of deadwood, an important component of biodiverse woodlands

- Culling of grey squirrels could lead to more problems than solutions. Culling may lead to an increased localised density, an increase in forest damage levels and increase the spread of disease.

- Red squirrel populations will continue to decline in the face of increased ecological displacement by grey squirrels and SQPV. Novel techniques need to be devised to protect red squirrels. These include setting island refugia, and developing an effective and humane way to eliminate grey squirrels.

- Large sums of money are being spent on red squirrel conservation. However, this money is not spent wisely. Whilst red squirrels are native to Britain, many of the populations are recently introduced European stock, and so even if red squirrels do eventually disappear from Britain, they could easily be reintroduced again. Globally, red squirrel populations are not threatened and the conservation effort in Britain is of little importance.

INTRODUCTION

The purpose of this document is two-fold. It aims to describe evidence from the scientific literature about the costs (financial and ecological), benefits and role of grey squirrel culling in red squirrel conservation while at the same time examining whether grey squirrel culling is a long-term solution to red squirrel conservation or whether other solutions need to be developed.

THE HISTORY OF RED SQUIRRELS IN BRITAIN

The Eurasian red squirrel (*Sciurus vulgaris*) is a widespread species found in most wooded areas of Eurasia from Iberia to Kamchatka Peninsula and Sakhalin Island (Russia), and Great Britain south to Mediterranean and Black Sea, north Mongolia, west and north-east China (Gurnell, 1991; Lurz *et al*., 2005; Wilson & Reeder, 2005). In Britain, the red squirrel was thought to be distinct subspecies (*S. vulgaris leucorus*) characterised by a distinctive annual bleaching of hair, especially on the tail and ears (Lowe & Gardner, 1983). However, recent DNA analysis indicated no evolutionary divergence between British and continental populations (Barratt *et al*., 1999). This is unsurprising for two reasons; first populations in Britain have been isolated for a relatively short time (8000 years) since the last ice age and may not have evolved sufficiently to acquire monophylognetic status (Barratt *et al*., 1999); second, red squirrels were deliberately reintroduced into Scotland and England from continental stock at various times during the last 150 years (Ritchie, 1920; Lowe & Gardiner, 1983), and many were also imported from the continent as a food source and may have escaped (Freethy, 1983). Further genetic analysis supports this earlier hypothesis, although it was suggested that most British squirrels are descended from more recent introductions from Scandinavia (Hale *et al*., 2004). Using museum specimens, Kitchener *et al.* (2003) suggested that the Cumbrian population of red squirrels remained a distinctive British subspecies, and that other populations were the result of introductions. However, further museum work showed a temporal loss of distinctive phenotypic characteristics from the Cumbrian population, which was caused by increased gene flow into the population following increased planting of woodland, which linked the Cumbrian and Scottish populations (Hale *et al*., 2001; Hale & Lurz, 2003). As a consequence, all British red squirrels represent a mixed genetic stock (Barratt *et al.*, 1999; Hale *et al*., 2004).

Populations of red squirrels are notably volatile, undergoing marked changes in numbers both in the long- and short-term. Historically, populations of red squirrel declined to near extinction during the 18th century as a consequence of deforestation, eventually necessitating the reintroduction of red squirrels from the continent (Yalden, 1999). During the 19th century, forest plantations originally planted at the end of the 18th century reached maturity. This led to an increase in the squirrel population to the extent they were considered a major pest and necessitated culling (Tittensor, 1975). Locally they became so numerous that red squirrel destruction clubs were formed and a bounty scheme implemented (Ritchie, 1920; Shorten, 1954). Large numbers of squirrels were killed; over fifteen years, the Highland

Squirrel Club killed 60,500 red squirrels in just one area (Ritchie, 1920). Later population declines during 1900-1930 have been linked to a disease epizootic (Middleton, 1930). Since the 1940s population size and distribution of the red squirrel in Britain have contracted, largely in parallel with the increase in range of the grey squirrel (*Sciurus carolinensis*).

THE POPULATION OF GREY SQUIRRELS IN BRITAIN

The grey squirrel is a native of eastern North America, inhabiting a range of forested habitats, particularly deciduous woodland. The grey squirrel has repeatedly been introduced to Britain between 1870-1930. Notable introductions include 100 in Richmond Park, Surrey and 91 in Regent's Park, London (Shorten, 1954). Introductions were not confined to southern England, but included releases all over Britain. With such large numbers released and at so many points, it is perhaps unsurprising that grey squirrel populations took hold in this country. Initially, populations spread locally; in 1920 populations were focused around initial release points, but by 1945 grey squirrels had expanded their range to much of southern and central England, although spread into East Anglia and the southwest occurred later. Later surveys in 1970 and 1990 indicated that grey squirrel populations had covered most of England and Wales, with two separate populations in Scotland; one was based around the mid-Lothian, Fife, Tayside and Glasgow, a second was limited to Aberdeen and the surrounding area (Lloyd, 1983; Gurnell & Pepper, 1993). The population in the Aberdeen area was thought to be isolated from the more southern population and its appearance was a result of a deliberate introduction. However, Staines (1986) suggested that the Aberdeen population was the result of natural colonisation from central Scotland, and the non-contiguous nature of some grey squirrel distribution maps in Scotland reflect poor survey coverage of some areas.

CAUSES OF RED SQUIRREL POPULATION DECLINE

Causes of red squirrel populations declines can be categorised into three factors: habitat loss, ecological replacement by grey squirrels and disease.

Habitat loss and red squirrel declines

Habitat loss has been an important factor in the decline of red squirrels in the past. The widespread destruction of forests led to the almost complete extinction of red squirrels in Britain (Ritchie, 1920; Gurnell, 1987). Only through reintroductions from continental stock and the increase in forestry plantations did the red squirrel recover. However, the frequency with which certain tree species have been planted are important. For example, pre-1920, 40% of planted woodland was oak; this habitat can lead to a competitive disadvantage against grey squirrels (see section on ecological replacement). Currently, habitat loss is not an important factor in red squirrel declines and forest coverage is increasing (Forestry Commission, 2001; Scottish Environment Statistics, 2006); however, the suitability of this new forest for red squirrels is low. Habitat preferences of red squirrels vary with location and densities (Bryce *et al*., 2002; 2005). It is considered that 'good' habitat for red squirrels are those that reds utilise, but grey squirrels avoid. These include Norway spruce, larch and Douglas fir (Bryce *et al*., 2002). Poor habitat was either selected by greys or avoided by reds; these include sitka spruce (avoided by both species) and Scots pine (used by both). Overall, the planting of forests in England and Scotland has not increased the area of suitable red squirrel habitat (Table 1), and in fact the increase in broadleaved woodland has been of greater benefit to grey squirrels (Table 1).

Table 1. The changes in woodland cover in England (1980-1998) (Forestry Commission, 2001) and Scotland (1980-1995) (Scottish Environment Statistics, 2006), with the suitability of habitat for squirrels based on definitions by Bryce *et al*. (2002)

Species	**Percentage forest change (England)**	**Percentage forest change (Scotland)**	**Suitability for squirrels**
Sitka spruce	+14	+61	Poor for both species
Norway spruce	-21	-28	Good for both
Douglas fir	+3	+1	Good for reds
European larch	-34	-39	Good for reds
Mixed/Japanese larch	-3	+21	Good for reds
Scots pine	-5	+8	Poor for both
Broadleaved woodland	+36	+68	Good for greys

Whether a habitat is 'good' for red squirrel is highly dependent on tree seed productivity. Coniferous woodland can have red squirrel densities equal to deciduous woodlands (Gurnell, 1987; Lurz *et al*., 1995; Wauters & Lens, 1995), but this is highly dependent on species composition and age structure of the forest; man-made coniferous woodland in northern England have the lowest seed productivity and lowest red squirrel density (Wauters *et al*., 2001). It has been suggested that introduced red squirrels from Scandinavia are better adapted to spruce dominated woodlands, and so are able to tolerate these habitats more than the 'native' red squirrel (Hale *et al*., 2004). However, quantitative data supporting this hypothesis are absent. The idea that coniferous plantation are 'good' habitat for reds is false; in many places they simply provide a refuge habitat into which grey squirrels have difficulty in spreading.

Ecological replacement by grey squirrels

There are areas of Britain where red and grey squirrels coexisted for a number of years (Teanganna *et al*., 2000; Bryce *et al*., 2002). In some cases, red squirrels populations become extinct after many years of coexistence (Harris, 1973/74; Reynolds, 1985). This contrasts with the disease-induced declines of red squirrels which are followed by rapid colonization by grey squirrels (see section on diseases). Due to this apparently slow pattern of replacement, it has been suggested that grey squirrels are out competing red squirrels. Data from coniferous woodland showed little direct interspecific competition with grey squirrel (Wauters *et al*., 2000); there was no evidence that either adult survival rates or the proportion of female breeding decreased (Wauters & Gurnell, 1999; Wauters *et al*., 2000), although however, both female red squirrel fecundity and juvenile recruitment were reduced in the presence of grey squirrels (Wauters & Gurnell, 1999; Gurnell *et al*., 2004). In deciduous woodland, grey squirrels are better able to exploit acorn crops and have a competitive advantage over hazelnut crops; this is predicted to lead to slow replacement of red squirrels by greys (Kenward & Holm, 1993). The different feeding abilities of the two species makes red squirrels more vulnerable to food shortages (Gurnell & Pepper, 1993), which may lead to a reduction in the number of breeding females and subsequent recruitment into the population. The presence of grey squirrels also makes it hard for juvenile red squirrels to establish territories. This competitive advantage is greatest in deciduous woodland; the rate of replacement is thought to be related to habitat composition, with populations coexisting for longer in coniferous habitats (Bryce *et al.*, 2002). However, as suggested by Gurnell *et al.* (2004), even in these habitats, it appears that red squirrel populations will decline and red squirrels will only persist where they have a competitive advantage over greys.

Diseases and squirrel population declines

Red squirrel populations seem particularly susceptible to diseases and historically, disease has caused many population declines (Middleton, 1930; Edwards, 1960; Vizoso, 1968; Scott *et al.*, 1981; Keymer, 1983). It is now known that a disease, squirrel poxvirus (SQPV), is a significant factor in red squirrel declines (Tompkins *et al*., 2002; Thomas *et al.,*2003). Whether SQPV was introduced to Britain along with grey squirrels is unclear (Daszak *et al*., 2000), but it is more likely that SQPV was endemic within the native red squirrel population, as the symptoms of this disease have been described from red squirrel populations prior to the introduction of the grey squirrel (Middleton, 1930). What is clear is that grey squirrels act as hosts without developing the disease (Sainsbury *et al*., 2000) and they aid the spread of disease into previously unexposed red squirrel populations (Daszak *et al*., 2000). They then take over the vacant ecological niche caused by the red squirrel's extinction (Tompkins *et al*., 2002). The speed of red squirrel loss is markedly faster in the presence of the disease than solely with ecological replacement (Ruston *et al*., 2006). By tackling the spread of this disease, red squirrel population loss will be markedly slower.

What will happen to red squirrel populations?

There are two main factors causing current red squirrel declines: ecological replacement by greys and disease. In the absence of SQPV, it is predicted that red squirrels would become restricted to those habitats where grey squirrels cannot out-compete reds. However, SQPV is an important factor. If this disease enters novel red squirrel populations, it is likely that reds will die out and be replaced by greys, even in these poorer quality habitats.

CONTROLLING GREY SQUIRRELS

There are four approaches to conserving red squirrels: stop grey squirrels spreading SQPV, stop greys colonizing new habitat and replacing red squirrels, control of the disease and increasing suitable habitat for red squirrels. Intuitively, the simplest method would appear to be to stop grey squirrels spreading, and so this is the approach most widely implemented. This is done through some form of population control: culling (poisoning, shooting, trapping), immunocontraception or biological control.

Grey squirrel population control: culling

There are four methods of culling: poisoning, spring trapping, shooting and live trapping. Of these, poisoning is banned in areas with red squirrels, and for all other locations it is discouraged due to the likelihood of non-target species poisoning. Spring trapping (a killing trap) is also discouraged due to the indiscriminate nature of the traps (Hodge & Pepper, 1998; Mayle *et al*., 2004). Three techniques predominate: poisoning (where not banned), shooting and live trapping.

Poisoning

Poisoning with warfarin is favoured in most commercial woodlands, where it is viewed as both cheap and effective (Taylor *et al.*, 1968; Pepper, 1990; Mayle *et al.*, 2004). There is some risk that poisoned squirrels carcasses may be consumed by scavengers. Fifty-seven percent of warfarin poisoned squirrels fell to the grounds and 25% of these were scavenged (Kenward, 1988). Warfarin has a short half-life and is not usually present at high levels in the bodies of poisoned animals. This is because death is relatively slow and there is ample time for much of the toxicant to be metabolized or excreted (Record & Marsh, 1988). Exposure to warfarin through scavenging is not thought to have a large risk of mortality to non-target species, but may have unknown sub-lethal affects (Townsend *et al*., 1981). However, direct exposure to warfarin can be important. Wood & Phillipson (1977) estimated that 55-65% of bait for grey squirrels was consumed by non-target species, primarily rodents; this can cause significant local population declines (Brakes & Smith, 2005). Poisoning of non-target species is another route to secondary poisoning in predators and scavengers (Brakes & Smith, 2005). Warfarin is the recommended poison to control squirrels, but a survey by McDonald & Harris (2000) showed that 46% of game estates used poisons other than warfarin to control grey squirrels. These second generation compounds have longer half lives than first generation poisons such as warfarin, and so the risk of secondary poisoning is increased (McDonald & Harris, 2000). Species regularly exposed to warfarin can evolve genetic resistance to its toxicity (e.g. Quy *et al.,* 1992). If this trait evolves in grey squirrels (Taylor *et al*., 1968), the use of other poisons may lead to even higher incidences of secondary poisoning in rare and threaten species (Carter & Burn, 2000; Mason & Littin, 2003). Furthermore, anticoagulants such as warfarin are described as “markedly inhumane” by the Pesticides Safety Directorate and there is pressure from the EU to reduce the use of pesticides in the countryside (Anon, 1997; Forestry Commission, 2006).

Shooting

Shooting can take place in two forms: shooting of individuals located whilst walking through a forest, or drey poking which involves targeting dreys with poles to flush out squirrels to be shot. The latter is considered more effective (Tittensor, 1975). Although shooting is another widely used method to control populations, it is viewed as insufficient to reduce squirrel numbers significantly (Hodge & Pepper, 1998).

Live trapping

Live trapping is considered the most effective technique to catch grey squirrels (Gurnell, 1999), and is the main technique used where red squirrels are present e.g. Thetford Forest (Gurnell & Steele, 2002). Traps are typically baited with whole maize and it is recommended that traps are checked twice daily (Tittensor, 1975; Mayle *et al.*, 2004). Captured grey squirrels can then be euthanased and any non-target species released unharmed.

Grey squirrel population control: immunocontraception and biological control

Immunocontraception relies on inducing an immune response which attacks the host's reproductive system. Delivery mechanisms are typically through either bait or a vectored mechanism such as a virus (Barlow, 2000). The idea to control grey squirrel reproduction is not new (Johnson & Tait, 1983), and there have been attempts to create a bait delivered contraceptive (Moore, 1997). Initial field trials indicated a drop in pregnancy rate from 50% to 15% (Pepper & Moore, 2001). However, as yet no effective mechanism has been developed (Rushton *et al.*, 2002) and recently funding into this topic has been ceased (Forestry Commission, 2006; JNCC, 2006). Whilst immunocontraceptives have been developed for a range of species such as elephants (*Loxodonta africana*) (Fayer-Hosken *et al.*, 2000) and brushtail possums (*Trichosurus vulpecula*) (Cowan, 1996), there are few data on their effectiveness as a management tool (Ramsey, 2005). For some populations of certain species e.g. white-tailed deer (*Odocoileus virginianus*) (Rudolph *et al.*, 2000), fertility control has led to a significant decrease in population size, whilst for other species, demographic compensation (increased longevity, increased reproductive rates or increased immigration) can negate the effects of fertility control (Twigg & Williams, 1999; Ramsey, 2005). As yet there is no clear consensus on the effectiveness of immunocontraception as a technique to manage large populations. It is also unclear how species with contrasting life history strategies will respond to fertility control (Caughley *et al.*, 1992; Hone 1992), and species, such as grey squirrels, with increasing populations or high reproductive rates may be most resilient to fertility control. In addition, it is likely that in species with high reproductive rates there will be selective pressure to evolve resistance to the immunocontraceptive (Magiafoglou *et al.*, 2003). Certainly, a lot more work needs to be done before the technique can be applied to a successful invasive species such as the grey squirrel.

Biological control can be in two forms, control through a disease or parasite (Rowe, 1983; Dobson 1988), or through the introduction of a predator (Rowe, 1983; Simberloff & Stiling, 1996). Examples of biological control agents include rabbit haemorrhagic disease (RHD) in Australia (Kovaliski, 1998). Currently no biological methods are available for grey squirrels, and there may be unknown ecological effects of introducing a biological control agent into the environment. As a consequence the only other option would be natural predators of squirrels such as pine martens (*Martes martes*) and goshawks (*Accipiter gentilis*) (Rowe, 1983). However, as a result of long term persecution, current populations of both predators are most abundant in areas containing red squirrels, not greys; predation on red squirrels is not thought to be a direct threat to population viability (Halliwell, 1997; Petty *et al.*, 2003), and it is highly unlikely that these predators would have a significant impact on grey squirrel populations. So whilst the use of natural predators as a biological control of grey squirrels appears an attractive option, it is unlikely to have a significant impact on either the spread of grey squirrels or population size.

EFFECTIVENESS AND COST OF CONTROL TECHNIQUES

It is not possible to eradicate the grey squirrel from Britain using current control methods (Gurnell & Pepper, 1993). Grey squirrels are resilient to control both through rapid recolonization of vacated areas and by increasing their reproductive rate to compensate for losses (Lawton & Rochford, 1999). There is widespread evidence suggesting that control techniques and programs have had little or no success in lowering the grey squirrel population. Recent calls for a grey squirrel bounty (Horne, 2006) are misguided. Previous bounty schemes during the 1950s culled 1.5 million squirrels but did little to impact the population even though they were a lot lower (Sheail, 1999, 2003; Forestry Commission, 2006). More locally, trapping in Thetford Forest did not lower the population of grey squirrels, despite trapping 2200 squirrels in 4600 ha over a three year period (Gurnell & Steele, 2002). A long-term poisoning campaign in Lady Park Wood, Gloucestershire, did not prevent woodland damage; in fact, it actually increased during this period (Mountford, 1997). The level of squirrel control through shooting had no effect on squirrel numbers (Fitzgibbon, 1993), and evidence from spring trapping suggests no reduction in the number of squirrels caught (E. Brun cited in Huxley, 2003). However, if selected and designed correctly, effective squirrel control can be targeted locally usually through poisoning rather than shooting or trapping (Kenward *et al.*, 1988a). Kenward *et al.* (1996) showed that all squirrels in a marked population could be removed in five weeks of poisoning when poisoning effort was widespread through a vulnerable wood. However, Lawton & Rochford (1999) showed that culling regimes only caused a temporary reduction in density, and that recolonisation can be extremely rapid. Recolonisation time varies from three months in an isolated area to only one month in an area that is not isolated (Mayle *et al.,* 2004). Poole & Lawton (2004) showed that following five culls, populations recovered to pre-cull levels in 3-10 weeks. In the short-term, culling may only have a temporary effect on the population. In particular, localised culling will be offset rapidly by immigration from unculled areas. If a source-sink system is created, this may lead to higher populations in culled areas and may actually increase the speed of grey squirrel spread (Pulliam, 1988).

The cost of control must also be considered as well as the effectiveness of culling squirrels. Cost of control varies primarily by method used. In most cases, the intensity of effort is insufficient for effective control. Costs are generally lowest in poisoning, but costs of other methods vary with intensity of use (Table 2). Give its low cost, poisoning is the preferred method of control; in 1992, 140,000 grey squirrels were poisoned, compared to 11,000 trapped (Pepper, 1992).

Table 2. The costs of different forms of grey squirrel control. * based on mean costs for different areas of woodland. ** indicates cost estimated.

Methodology	**Cost/ha/annum**	**Source**
Live trapping	£2.61	Gurnell *et al*. (1997)
Warfarin	£0.21-£6.00*	Kenward *et al*. (1988a)
Warfarin	£3.92	Kenward & Dutton (1996)
Spring trapping	£12.50	E. Brun cited in Huxley (2003)
Immunocontraception	£12.84**	Ruston *et al*. (2002)
Warfarin	£17.62	Huxley (2003)
Spring trapping & shooting	£23.75	Huxley (2003)
Live trapping	£59.49**	Ruston *et al* (2002)

Costs of squirrel control can vary markedly (Table 2); for example, costs of warfarin control per hectare decrease with increasing wood size (Kenward *et al*., 1988a) and increase with intensity of effort (Kenward & Dutton, 1996). The costs of culling techniques must be offset by the benefits, which include financial costs through reduced damage to tree (see section:

other perceived negative impacts on grey squirrels) or whether it can prove an effective method to conserved red squirrels. Given this cost-benefit of squirrel control, warfarin poisoning is the favoured technique, despite the concerns over humaneness and its indiscriminate nature.

There have been recent calls by a number of agencies including Scottish Natural Heritage to cull grey squirrels to control spread into areas inhabited by red squirrels (Horne, 2006). However, past experience shows that there is no evidence to suggest this will be successful. The most successful eradication of grey squirrels has been on Anglesey, Wales, where the removal of 6,000 squirrels in five years has allowed red squirrel populations to increase (Shuttleworth *et al*., 2002). The success of this effort has been in part due to the geography of Angelsey; being an island with limited connections to the mainland has meant grey squirrels were unable to repopulate culled areas. In contrast, there has been considerable trapping effort in Thetford Forest, East Anglia, without any discernible effect on grey squirrel numbers (Gurnell & Steel, 2002). The cost of controlling mainland populations is large; Rushton *et al.* (2002) estimated that it would cost £300,000 per annum to ensure the persistence of red squirrels in Thetford Forest. Similarly, in Redesdale Forest, Northumberland the cost would be £200,000 per annum. The key aspect of squirrel control is immigration into areas following control, and so culling would be more productive in isolated populations. Recent plans by Aberdeen City Council to cull grey squirrels seem particularly misguided, as it is suggested that grey squirrel populations in Aberdeen City and Deeside are isolated from those further south (Anon., 2006). Yet this assertion contradicts other evidence; Staines (1986) suggested that Aberdeen's grey squirrels immigrated from the south, and maps in Poulsom *et al.* (2005) indicate a contiguous grey squirrel population all along the east coast of Scotland. So culling grey squirrels in Aberdeen will have no effect on the grey squirrel population and will not aid red squirrel conservation; whilst culling may lower population size in the short term, the high dispersal abilities of grey squirrels means that recolonization is inevitable. Modelling by Rushton *et al*. (2006) suggested that during a ten year period, culling of greater than 60% of the population per annum was necessary to stop grey squirrels spreading SQPV into the Cumbrian red squirrel population, and hence to ensure red squirrel persistence. Targeted or intensive culling in areas where grey squirrels are spreading may be effective, but must be very long term and is thus expensive. However, this is a prediction based on computer modelling and there are no field data to show whether such intensive culling will prevent the spread of SQPV. So, what the costs (ecological and financial) and benefits of intensive culling remains unclear. In contrast to areas where grey squirrels are spreading, it is not considered practical to exterminate grey squirrels where they are already established (Mayle *et al*., 2004).

OTHER METHODS TO STOP RED SQUIRREL DECLINES

There are four alternative approaches to red squirrel conservation that do not involve culling grey squirrels. The first is the establishment of red squirrel populations on islands that have no grey squirrels. Current islands that harbour red squirrel populations include the Isle of Wight, islands in Poole harbour and Angelsey (Harris *et al*., 1995; Rushton *et al*., 1999). Red squirrels have been introduced to the isle of Arran in Scotland (Poulsom *et al*., 2005). There are several other islands, particularly in Scotland, that currently have suitable woodland but no red squirrels (Scottish Squirrel Group, 2004); including Mull in Scotland (Shuttleworth, 2005). Establishing viable populations on islands will secure the future of red squirrels in Britain. In addition, should grey squirrels ever become introduced onto these islands, the experience on Anglesey has shown culling would be an effective strategy to remove them.

The second aspect that would aid red squirrel conservation would be the development of a SQPV vaccine. While this would not stop ecological replacement of red squirrels, it would slow their decline. Recently McInnes & Middleton (2005) estimated the cost of developing a SQPV vaccine. Initial costs ran to £416,000 for three years; however, they acknowledge that this does no include extensive field trials, nor an indication of timescale. Though large, these costs are smaller than the £1.1 million planned for red squirrel conservation in northern England (NWT, 2006). SQPV is widespread in grey squirrels in northern England, where it has already been found in red squirrels (McInnes & Nettleton, 2005), and so despite the £1.1 million pledged to their conservation, red squirrels populations in northern England will continue to decline as a result of SQPV.

In the absence of SQPV, red and grey squirrels have been shown to coexist for many years (e.g. Harris, 1973/74; Bryce *et al.*, 2002). This is because in some habitats, grey squirrels do not have such a competitive advantage over red squirrels. Without SQPV and any grey squirrel intervention, it is probable that red squirrel populations would survive in areas where they have a greater competitive advantage over grey squirrels. Habitat is a key aspect to conserving red squirrels (Lurz *et al*., 1998), as they require a dependable seed supply (Lurz *et al*., 1998; 2000), which depends on tree composition (Lurz *et al*., 1998) and forest age structure (Gurnell & Pepper, 1993). To ensure a constant seed supply may mean altering felling patterns and forest design plans (Lurz *et al*., 2003). Red squirrels appear to have the ability to utilise production conifer plantations (Lurz *et al*., 2000), which presents a paradox, as the majority of commercial forestry in Britain comprises blanket, similar aged, non-native coniferous species with low biodiversity levels (Willis & Garrod, 1998). However, changes in management practises are being urged so that future plantations have higher biodiversity levels. These include recommendations such as leaving some stands to develop old-growth conditions (Fuller & Brown, 2003; Humphrey, 2005), increase structural diversity by leaving deadwood, increasing tree species composition, habitat restoration (e.g. to peatlands), mimicking natural disturbances regimes and using species of local genetic origin (see Quine, 2003). If such regimes are implemented, plantations may have great benefits to biodiversity (Humphrey *et al*., 2003), but without these changes, planting more monoculture plantation even to aid red squirrel conservation would be an ecological disaster.

Ecological replacement of red squirrels by greys is linked to the reduced ability of juvenile reds to be recruited in the population (Wauters & Gurnell, 1999; Wauters *et al*., 2000) and reduced fecundity, possibly through reduced breeding condition (Gurnell *et al*., 2004). Supplementary feeding of red squirrels may be one way to counteract this affect and so may help increase red squirrel persistence, particularly in deciduous woodland. This could only occur in the absence in SQPV, but this strategy could be useful if found to promote red squirrel population persistence.

OTHER ECOLOGICAL AND ECONOMIC IMPACTS OF GREY SQUIRRELS

Other negative impacts of grey squirrels: tree damage

Other than the well documented decline in red squirrels, grey squirrels are cited as having a major economic impact by damaging trees in commercial plantations. Much evidence supports the damage that grey squirrels can cause to woodland (Kenward, 1983); however, red squirrels are also known to causes significant damage to trees (Tittensor, 1970), to the extent they were considered a major pest prior to the introduction of grey squirrels (Ritchie, 1920). Both species (Table 3) and age of tree influences grey squirrel damage. The two primary species damaged across several studies were sycamore and beech; other species are attacked to varying degrees depending on site (Lawton & Rochford, 1999). Thin barked species of between 10 and 40 years are at particular risk (Kenward *et al*., 1988). Damage can result in loss of apical dominance, infection of wood through the wounds, loss of vigour or even death (Gurnell & Mayle, 2003). Several factors are known to affect the rate of damage. Juvenile squirrel density is correlated to bark stripping intensity (Kenward *et al*. 1988a), whilst tree quality gave the best correlation to damage levels (Kenward, 1989). The percentage ground cover (Kenward *et al*., 1991), number of seed bearing tree species (Kenward *et al*., 1988b) and growth rate of the attacked tree (Mountford & Peterken, 1999) are other important variables affecting level and intensity of grey squirrel damage. Damage is not linked to food availability (Kenward *et al*., 1988a). Identifying factors that can predict damage is of particular use in planning control strategies (Mayle *et al*., 2004). Current silviculture techniques may increase damage, as the choice of fast-growing species (Table 3) and growing trees close together encourages fast vertical growth, which all increase the susceptibility of woodlands to damage (Lawton, 2003).

Table 3. The percentage of stands of different species showing occurrence of damage (Mayle, 2003 cited in Huxley, 2003) in comparison to the percentage area of woodland in England (Forestry Commission, 2001)

Tree species	% stands showing damage	Area (% total woodland)
Sycamore	100	4.9
Beech	66	6.5
Oak	40	16.1
Ash	33	10.6
Lodgepole pine	33	-
Scots pine	16	-
Norway spruce	16	-
Larch	8	4.7
Sweet chestnut	8	-

The financial cost of grey squirrel damage is somewhat controversial and must be balanced against the costs of squirrel control over a long period. For example, Kenward & Dutton (1996) estimated the costs of moderate to severe squirrel damage to beech. Over an 85 year rotation this was estimated at £1700/ha (Kenward & Dutton, 1996). Considering that the main vulnerable age group is 10-40 year (Mayle *et al*., 2004), annual cost of damage works out at £57/ha/annum. Over the thirty year period, the cost of squirrel control with warfarin is considerably cheaper (Table 1), but only if it is sustained and totally eliminates damage. As a consequence, the costs of control may outweigh the benefits (Lawton & Rochford, 1999; Forestry Commission, 2006). If taken across all woodland in Britain, the cost of squirrel damage can be viewed as substantial (Huxley, 2003), but it is difficult to extrapolate financial losses over both a period of cropping and with variable damage intensity.

At present we know that the exact benefits of controlling grey squirrels can be highly variable. For example, both Mountford (1997) and Rayden & Savill (2004) cite continued tree damage despite grey squirrel control programs. Squirrel control may even increase damage to woods; agnostic behaviour is cited as one reason for squirrel damage and this is higher when populations are increasing or when large numbers of immigrants are moving into a vacant area, conditions that can be caused by culling of squirrels (Lawton & Rochford, 1999). There are two strategies to control grey squirrel damage: to control grey squirrel numbers or controlling the extent of the damage (Lawton & Rochford, 1999). To counteract the need for squirrel control, better use of silviculture techniques, including the selection of less susceptible species and reducing planting density, could greatly reduce squirrel damage, and so reduce both the need for continuous control, which in turn has considerable financial benefits. The only way to further understand this issue is to model the economic costs of grey squirrel damage, and the costs and benefits of different control strategies, both culling and habitat management.

Other negative impacts of grey squirrels: bird predation

Grey squirrels are often cited as predators of bird's eggs and fledglings (Monckton, 1991), yet proper quantitative data are lacking (Hewson & Fuller, 2003; Hewson *et al*., 2004) and the majority of evidence is anecdotal. A recent survey indicated that of eight woodland bird species showing declines, only two rarer species may have showed a decline related to grey squirrel abundance (Amar *et al*., 2006). However, this evidence cannot be directly linked to predation. Of the remaining six species, the authors suggested that changes in woodland stand structure, such as increased woodland age, reduction in active management and increased deer browsing, may be responsible for these declines (Amar *et al*., 2006). The focus on grey squirrels ignores the fact the red squirrels themselves are important predators of bird's nests both in urban (Jokimäki & Huhta, 2000) and rural environments (Nour *et al*., 1993). It has also been suggested that grey squirrels compete with hazel dormice (*Muscardinus avellanarius*) for food and woodland bats for resting sites (Hewson *et al*., 2004). However, direct evidence to support these hypotheses is absent. Both red and grey squirrels fill similar ecological niches; as a consequence it is likely that red squirrels too are important predators of bird's nests and competitors in the same way greys are. The focus on the negative aspects of grey squirrels ignores the same role played by the native red.

Positive impacts of grey squirrels

A survey in 2002 by The Mammal Society indicated that 45% of people liked grey squirrels whilst only 24% dislike grey squirrels (Fig. 1). Clearly, many people enjoy the grey squirrel as part of the environment (Mayle *et al.*, 2004), but outside any intrinsic value, there has been no direct focus on the role of grey squirrels as beneficial to the environment. Damage to trees can be beneficial (Forestry Commission, 2006), as wounding can provide habitat for saproxylic fungi and invertebrates, which in turn provide food for woodland birds. Trees killed by squirrel damage can also provide valuable nesting sites for a range of species. Deadwood is an important part of woodland biodiversity (Humphrey *et al*., 2002). Bark stripping in particular is focused on sycamores (Table 3), an invasive species (Royal Forestry Society, 2006). Grey squirrels may actually help control sycamore growth in some forests. The extent to which grey squirrels act as seed dispersers is unknown, though they excise the radicle of acorns, causing germination failure (Pigott *et al*. 1991); however, whether this alters the long term dynamics of woodland is unknown.

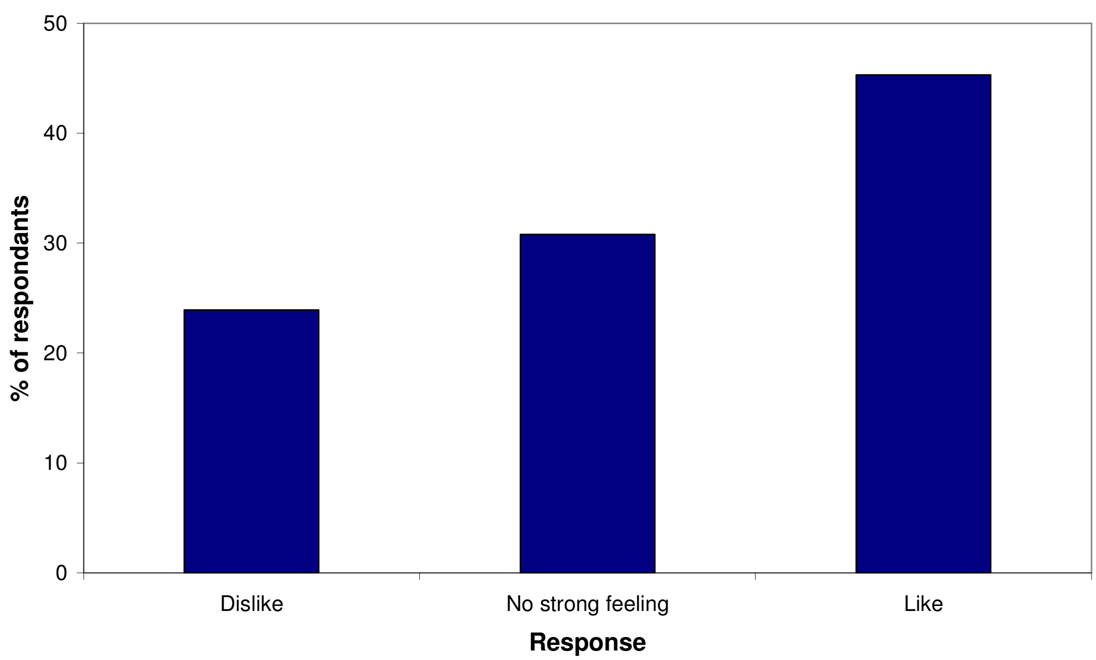

Figure 1. The percentage of respondents (n = 3606) who disliked, had no strong feeling, or liked grey squirrels, based on a scale of 1-10 (1-3: dislike; 4-7: no strong feeling; 8-10: like)(Baker & Harris, *unpublished data*)

WHAT ARE THE IMPACTS OF CULLING STRATEGIES ON GREY AND RED SQUIRRELS

The evidence as to whether grey squirrel culling benefits red squirrels is controversial. As has been shown on Angelsey, the removal of grey squirrels led to a population increase and recolonization of areas of the island by red squirrels (Shuttleworth *et al*., 2002). This contrasts with Thetford Forest, where long term trapping found no benefits to red squirrels (Gurnell *et al*., 1997; Gurnell & Steele, 2002); control strategies, although expensive, are predicted to allow red squirrel populations to persist (Rushton *et al*., 2002; 2006). However, the exact positive or negative affects of grey squirrel control is unclear. In American red squirrels (*Tamiasciurus hudsoncius*), removal of individuals led to immigration of males and female of breeding condition (Klenner, 1991). Ultimately immigration can compensate for culling losses e.g. in red foxes (*Vulpes vulpes*) (Baker & Harris, 2006). In addition, both the increase of reproductive individuals in an area, or overcompensation by a culled population, can lead to an increase in density (Choisy & Rohani, 2006) and associated tree damage.

Culling also has serious implications for the spread of disease; culling can ultimately increase the possibility of cross-species transmission (Donnelly *et al.,* 2003, 2005; Chisy & Rohani, 2006), by altering density or by disturbing population spatial structure (Tuyttens *et al*., 2000; Woodroffe *et al*., 2005). In the context of grey squirrels, increased culling could lead to greater movement of individuals which may increase the spread of SQPV to novel red squirrel populations.

HOW CAN WE CONSERVE RED SQUIRRELS?

Conserving red squirrels in Britain remains a challenge. There is no longer a ‘native’ red squirrel due to the frequent introductions from Europe and habitat defragmentation which has allowed gene flow between previously sub-divided populations. The red squirrel is widespread and common over much of its distribution (Lurz *et al*., 2005), and so it is questionable why such large sums of money should be spent conserving this species. Conservation effort on red squirrels in Britain is disproportionate to its importance in global conservation. Red squirrels can be reintroduced again to Britain, if an effective and humane way of reducing/eliminating grey squirrels is eventually found. There appears to be little evidence to support the benefits of culling grey squirrels for red squirrel conservation, particularly in the long-term. Grey squirrels cannot be exterminated from Britain by culling.

Previous attempts to control grey squirrels when grey squirrel distribution was markedly smaller did not stop or slow the spread. With SQPV and continued ecological replacement by grey squirrels, red squirrels will continue to decline in Britain.

Since culling is not a tactic that will benefit red squirrel populations, is long-term and costly, novel techniques need to be considered in grey squirrel population management for red squirrel conservation. Creating island refugia would ensure their persistence in Britain, while developing a SQPV vaccine would markedly slow population declines. A significant step forward would be to identify techniques that would lead to a decline in grey squirrel populations. These might include the release of a biological control agent or a= virus-vectored immunocontraceptive (VVIC), although currently prognosis for either technique is very low. Concern would be raised about transmission of a VVIC to red squirrels; however, even if red squirrels also became extinct along with greys, red squirrels could be reintroduced, as has happened in the past. Another possibility would be to examine ways of allowing red and grey squirrels to coexist.

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