people's trust for **endangered species**

The state of Britain's mammals

a focus on invasive species

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Cover image: grey squirrel Laurie Campbell, rabbits Dave Bevan

FOREWORD

The People's Trust for Endangered Species (PTES) has been funding and carrying out research and conservation work on endangered species around the world for over three decades. In that time we have devoted ever more of our efforts and funds to work here in the UK, in particular on our beleaguered mammal species. We no longer have the megafauna that draws people to Africa and Asia, and as an island the diversity of our animals is substantially less than on the continent. This is why it's even more important that we work now to ensure a future here for those species we do have. As we move into the second decade of the new millennium there is little respite for the natural world. The problems caused by habitat destruction and fragmentation are well documented and continue at an alarming rate. The changing climate will also have far-reaching impacts on many of our species and habitats, in particular those animals with more complex adaptations to life such as hibernation and migration. It is now more important than ever to consider the range of threats facing our biodiversity.

In 2000 PTES commissioned a report by David Macdonald and Fran Tattersall of WildCRU to document the state of Britain's mammals so that we had a clear picture of how all of our species were faring, and the challenges facing conservation, so we could better understand all the issues they faced. The report highlighted four key threats to our native animals: conflict with non-natives species, toxins and pollutants, disappearing and fragmenting habitats, and finally conflict with people. Now ten years on from the production of *Britain's Mammals: the challenge for conservation* PTES has commissioned this report to look in detail at the problems caused by invasive animals on our native mammal species. As highlighted in the report, two of our fastest declining mammal species are suffering from such a threat: water vole numbers have been decimated by predation from the voracious American mink, whilst the red squirrel has suffered numerous impacts at the hand of its American cousin, the grey squirrel. These impacts are compounded by the other issues laid out in the report, and resolving some of these may be the key to preventing the extinction of these two iconic species.

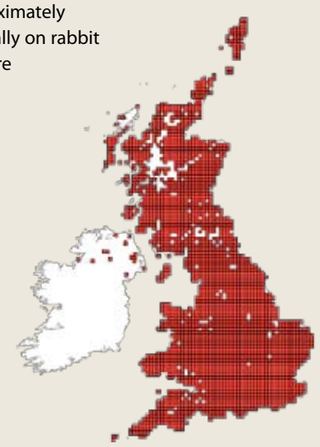
PTES is at the forefront of tackling these issues. Huge achievements have been made in the last decade: safe guarding key sites for water voles has proven to be an invaluable way of protecting whole populations from the American mink, whilst advances in the understanding of the squirrel poxvirus and buffering strategic woodlands for reds is helping protect them from the advancement of greys. However there is still much to do and this report helps to highlight where our efforts still need to be focused.

Jill Nelson
Chief Executive
People's Trust for Endangered Species

Rabbit *(Oryctolagus cuniculus)*
Rabbits, originating from the Iberian Peninsula, were introduced to the UK for meat and fur by the Normans in the 12th century, whence they have been transported widely, and with devastating consequences, to Australia and New Zealand[1]. Paradoxically, therefore, their status is to be endangered in their native range whilst constituting a pest in much of their introduced range – and, in the UK, to be both an agricultural pest and, in places, a conservation asset[2].

In the UK, rabbits are not only an important part of the prey base of native predators, for example buzzards[3], foxes, polecats and stoats[4], but also of the non-native invasive American mink, with the result that where rabbits sustain more abundant mink, water voles are further disadvantaged[5,6]. Rabbits are also vital ecosystem engineers whose grazing maintains calcareous grassland, dune and heathland habitats, and the often rare species that depend on them (e.g. the silver spotted skipper butterfly[7]).

Rabbit populations have fluctuated greatly in the past 60 years. The myxoma virus, introduced into Britain in the 1950s to control rabbits, resulted in 99% mortality[8], but a few survivors were resistant and their survival, along with a reduction in the virulence of the virus, enabled rabbit populations to recover widely, although generally not to their overall pre-1950 levels[9]. More recently rabbit haemorrhagic disease (RHD) arrived accidentally in Britain in 1994; the first outbreak was observed in China, but viral genetics suggests multiple origins of virulent forms[10] from harmless strains, as first proposed by Chasey & Trout (1995)[11]. Rabbits have recently become increasingly recognised as reservoirs of zoonotic disease for humans, such as E. coli VTEC[12], and livestock, including paratuberculosis[13]. Rabbits cause locally serious economic losses to forestry interests[14] while damage to the agricultural industry, totalling approximately £115M annually[15], represents the single biggest negative economic impact caused by wildlife in the UK. Evidence from several survey types suggests a decline in numbers since the 1990s of c.20% nationally[16]. Approximately £5M is spent annually on rabbit control and tools are available to ensure that management is cost-effective[17]. Landscape-scale control of rabbits may not be desirable for specific localities where their positive grazing effects are needed[2].



PREFACE

Many members of the public have heard that non-native introductions are an issue. There are cases, in Britain, where there is some consensus that the uninvited visitor is 'a bad thing', a generally sensible view occasionally stretched by value-laden innuendo, such as referring to grey squirrels as 'American tree rats'. But that same bushy-tailed visitor might be judged 'a good thing' by millions of suburban families enchanted by its acrobatics in park or garden. Grey squirrels, of course, are an economic pest (just as the much loved and lamented native red 'Squirrel Nutkin' had been before them). While the ethicist might struggle to see why it is meritorious to poison grey individuals but criminal to poison red ones, most people agree that, with hindsight, replacing a native pest of forestry with a non-native one was a mistake.

This one example – the squirrel dilemma – at once makes clear that the biology of invasions, itself technically complicated, is entrenched in economic and ethical challenges that thwart consistency and guarantee controversy: in short, a typical issue in conservation. So, when the People's Trust for Endangered Species invited us to focus this update on a single theme, we selected non-natives.

If the public is broadly aware that non-native species are problematic, what do biologists think? They too obviously see the error of shifting species to new homes where they become economic pests or threats to public health. But the reasons why biologists think such assisted passages are a mistake go further than such purely practical considerations. They are proximately to do with maintaining local biodiversity and community composition, but ultimately to do with leaving processes to run a course that is not man-made.

The greatest devastation a non-native species might wreak on native biodiversity is to cause extinctions, and fears of this possibility have been so clamourously repeated in the conservation literature that they have gained folkloric acceptance in everyday life. Non-natives are widely cited as the second greatest global threat of species extinction (following habitat loss), but this claim is exaggerated, having been passaged through countless Chinese whispers from a rather preliminary analysis that considered only the USA (and included the very special case of Hawaii)[18]. The generality is that most invasive species do not cause extinctions, or even devastate native biodiversity, but they do generally change things, often in ways that conservationists perceive as being not for the better, and which are tricky to manage, as will be made clear by the cases of non-native mammals in Britain that we will discuss in this report.

Of course, there's nothing unusual about one species being responsible for the movements of another: doubtless the first Smilodon to cross the Panamanian land bridge from North to South America took a whole community of fleas with it. Furthermore, nobody values any the less the beautiful and endangered island grey foxes of the Californian Channel Islands because their ancestors were transported there over 2 000 years ago in Amerindian canoes[19], any more than they discriminate between those red foxes in the USA whose ancestors evolved there, and those – now occupying much of the Eastern USA – whose ancestors were imported from Britain to the American colonies so that George Washington's generation could hunt them[20]. No, what biologists worry about is that the disruption that has always arisen through natural processes when an immigrant arrives has, recently, happened very often because of people.

Most discussion dodges the issue of how to define 'recently'! Suffice it to say that it lies somewhere between the time when, 4 000 years ago, early people paddled ancestral Asian dingoes to Australia (where, however much they may dislike them, few Australians would deny their Australianness), and around 1845 when colonists did much the same with British red foxes (whose Australianness every Australian would deny). There is an issue here about 'naturalness', touching on a profound question of whether people are part of Nature and, if not, when they stopped being so. Some biologists attach very high value to natural processes, especially as they determine the geographical ranges, and hence natural communities, of species. It is a moot point whether a wider public can be convinced to attach a similarly high value to this form of naturalness, in the context of the many other dimensions dictating how and why they value Nature.

Things seem set to worsen. The biogeographical fall-out of the inter-continental musical chairs now being catalysed by man-made climate change further complicates the consequences of species being redistributed as they leak from unprecedented global trade[21]. In China this has led to a tenfold increase in the number of invasive species between 1990-2005[22]. In the United States, 35% of vertebrate families in which there is live-trade are now established as introductions outside of their native range[23]. Natural communities may become more susceptible to invasions insofar as their resilience deteriorates under pressure from habitat loss, hunting and climate change.

These global concerns spawned the Invasive Species Specialist Group (ISSG) in 1994[24] and the Global Invasive Species Programme (GISP) in 1997[21]. In May 2008 Defra, the Scottish Executive and Welsh Assembly Government launched the Invasive Non Native Species (INNS) framework strategy for Britain to draw together the practicalities of prevention, detection and control of species introductions, and to foster public engagement on managing invasive species. Most (84%) respondents (not, of course, a random sample) were supportive of lethal control policies, particularly those that were designed to address health, native species or economic issues[25].

Several times already we have mentioned the public's view. This is because, while the introduction of non-native mammals may be a biodiversity issue, their removal will almost invariably include welfare issues and, in travelling the road from science to policy, will necessitate judgment. In that context the public's view will be decisive. So, in this personal perspective on introduced mammals in Britain, our purpose is not only to provide a ready reference for professionals (who should find all the key facts they might need between this one set of covers), but also to clarify the topic for an informed public. Paradoxically, this attempt at clarification involves revealing the issue to be bedevilled by hazy boundaries, value judgment and inconsistency. Is consistency important? Yes, but a lesson of this overview of non-native mammals in Britain is that they raise issues that defy any single or too formulaic solution – consistency is important, but judgment is more so.

David Macdonald and Dawn Burnham with Fly and Qara, brother and sister trainee wildlife detection dogs.

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Terry Whittaker

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INTRODUCTION

What is a non-native species?

Non-native animals and plants are those moved around the globe beyond their native range, either intentionally, or as an unexpected consequence of movement of people or products[25]. The consequences of such introductions vary from negligible to devastating. In the UK, 5% of all priority species with Biodiversity Action Plans (BAP) list non-natives as a threat (9% for vertebrates), and non-natives are identified as a threat to 32% of priority habitats.

Most of Britain's non-native mammals were brought here deliberately, giving contemporary conservationists pause to wonder which of their actions will be judged ludicrous, or perhaps improper, with hindsight. However, even the Victorian penchant for exotics – which added muntjac, sika and grey squirrels to our worries – had its gainsayers: in 1866 Krefft cautioned, '*The author protests against the wilful introduction of alien species without permission of competent authority*'[26]. Escapes continue – the red-necked wallabies of Derbyshire added marsupials to Britain's fauna (though they are now dying out there). Some were deliberate such as the release of 6 000 farmed mink liberated by animal rights activists from the New Forest in 1998. Many of these returned voluntarily to their cages, and most of the remainder doubtless starved, but the survivors bolstered the numbers that had already escaped causing a blight on native species. Overall, as this report concludes, non-native invasive species often damage and always alter native biodiversity, and these generalisations apply to Britain's non-native mammals.

Invasion terminology

The vocabulary of biological invasions blurs the technical and day-to-day usages of similar words (e.g. exotic, imported or alien), and can risk moralistic or jingoistic nuances[27, 28]. Equally there are no agreed measurements of the level of impact, or its type, other than it should be 'major', that an incoming species must exert on a community in order to be considered invasive. Only 10% of introduced species become established, and of those only 10% become pests[29]. However, that small percentage is not an inconsequential number of invasive species that can cause havoc within native ecosystems – the extinction risk caused by invasives may be second only to that of habitat destruction[30]. Non-native species have been introduced worldwide, including meadow grass to Antarctica[31] and some, like the house mouse, are distributed globally[32] (commensal rodents introduced to islands are implicated in the extinction of at least 11 small mammal species[33]).

Compared with natural colonizations or recolonizations that occur on an evolutionary and geological time scale, invasions are characterised by their speed. One recently proposed definition attempts to circumvent geographic boundaries and the degree of impact, by taking a mechanistic approach: '*A biological invasion consists of a species acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population*'[27]. This definition does not distinguish between native or non-native species, but is based purely on ecological processes in response to a change in (for natives) or of (for non-natives) the environment. For context, native mammals that might be considered invasive (and variously judged benign or malign by different people), insofar as a change in food availability has radically increased their abundance, include the badgers of agricultural pastures and the foxes of suburban gardens. However, this report focuses only on non-native species.

For the purpose of this report, in line with the Convention on Biological Diversity's[34] definition adopted by the European Alien Species Gateway[35] and the Global Invasive Species Database[36], we use invasive to mean those species whose arrival was mediated by humans (non-natives) and that produce undesirable impacts[37]. We also consider other categories of non-native mammals that, whilst considered substantially less harmful, certainly alter the natural British community; some of these may have the potential to become invasive.

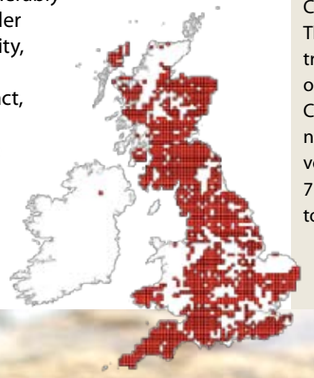
When are non-natives part of the natural community?

Some non-native British mammals arrived long ago, but for how long must a species be resident before it is accepted as part of the natural British community? Technically, ecologists refer to naturalized species meaning those non-natives that are established in the wild in self-sustaining and self-perpetuating numbers without support, and independent, of humans[38]. This ecological meaning is distinctly different to the colloquial usage that implies the acquisition of citizenship. Is the qualifying residency for ecological citizenship measured in years or generations, and is it affected by the extent to which they are a nuisance (either to people or to native biodiversity)? At what point is it no longer appropriate to attempt a non-natives control just on the grounds of its non-nativeness? Answers to none of these questions are clear from everyday attitudes to Britain's non-native mammals[25]. Fallow deer, brought to the UK by the Normans, are commonly treated as native, but lagging nearly a thousand years behind, muntjac are not. Most American mink in England probably descend from ancestors that have bred in the wild here for more than 50 generations, and there may have been closer to 150 generations of grey squirrels, but there are few calls to consider either as adopted natural members of the ecological community. The Romans brought rabbits to Britain deliberately (initially held captive in stone-walled leporaria, for the delicacy of their embryos – though it was not until the 12th century that they were free-living in England) as they did black rats, unwittingly; so both have been resident for at least as long as brown hares which were also introduced.

Inconsistency and prejudice are rife in media coverage of non-native species – as is muddled thinking (one example being to consider the cost of eradicating a species as part of the evidence that it is economically damaging). Conservationists too should be aware that inconsistencies may arise. The hatred focused on American mink eating Hebridean sea birds is relentless, while the protests at killing hedgehogs that do much the same – also introduced to the Hebrides – is passionate (see pages 20-21). The attitudes expressed about mammals, birds and even fish differ from those applied to various invertebrates.

The media, and even some biologists, are much more inclined to mention the non-native origins of some species than others (vide 'the American tree rat'), an instance of bio-xenophobia partly, but not wholly, influenced by the nuisance they are perceived to cause. There is an interesting distinction between whether that nuisance afflicts human (economic) wellbeing or native biodiversity[28]. The grey squirrel causes economic damage to forestry by bark-stripping, and severely threatens native red squirrels, through a combination of exploitation competition and disease. American mink have little economic impact, but have devastated populations of the native water vole and some birds. Mink have been in the UK for almost as long as grey squirrels (and may even be distributed as widely, having colonized Scotland as far north as the Great Glen). However, whereas many millions of people are charmed by the highly visible grey squirrels, almost nobody speaks up for the elusive (but deeply beautiful and marvellously adapted) mink.

We suggest that the decision to consider a naturalized non-native species as an ecological citizen hinges solely on the nature of the damage it causes to native biodiversity. For as long as that damage is judged intolerably undesirable then the intruder remains a pest to biodiversity, and efforts to remove it, or otherwise mitigate its impact, are justified indefinitely. There comes a point where a non-native has been exerting its influence on native biodiversity for so long that a new community has emerged,



Laurie Campbell

American mink *(Neovison vison)*

In response to demands created by the fashion industry, mink were imported from northern America to stock British fur farms in 1929[45]. Following numerous escapes they had become widely established in the wild across Britain by the 1970s[46]. Today, they are found from the south of England as far north as Ullapool and the Dornoch Firth in Scotland and on Harris and Lewis and the Uists in the Outer Hebrides. Signs found further north on the mainland may be from transient individuals[47,48]. The spread of mink in the UK may have been facilitated by the coincidental, but unrelated, reduction in their potential native competitors the otter (due to poisoning from environmental pollution and persecution) and the polecat (nearly hunted to extinction as vermin). Both polecats and otters are now increasing in the UK[9], but there is no evidence that the presence of a healthy otter population prevents mink from spreading. Although mink signs tend to decline where otters re-establish[49,50], mink can coexist with otters; seemingly by altering their behaviour in response to the presence of their competitors[51,52,53].

The mink's predatory adaptability has had detrimental consequences for British wildlife, most notably for water voles, and for island populations of ground-nesting birds[45]. The water vole has suffered a dramatic decline in numbers in the UK which can be attributed in large part to American mink, and the presence of this species is also considered inimical to the water voles' recovery[54]. In the uplands the spread of mink and impact on water voles is facilitated by the presence of rabbits in those prey-poor environments (giving rise to a pattern of apparent competition between water voles and rabbits[6]). Experimental studies have shown it is possible to control mink on short stretches of lowland river[55], and various removal projects have been undertaken for water vole protection (East Yorkshire; Cheshire; North Wales; Norfolk, Suffolk and Essex; Upper Thames; Somerset and Dorset[56]). Mink can be efficiently trapped (and humanely dispatched) using live traps on floating rafts designed by the Game and Wildlife Conservation Trust. In the Cairngorms National Park and northeast Scotland, major mink control efforts assisted by volunteers[57] have resulted in an area already exceeding 7 000 km^2 being mink free. American mink have not spread to the far north of Scotland, and genetic analysis has shown differentiation between populations in west and north-east Scotland suggesting that the Cairngorms form a barrier to dispersal, but that the Great Glen area acts as a corridor from west to east Scotland[58]. So, following methods used in the West Country by the Environment Agency and the British Association for Shooting and Conservation, a cordon sanitaire designed to halt their spread further north is underway. This involves monitoring and trapping along rivers and the coastline from Ullapool to the Dornoch Firth[47,57]).

American mink may be declining in their native range in Canada, and suggested explanations include interbreeding with feral captive mink (perhaps poorly adapted for survival in the wild) and over-hunting[59].




to which the intruder is integral so that it fulfils a functional role in the ecosystem. Its removal would no longer rescue or restore the original natural state. Then, from a biodiversity perspective, it may become fruitless to continue eradication attempts with the aspiration of ecosystem repair. At that point the intruder's origins alone no longer justify killing it. From a biodiversity standpoint, rabbits and hares fit this mould, as might fallow and roe deer (although their cases are complicated since both might be considered reintroductions – see pages 15 and 29). If the naturalized non-native causes economic or other damage to human wellbeing, then however long its tenure it will be considered a pest. To varying extents this is the case for rats, fallow deer, muntjac and edible dormice. Disentangling the impacts on people and nature provides a sensible (but not incontrovertible) argument for continuing the attempt to eradicate or manage some invasive mammals in Britain. This justification offers a rationale for taking action against mink in many parts of the UK, and grey squirrels (at least in Scotland) because they are non-natives *and* continuing to damage native biodiversity in ways that could still be halted and reversed *and* insofar as it is feasible to do so. In contrast, it would no longer seem sensible to kill rabbits on the grounds that they are non-native, although it is entirely understandable to do so where and when they are economic pests.

So, how long does it take to qualify for ecological citizenship? We suggest the answer is not measured in years or generations, but in the nature of the impacts and the feasibility of remediation. It could be foolishly purist to be relentless in postponing acceptance. Some non-natives devastate native biodiversity, but others are not malign, so there can be higher priorities for conservation than weeding them out, and worse outcomes than accepting a new member of the ecological community. Around the world, the balance of pros and cons falls in favour of some non-natives. For example, and perhaps illustrating the concept of an 'empty' niche, raccoon dogs so far appear to have fitted in alongside badgers and foxes in Finland. Indeed, and importantly, invasive species have fitted in so many places, increasing species diversity, that the notion that natural communities are generally saturated with species seems untenable, and furthermore, there is no evidence that species-rich environments are any more resistant to invasion than species-poor ones. The elephants of Sabah probably descend entirely from 17th century imports from Sumatra, but the Sabahans consider them a national treasure worthy of protection. On Guadeloupe endemic raccoons were recently found to have been introduced from the eastern USA in the past few centuries but they remain valued symbols of the local national park[39,40]. Even in the UK, we personally find it hard, on balance, to disguise our pleasure at seeing muntjac, or to feel too anxious about the spread of edible dormice!

When are introductions reintroductions?

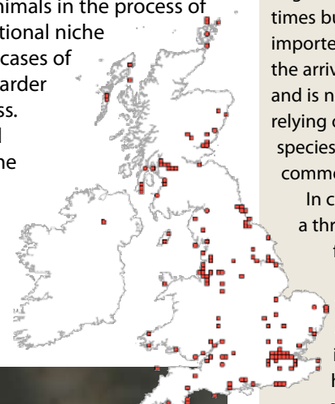
Another distinction that is less straightforward than it first appears is between introductions and reintroductions. Several British mammals have been exterminated during historical times and Article 22(a) of the European Habitats Directive makes it an obligation of member states to consider their reintroduction if species, as listed in Annex IV, are native to their territory where this might contribute to their conservation. Introduced species, in contrast, have no history here. This distinction, which leads to the simple judgment that from a biodiversity perspective, introductions are bad whereas reintroductions are good, also has blurry edges and we might ask for how long a species must be absent before it loses its native status?

One practical criterion might be whether there is still appropriate and sufficient habitat to support them. Beavers, for example, were last recorded in the Cronikils of Scotland by Hector Boece in 1526, whereas in England they were rare by the 10th century (although some say they may have survived until 1789)[41] – so they lost their foothold in the UK as long ago as brown rats gained theirs. There is thus consistency in continuing to call beavers native and brown rats non-native. Brown bears, lynx and wolves were largely gone by 3000bp, 450 and 1700, respectively; so if their re-entry tickets remain valid, does that mean that despite their 900-year residency, fallow deer remain non-native? Do elk, last resident in these Isles 10 000 years ago, retain their candidacy for reintroduction; and since fallow deer naturally became extinct during the last glaciation were the Romans introducing or reintroducing them? These remarks are not to display an obsession with consistency, but rather to raise a gentle alarm to the hazards of attempting too formulaic a set of definitions. Nonetheless, it is well to be alert to inconsistencies: the level of scrutiny brought to bear on proposals for a carefully managed return to Britain of beavers (a species generally rather liked in its Continental range) contrasts oddly with the slow-burning reaction to the escapes, and hence de facto reintroduction, of wild boar (generally loathed by Continental farmers).

Are feral domestics a special case?

A final hazy distinction lies between wild invasives and various feral domestics. Feral animals are those that have lapsed from domestic into wild[38]. Around the world, feral domestics threaten native biodiversity, by eating it, as do the feral goats, cats and dogs of the Galapagos, or by spreading infections (rabies outbreaks in wildlife are frequently caused by domestic dogs) or heavily selected genes. In Britain our nine million domestic cats were estimated to kill around 60 million mammals and 30 million birds during the course of a survey lasting no more than five months[42]. Ferrets and domestic cats are involved in another serious conservation issue, cross-breeding with native polecats and wildcats respectively. As a special case of invasions, how bad are domestic genes? They may disrupt adapted genomes, but their main threat is to the naturalness of evolutionary processes (see Issues page 24). Most conservationists would – rightly in our view – favour a stringent policy of killing feral domestics likely to cross-breed with wild relatives, but the difficulty of defining, genetically, Scottish wildcats[43] makes a quest for natural purity compromising (see page 22). There is also an ethical debate as to how the value of a wildcat's 'natural' life is measured relative to that of a domestic cat's 'feral' life (see pages 22-23). A certain degree of pragmatism seems legitimate – a flip of the Ice Age coin determined that no polecats colonized the Isle of Man, so we are not particularly exercised by the fact that feral ferrets have filled that niche, courtesy of humans. Indeed the heck cattle and Konik ponies of the Oostvardenplassen in the Netherlands are deliberately released as feral animals in the process of 'de-domestication' to fill a functional niche in a restored ecosystem[44]. The cases of commensal rodents are even harder to define in terms of naturalness. Both black and brown rats, and house mice, evolved without the compulsion to live and travel with people, but their natural range is defined by their hosts' range, making us question whether their travels with people should be defined as unnatural.

Dave Bevan



Dave Bevan

Brown rat *(Rattus norvegicus)*

Thought to originate from Asia, the brown rat was first recorded in England in 1720[9], presumably having arrived by ship. It is now widespread throughout the British Isles in both rural and urban areas, with only some coastal islands and mountains uncolonized. Brown rats are indisputably pests: they contaminate stored food products and carry infectious diseases, such as toxoplasmosis and cryptosporidiosis[60]. They may also damage seabird colonies, by destroying eggs and chicks and are pests of game-rearing. Their numbers are likely to be affected by climate change, because their survival increases in warmer springs. Improved over-winter survival is thought to have increased their impact on seabirds, which, in turn, is thought to have increased in recent years[61].

Rat populations can be managed by using rodenticides, lethal spring traps, cage traps then gassing with aluminium phosphide or shooting[62]. Reducing the availability of cover around farm buildings, where rats are commonly found helps reduce brown rat populations[63]. Use of rodenticides, particularly anticoagulants is common; however, individual rats that take only a sublethal dose become bait shy, and over time natural selection favours development of population-level genetic resistance to the most commonly used poisons. Collateral damage to other wildlife which can be poisoned via secondary poisoning or direct consumption is a special concern[64]. Brown rats have been eradicated from a number of islands around the UK to aid seabird conservation[65].

Black rat *(Rattus rattus)*

The black rat originated in Asia. It was introduced to England by the Romans, and possibly died out in Saxon times but has been present since the 10th century, imported by shipping. It was widespread in Britain before the arrival of the larger and more aggressive brown rat, and is now found only on islands and in mainland ports, relying on shipping for repeated introductions[66]. The species remains widespread worldwide and is much commoner than the brown rat in New Zealand[67].

In common with brown rats, black rats are considered a threat to seabird colonies and have been eradicated from Lundy[68] except on the Shiant Islands where little evidence for black rat predation on seabirds was found. Currently low numbers mean that any impacts of black rats are localised, and the improvements in the storage and transport of food has reduced immigration[66]. Now that these natural symbionts of man are rare in Britain there is some debate as to whether they should be eliminated or protected[9]. There is however, no British gene pool to conserve.

The black rat is generally outcompeted by the brown in temperate climates. It is possible that increasing temperature might favour the black rat, allowing it to expand its range in cities around ports at the expense of the brown rat.

An argument for elimination of invasive *R. rattus* (along with *R. exulans* and *R. norvegicus*) is the harm it causes to global biodiversity (especially on islands), although ranking the impacts of these three commensal rats is difficult[33].

BRITISH MAMMAL COMMUNITY

The British mammal community consists of around 66 wild resident species and seven feral domesticated species, with another 30 species (bats and marine species) that are considered occasional visitors[9]. The majority of residents consists of bats (16 species), rodents (14 species) and cetaceans (ten species). The bulk of mammal biomass in the British countryside is domestic stock (approximately 97%[69]). Such is their dominance that the maintenance of many plant communities of conservation concern (e.g. lowland moorland, chalk grassland, upland moorland) involves careful deployment of various domestic species.

The current mammal community contains fewer species than might have been expected from body weight to abundance relationships and, in particular, fewer carnivore species[9]. In the last 10 000 years, 12% of British mammals have been lost to extinction – most of them big (such as elk, reindeer, auroch) and including all three native large carnivores (brown bear, wolf, lynx). The loss of large carnivores may facilitate competitive release of smaller ones: for example, wolves kill foxes, but both foxes and the invasive American mink (which wolves also kill in their native range[70]), live free of wolf harassment in the UK. Substantial losses to the native British mammal community coupled with the loss of habitat for native mammals to agriculture (comprising around 75% of the UK land mass)[71], may have opened the door particularly to mammalian non-native invasions. (By the way, it has also facilitated increases in some native mammals – badgers are far more numerous on lowland British farmland than they are in the wild wood).

The precise number of non-native mammal species in Britain depends on some hazy distinctions. The purist might consider all those transported outside their natural geographical range to be non-native, irrespective of how long they've been here. In that case, Britain has 14 non-native mammalian species, of which five arrived about 1 000 years ago: rabbit, fallow deer, ship rat, house mouse, brown hare while the others arrived a hundred or so years ago: grey squirrel, American mink, sika and some roe deer, muntjac, Chinese water deer and edible dormouse, ferret and brown rat. Other recently introduced species have become established sufficiently to breed but are apparently not – at least, not yet – invasive: prairie dog, short-clawed otter and red-necked wallaby[72]. Raccoon, raccoon dog, skunk, coatimundi, chipmunk and sugar glider, all escape occasionally from captivity, but there is no evidence that they breed in the wild (some would include pumas and leopards on this list!)[72].

Although it might be argued that the Convention on Biological Diversity requires member states to monitor them (because how, otherwise, could they demonstrate delivery of the obligation to prevent their spread), the distribution and abundance of non-natives is not always well-known. Despite a succession of reports and proposals[73,74,75,76] the monitoring of British mammals in general, and of non-natives, including invasive species in particular, remains substantially ad hoc, undertaken largely by volunteer recorders[77]. A new public engagement project, Recording Invasive Species Counts (RISC)[37,39], launched on 22 March 2010, includes one mammal, muntjac, as one of six non-natives for public recording. Unusually, mink have been included in four systematic national surveys, largely piggy-backing on interest in otters[78] and the detailed data these provide highlight the value of proper monitoring[49]. The National Biodiversity Network (NBN)[79] Gateway holds records for many species which in turn inform the GB Non-Native Species Secretariat (NNSS), the European Alien Species Gateway[35] (DAISIE) and the Global Invasive Species Database (GISD)[36] (see table). For zoos, wildlife parks and animal sanctuaries, and licenses granted under the Dangerous Wild Animals Act, lists of the numbers of animals are held by the relevant local authorities but are not collated centrally[72]. If these, the non-native pet trade and the existing Natural England's Wildlife Management and Licensing Service for non-natives were included with the data coordinated by the NNSS, the risk of escapes and establishment of non-native species could be mapped centrally, along with other action directed towards non-native species in Britain.

Do mammals feature highly as invasives?

Of the 36 mammals listed as non-native invasives in GISD, the majority (32) were introduced intentionally and the remaining four are all commensal rodents. The reasons for introduction were varied (and often different for one species in separate locations) but many involved broadly economic aspirations (ten are feral domestics, five were introduced for fur farming, four as bio-control agents and two as laboratory animals which subsequently escaped). Direct releases into the wild were mainly for game and bio-control agents, or as fur bearing animals. Mammals have also been introduced for acclimatization, aesthetic and cultural reasons. Compared with other vertebrate species listed on GISD the 31% of mammals are the second most numerous invasives, outdone only by fish at 39%. Globally, deer contribute the highest proportion of invaders of the mammal families[80]. Fourteen mammal species feature on the GISD100 worst-invasive-species list[31], perhaps over-represented because their impacts on often beloved native mammals are so noticeable and because they are well studied (see table for UK offenders).

Once introduced, mammals appear more likely to be successful than other vertebrates. In Europe and

Dave Bevan

North America, of those species that survived the first difficult step of initial introduction, the percentage of introduced mammals that then became established was high (84.6% for Europe to North America and 77.8% for North America to Europe) compared with birds (27.05% and 28.6%) and, to a lesser extent, freshwater fish (58.3% and 63.2%)[81]. The introduction effort (propagule pressure) and human affiliation may both contribute to the success of mammalian invasions. Many mammal species are adaptable, especially those with a large native range and therefore wide environmental tolerances or an ability to use a wide range of resources[83]. At the time of introduction, being a generalist helps[82], as does originating from an area similar in climate to the new range[83]. Species traits also have an impact on the likelihood of a mammal becoming invasive. But traits that favour one stage of the invasion process may not favour another[84,85]. Herbivorous mammals have better odds of becoming successful as non-natives than do carnivorous ones; carnivory appears to be a hindrance at the introduction stage but thereafter offers better odds for establishment and spread[85].

INVASIVE MAMMALS IN THE UK

Species	Native range	UK origin	UK threat/ significance	Regulation/Legislation	TMP[A] 10 year trend	GISD[B] (UK Status)	DAISIE[C] (UK status)	GB[D] NNSS
American mink	North America	Fur farms 1929	Predates native water vole	WCA Schedule 9 and DIAA 1932	37% decline	Present/Controlled	Worst 100	yes
Ferret	Europe	Rabbit hunting 12th century	Hybridisation with polecat		-	Reported/Established	yes	-
Muntjac	China & Taiwan	Woburn Park 1901	Pests in conservation woodland	WCA Schedule 9	Increase 130%	-	yes	-
Japanese sika	Japan	ZSL 1860	Hybridization with red deer, impact on forestry	WCA Schedule 9	Increase 37%	-	Worst 100	yes
Chinese water deer	East China & Korea	Whipsnade 1929	Minimal impact; UK population may represent 10% of global population	WCA Schedule 9*		-	yes	-
Fallow deer	Anatolia	11th century Normans	Browse impact on woodland and arable damage		Stable (check with DI)	-	-	-
Grey squirrel	North America	Multiple introductions 1876	Competition & disease transmission to red squirrel	WCA Schedule 9 and DIAA 1932	Increase 49%	Worst 100	yes	yes
Edible dormouse	Europe & Anatolia	Tring 1902	Potential impact on forestry & nuisance to dwellings	Schedule 9 & 11(2) WCA	-	-	yes	-
Rabbit	Iberian peninsula	12th century Normans	Agricultural pest; prey to natives & ecosystem function for grazed calcareous grassland	Agriculture Act 1947, Pest Act 1954	31% to 38% decline	Worst 100	-	-
Brown rat	Asia	Shipping 1720	Pests to agriculture, health and native bird colonies		Increase 88%	Present/Controlled	Worst 100	-
Black rat	Asia	Romans	Rare in Britain	WCA Schedule 9	-	Eradicated(100)	-	-
House mouse	Africa and Asia	Iron Age (pre-Roman)	Pests to agriculture, health and native species		Stable	Worst 100	-	-
Brown hare	Europe	Romans	UK BAP species since 1995 - hare coursing illegal with dogs		Unclear trend	-	-	-
Feral cat	Eastern Mediterranean	Romans	Predators of native small mammals and birds		Decline 16%	Established (100)	-	-
Red-necked wallaby	South America & Tasmania	Whipsnade 1940s	Potential threat to capercaillie on Loch Lomond island	WCA Schedule 9	-	-	yes	-
Coypu	South Australia	Fur farms 1920s	Pre-eradication impacted on agriculture, waterways and marshland species	WCA Schedule 9** and DIAA 1932	-	-	- (Worst 100)	Eradicated

[A]TMP: Tracking Mammal Partnership (JNCC); [B]GISD: Global Invasive Species Database (ISSG, IUCN); [C]DAISIE: Delivering Alien Invasive Species Inventories for Europe; [D]NNSS: GB Non-Native Species Secretariat (Defra, Scottish Government, Welsh Assembly)
*Added to Shedule 9 Wildlife and Countryside Act 1981 from 6 April 2010 , **To be removed from WCA Shedule 9 from 6th April 2010, DIAA 1932 Destructive Imported Animals Act 1932




ECOLOGICAL EFFECTS OF INVASIVE SPECIES

The ecological effects of invasive species defy simple classification, but we group them here under five headings:

Predation

Globally, predation is the cause of about a third of the documented negative impacts of invasive mammals. Carnivores represent 19% of mammalian introductions but only 5% of mammalian species[86]. The interactions of non-native predators and their new prey are as varied as those between native predators and their prey. Whether they are problematic, limit their prey's populations or even threaten their extinction, depends on the pattern of prey mortality and its density dependence, which may vary from place to place; all of which makes generalisations and predictions difficult. Sometimes, however, the impact can be catastrophic. The Nile perch is famously responsible for the extinction of about 100 species of cichlid fish in Lake Victoria[87]. In Britain the invasive American mink has devastated the native water vole populations of lowland rivers. Water voles have no effective defence against American mink, their vulnerability worsened by the reduction, due to agriculture, of riverside habitat to narrow ribbons. Perhaps water voles will survive for long enough in the company of mink to evolve adaptations to cope with them as, apparently, red-legged frogs, *Rana aurora*, have to the arrival of bull frogs, *Rana catesbeiana*, in California[88].

As many as a quarter of mammalian invasions involve problems linked with herbivory and the consequent impacts on vegetation and soil stability and, thus, the native species depending on them. Feral goats have severely degraded the food supply for the Galapagos giant tortoise[89], whereas rabbit grazing precipitated a landslide which threatened Macquarie Island's largest king penguin colony[36]. Closer to home, grey squirrels cost the forestry industry around £10M per rotation in bark-stripping, and rabbits consume agricultural crops, raising the interesting point that it can pay farmers to foster foxes that eat rabbits[90].

Competition

Ecologists know that competition between species is difficult to demonstrate; however invasive species provide unwelcome but revealing experiments that elucidate the effects of both indirect 'exploitation' and direct 'interference' competition. Exploitation competition occurs when species' interactions are indirect, for example one species eats its rival out of house and home. A British example might be grey squirrels competing for tree seeds cached by reds in spring. Interference competition occurs through individuals interacting directly, members of one species diminishing the fitness – reproduction or even survival – of the other. The American mink provides a vivid example, but this time on the Continent, where it has caused a drastic decline of the native European mink, through intraguild (i.e. amongst species with similar ecological trades) competition[91]. In short, the invading American mink uses its greater bulk to attack and drive out the European mink. Though there is intraguild competition between American mink and the recovering otter population in the UK[53,92], it seems that behavioural adaptation by the mink may ameliorate the competition[52].

Sometimes it can be tricky to distinguish which type of competition – exploitation or interference, or both – is operating when a non-native species invades a community. On the Galapagos, for instance, at least four species of endemic rice rats appear to have been driven extinct by black rats[33] – invasive there as here. But was competition responsible? The answer was illuminated by the fascinating case of one native, the Santiago rice rat, that has survived alongside black rats introduced 300 years ago. A combination of experiments, some involving black rat removal and others providing supplementary food, teased out the conclusion that the black rats exerted interference competition, not exploitation competition, on the endemic Santiago rats[93,94]. Nonetheless, the Santiago rice rat may have survived by eating less preferred Opuntia cactus fruits, which black rats do not eat, to avoid encounters with black rats when breeding (a competitive refuge), and to survive the periods of scarce food in the dry season[95].

Disease

Sometimes considered as another form of indirect competition, infectious diseases transported by invasives that are relatively benign to them may have dire consequences when introduced to new communities. The grey squirrel not only competes with reds but also carries the squirrel poxvirus, which causes higher mortality rates in the red squirrel than it does in the greys[96]. Another British example, although not a mammalian one, concerns the signal crayfish, introduced from North America to Britain in 1976. By 1988 it had colonized more than 250 British waterways[97]. The invading signal crayfish frequently carry crayfish plague, *Aphanomyces astaci*, a fungus-like infection, to which they are highly resistant but which is lethal to all of the native European species, including the British white-clawed crayfish. These introduced crayfish illustrate again the multiple impacts of invasives, because even in populations in which the signal crayfish do not appear to be carrying the crayfish plague[98], the aggressive signals also oust the white-clawed crayfish[99] through interference competition, and they mate with them, preventing production of young white-clawed crayfish; and exploit the same foods in the same habitats. As they can reach a higher biomass in those habitats[100], they also have significant impacts on a wide range of other aquatic fauna and flora[101] (they are also heavily preyed upon by American mink, although whether this can limit their numbers is unknown).

Worldwide, a class of invasive mammals that often spreads infectious disease is domestic – for example, dogs spread distemper to the Serengeti's lions[102], and rabies to Ethiopian wolves[103]. In Britain, the brown rat is a reservoir for diverse parasites and pathogens that infect humans and domestic stock[104]. On the other hand invasives can sometimes act as alternative hosts for parasitic infections, thereby reducing the risk to native hosts through a dilution effect. Introduced bank voles in Ireland caused a decline in flea-transmitted *Bartonella haemoparasites* in native wood mice[105].

Hybridization

When natural geographical barriers to isolation are removed, populations of native species can be threatened by hybridization or cross-breeding with closely related introduced species. The most notorious example in Britain is probably the case of the American ruddy duck that first escaped private collections in 1965, and spread throughout Europe, posing a serious threat to its endangered, native relative, the white-faced duck in Spain. By 2000 an estimated population of 6 000 ruddy duck had become invasive in Britain, but an ongoing programme of control has reduced this figure to less than 500 birds. There are now at least 15 countries in the Western Palaearctic taking actions to control ruddy duck populations[35]. A mammalian example is the hybridization between red deer and sika[106]. Hybrids are fertile, and further hybridization or back-crossing to either parental type is rapid, threatening the genetic integrity of the native species.

Two other British cases involve cross-breeding with domestic species. The recovery of the polecat was jeopardised by cross-breeding with feral ferrets, though indications are that true polecats have the competitive edge. Perhaps the most catastrophic example is the threat that cross-breeding with domestic cats poses to the Scottish wildcat[43] (see pages 22-23).

Ecosystem

Some invasions affect entire ecosystems and upset a large fraction of the biological community. Predation on seabirds by introduced rats on offshore islands in New Zealand reduced the fertility of forest soil by disrupting sea-to-land nutrient transport by seabirds. This affected both organisms below and above ground, including plants and the ecosystem processes that the latter drive[107].

An interesting example in the context of the reintroduction of European beavers to Scotland[108,109] is the case of invasive North American beavers on Tierra del Fuego. Now numbering 50 000 they were introduced in 1946 and have changed the vegetation of upland stream valleys from Nothofagus (beech) forest to grass and sedge dominated meadows[110].


Eliana Sevianu

Edible dormouse *(Glis glis)*

Considered a delicacy by the Romans, who kept them in charmingly-named gliraria, the edible dormouse is naturally found throughout Europe into northern Spain to the west and into Russia in the east, reaching as far as Turkmenistan, northern Turkey and northern Iran and some Mediterranean islands[111]. It may be declining in the northern parts of its range, but to the south it is considered an agricultural pest in years of peak abundance. The UK's population of edible dormice was established in 1902 in Tring, Hertfordshire having escaped from a private wildlife collection. The population is thought to number between 10 000 and 30 000 individuals, currently restricted to the Chilterns, where the species can be locally very common and is thought to be gradually expanding its range[9]. Illegal translocations have resulted in recent records from Dorset, Hampshire and Essex. Edible dormice are economically significant, stripping bark in woodlands, damaging forestry and fruit crops and, indoors, chewing wood and wiring[112], triggering alarm systems and causing general nuisance.

The edible dormouse is listed on Schedule 9 of the Wildlife and Countryside Act, making it illegal to release any captured individuals without a licence. While certain methods of killing the edible dormouse are prohibited under Section 11 (2) of the Wildlife and Countryside Act (e.g. snaring, poisoning, using crossbow, explosive or electrical devices), a general licence is available to kill them using live-traps and humane dispatch or spring traps, if they are causing public health problems or serious damage to orchards or forestry. Since 2002, 67 licences have been granted, affecting 3 673 individual dormice. Most (65) were issued for preserving pubic health and safety whilst two licences, (involving 525 animals) were for scientific research. As yet, there have been no applications for licences for preventing serious damage to growing timber. Nest tubes are an alternative trapping method[113].

The edible dormouse is amongst the species whose range may expand if climate change leads to warmer springs[114]. Range expansion is currently limited in the UK by habitat constraints, but since translocations bypass these, expansion is likely to be due to human intervention. The species undergoes periodic failure to breed (particularly in poor mast years), balanced by having a long life (at least nine years). A population studied near Tring has increased exponentially in the last five years[115].




COMMUNITIES AND PRINCIPLES

The natural behaviour of unnatural communities

In natural communities new species arrive via dispersal, including the axiomatic case of fleas upon the backs of yet larger fleas. The process is no different in principle for non-native species except that it is, metaphorically at least, on the backs of people that they are transported. If the process of transportation by people is simply a metaphor for dispersal, albeit an accelerated one, is there anything fundamentally different in the ways that non-native species interact with ecological communities, that distinguishes them from interactions within native communities? The short answer is no – the same ecological principles apply (although non-native species do offer revealing, if unwelcome, 'experiments' in how ecological principles work). What differs is the desired outcomes. Conservation biologists are often keen to sustain or increase the numbers of native species, and to reduce, or eradicate, non-natives. In this respect, however, there is no difference in principle between non-natives and any other category judged to be at the undesirable end of the asset/pest continuum.

Not only do introduced species interact with native ones, but through successive invasions they interact with each other in newly assembled communities that have their own dynamics. This complicates the Convention on Biological Diversity Article 8(h) which calls for the control of introduced species within the context of natural ecosystems and their restoration. For example, dingoes, themselves originally introduced into Australia, currently deliver a net conservation benefit by eating other invasive species[116] (with the added complication that dingoes are threatened by feral dog hybridization[117]). Similarly, there is a complex network of competition between the several deer species introduced to the UK. Removing an invader may trigger a 'surprise effect' – i.e. the rapid increase of hitherto unnoticed species[118].

Invasion principles

Why do some species become invasive? One of many ideas is the 'enemy-release' hypothesis[119] which is that in their new surroundings, invasive species are freed from control by their natural enemies. This plausibly explains why rabbits (and house mice) reach plague numbers in New Zealand where invasives have exterminated half the native birds since 1200 AD[120]. The removal of large native predators may, similarly, trigger 'meso-predator release'[116] including, for example, the feral cats whose proliferation decreased the diversity of scrubland birds in Californian sage-scrub[121]. Turning this phenomenon on its head, the introduction of a new prey species can lead to an increase in native predators which then impacts native prey through 'hyper-predation' as illustrated by the increase in Californian garter snakes, fuelled by introduced fish, which over-hunt the native cascades frog[122]. A similar imbalance – called competitive release – occurs if the control of one competitor produces advantages for its rivals[123]. Thus, on Santiago Island, Galapagos, removing invasive black rats led to an increase in house mouse numbers[94].

This example, as correctly anticipated in Jared Diamond's *Evil Quartet*, illustrates cascading secondary effects. The red and fallow deer, introduced in the 1920s to Argentina's Nahuel Huapi National Park, browse native trees heavily, reducing their abundance, thereby benefiting exotic trees[124] – a succession where one invasion leads to another and so forth precipitating 'invasional meltdown'[125]. All these ecological phenomena can be illustrated by non-native species, but each operates equally within natural communities, just as the biology of natural colonists mirrors that of introduced ones. In terms of species, as distinct from system, attributes that might favour invasions[126], reported that non-native birds had relatively larger brains than did natives – this attribute may be associated with a capacity to adapt to novel environments, whether at home or abroad.


Dave Bevan

One plausible generalisation for which environments are more prone to invasion is that incomers are more likely to gain a foothold in environments where resource availability fluctuates[127] (an idea, at the level of community composition, that has parallels with the Resource Dispersion Hypothesis at the level of social group composition[128]). Are islands particularly prone to invasion, as Charles Elton[129] (1958), Oxford's founding father of ecology, believed? Maybe, but no relationship was found between land mass size and the success of mammalian, or avian, establishment[130]. Nonetheless, the perception that islands are particularly vulnerable to invasions[131] is painfully illustrated by New Zealand where invasives have contributed to the extinction of half of the breeding bird fauna[132]. British colonists selected 'innoxious' species from home to aid their own acclimatization[133]; in a sphere not short of irony, it is noteworthy that one of these, the rabbit, was itself an invasive non-native to Britain.


Laurie Campbell


Dave Bevan

Chinese water deer *(Hydropotes inermis)*

Native to East China and Korea, Chinese water deer were brought to London Zoo in 1873. Wild populations have been established from escapes from Whipsnade Zoo in 1929 and Woburn Abbey, along with deliberate releases. There are now populations scattered through East Anglia, with strongholds around Woburn Park, Whipsnade Zoo and in the Norfolk Broads[134]. Their numbers are steadily rising, from around 650 in the 1990s to 1 500 in 2004 increasing at 2% per annum between 1972 and 2002, and more rapidly around the Norfolk Broads[135]. They occupy grassland, arable, reeds, scrub and woodlands, but prefer wet areas[134].

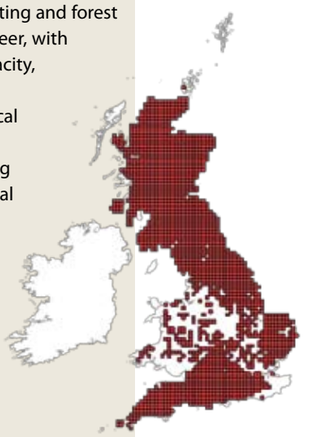
There is scant evidence that Chinese water deer cause problems – they occur at low population densities and eat herbs, sedges, reeds and woody browse species such as bramble, rather than agricultural crops and commercial forest species[134]. They may suffer competition from muntjac.

In its native range, the Chinese water deer is rare, assessed as 'Vulnerable' on the IUCN Red List; and may have declined by as much as 30% in the last 20 years. The species is threatened by poaching, habitat loss and environmental change[136]. The introduced UK population may represent as much as 10% of the global population[134], and the UK is the only place in the world where it is legal to hunt them. However, Chinese water deer have the potential for more rapid population growth than do other deer, because they have a short gestation period, large litter size, reduced suckling phase, rapid body growth and early sexual maturity[137].

At their current densities, Chinese water deer appear not to cause significant damage, and can be managed by fencing[134]. They are recorded in 0.6% of DVCs in England with a financial cost estimated at £30 000 - £40 000[138].

Roe deer *(Capreolus capreolus)*

Although often considered as native[135,139,140], the purist can maintain that roe deer are native only in Scotland, since they were reintroduced to England from Continental stock in the 19th Century after having been extirpated there in the 18th Century (probably due to over-hunting and forest loss). Roe are the most widespread British deer, with an expanding population[135]. With their capacity, in the right conditions, to bear triplets, roe have a high potential for range and numerical expansion[141]. They are commonly found in woodlands and also deep heather, spreading in recent years to open scrub and agricultural land[142]. They cause damage in orchards and to other horticultural crops, in coppice woodlands and in forestry plantations[143]. Roe deer are currently culled both as a management policy to reduce damage but also as a game species. Roe are involved in approximately 9% of recorded DVCs per year, with a potential economic cost of around £6M[138].



PREVENTION AND PREDICTION

Although the risks of introducing species are well documented, globalisation and irresponsibility combine to ensure that the threat of further introductions – both deliberate and accidental – remains high. International transport is increasing – the value of UK trade imports in 2008 had more than trebled to £344 818M from £102 264M in 1988[144] – and with it the opportunity for introducing non-natives (although these trends doubtless differ between taxa, and tightened regulation and heightened awareness may mean that introductions of non-native mammals will diminish). In general, there is evidence that introductions from Europe to America have peaked, and may be declining, while the flow in the other direction may not[81], and other routes are becoming more important – e.g. from Asia. For mammals, conduits include intentional importation for the pet trade. Obviously prevention is better than cure[34,145]. One approach would be to devise a code of conduct for each of the major introduction pathways to the UK[146]. Approaches include 'white' and 'black' lists. New Zealand and Australia operate a 'white list' of the only species whose live import is approved[147]. A black list enumerates species banned from import, which includes all the obvious candidates such as any species of mink, squirrel, fox and mongoose[148].

In the UK, the GB Non-Native Species Risk Analysis Mechanism (established in December 2006) is used to aid prioritisation of resources, to help enable effective rapid responses and for underpinning decision-making. This mechanism involves risk assessments on non-native species carried out by independent experts, reviewed by the Non-Native Risk Analysis Panel (NNRAP) and open for public comment. Increasingly, risk evaluations and planned strategies need to anticipate climate change[149]. Altered environmental conditions may change the competitive relationship between species or increase the chance of survival for escapees and accidental releases.

Terry Whittaker

The financial costs of managing invasives is potentially huge – there are 10 822 species listed on the European Invasive Species Gateway (DAISIE), and about 10% of those have significant ecological impact – already costing the EU a minimum of 12 billion euros per year[150]. Some have suggested using the 'Polluter Pays' approach[151,152], charging fees to those linked to intercontinental introduction pathways, either by owning or travelling on vessels, or receiving or importing live animals and plants. The idea is that these fees could fund preventative and capacity-building measures, and administration (for example by World Trade Organisation, Convention on Biological Diversity and International Plant Protection Convention). A nice idea in theory, but in practice attributing blame would be a huge challenge.

So, is it possible to predict whether a particular mammalian species is likely to become invasive, or even to establish a foothold? Yes – kind of! First, basic probabilities affect the outcome, so that all else being equal, the greater the number of introduction episodes, and the greater the numbers of individuals introduced (i.e. 'the propagule effect'), the greater the likelihood of that species establishing. However, even a few individuals can seed an invasion: only seven and eight individuals, respectively, established populations of sambar and hog deer in Victoria, Australia[83,153] and four sika established the Powerscourt Park herd in Ireland (see column right). Second, the species' life-history will affect its capacity as an invader: assuming the right match of climate and resources, an invader must have the ability to increase its numbers from an initial condition of being rare. An obvious prerequisite is that birth rate exceed death rate in its new home, a consideration which focuses the attention of biologists on density-dependent mortality, which is likely to vary with circumstances. Indeed, even in principle, species traits alone are poor predictors of the likely outcome; because circumstances vary so widely (e.g. the niches of local competition and enemies can all shift in largely unpredictable ways with the invader's arrival[154]). The invasion pressure (IP) model incorporates the number of propagules (i.e. potentially reproductive individuals) and the probability that a propagule will establish. It can be graphically expressed as an 'invasion cliff', with lowland where invasion is unlikely and highland where invasion is almost certain, separated by a tipping point. The cliff effect helps explain time lags in spreading, invasion irruption and collapses, and why invasions are so difficult to predict[127]. Case studies, and the opinions of experienced biologists help in predicting which species are the biggest risks, and computer simulations offer a way of predicting how an invader might spread (species with extensive natural ranges tend, as invaders to be widespread too[127]). For example, so-called diffusion models take account of the initial location, speed and direction of simulated invasions across patchy landscapes, and may help planners anticipate the most effective control strategy[155]. Perhaps the most reliable guide to the risk posed by a newcomer is its track-record: if a species is a pest elsewhere, then it is more likely to be a pest in a new setting.

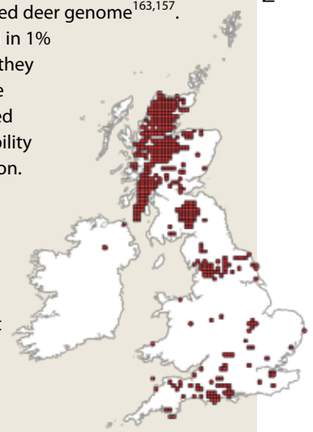
Laurie Campbell

Sika *(Cervus nippon)*

Two of the 13 extant subspecies of sika – the larger *C. n. hortulorum* found on mainland Asia and the smaller Japanese sika (*C. n. nippon* – one of six subspecies found in Japan) – have become widely established in Europe with self-sustaining populations found in Austria, Germany, Czech Republic, Denmark, France, Poland and Switzerland[156]; however, only *Cervus n. nippo*n is widely established in the UK[157], and genetic evidence indicates that sika in Britain are closely related to the native populations of Kyushu in the Nagasaki region of Japan[158]. The first sika – of both subspecies – recorded in Britain were presented to the Zoological Society of London in 1860[159]. Subsequently, parks were stocked with sika until the 1930s, many derived from the Powerscourt Park herd in Ireland, established in 1860 with four individuals. Inevitably releases and escapes led to established feral populations throughout the British Isles[159]. Studies from 1972 to 2002 suggested that sika populations were expanding then at 5.3% per annum[135]. They favour deciduous or mixed woodlands, and sometimes acid heaths[159,140], but in Scotland they often inhabit commercial conifer plantations, hence some peoples' confusion in calling them 'sitka'.

Sika 'bole score', scraping their antlers down tree trunks during the breeding season[143], causing economic impact on commercial forestry[157]. In Japan, sika are considered to be forestry and agricultural pests[160]. Hybridization between sika and red deer is a serious concern to conservationists. In 1972 sika occupied 7% of red deer range and by 2002 36% of red deer range[135]. However, despite widespread hybridization, sika and reds remain genetically distinct (e.g. in the New Forest[161] and Kintyre[106]). Senn and Pemberton (2009) suggest that in a hybrid swarm in Kintyre there has been breakdown of assortive mating (i.e. the tendency of red and sika to breed true. Hybridization is resulting in phenotypic changes producing red-like and sika-like deer[162]).

In the New Forest, culling is targeted to prevent increasing overlap between red deer and sika, but in Scotland, where this may be too late, island refugia have been established to conserve the red deer genome[163,157]. Sika are recorded in 1% of DVCs, though they are thought to be under-represented due to the possibility of misidentification. Around 75% of sika DVCs occur in Scotland, the rest in England, at an estimated economic impact of £50 000 - £80 000 per year[138].



REGULATION

Since 1993 the Convention on Biological Diversity (CBD) became, and remains, the primary global mechanism for environmental regulation. Under Article 8(h) of the CBD, signatories are required to prevent the introduction of, and to control or eradicate those, alien species which threaten ecosystems, habitats or species. The CBD (COP 6, Decision VI/23)[34] lists fifteen guiding principles, all in accordance with the precautionary approach: states should seek to pre-empt and minimize the risks to other states, undertake research and monitoring, and promote education and public awareness of invasive alien species. Prevention principles involve border control and quarantine measures, the exchange of information and the cooperation of states in areas such as agreements on trade regulation and capacity-building for shared technology or training programmes. The intentional introduction of species should be permitted only where they have been proven not to threaten biological diversity, and unintentional introduction pathways should be closely regulated, particularly in risky sectors such as shipping and horticulture. Techniques used for eradication, containment or control should be safe to humans, the environment and agriculture as well as ethically acceptable to stakeholders in the areas affected by the invasive alien species. The three-stage hierarchical approach advocates that:

- prevention is more cost effective and desirable than cure
- priority should be given to prevention, otherwise eradication should be attempted if it is feasible
- if eradication is unfeasible, the next priority is for long-term containment and associated control measures.

In line with the CBD, the Invasive Non-native Species Framework Strategy for Great Britain adopts this hierarchy, and emphasises prevention[145]. It also specifies, as a key action, the development of legislative proposals to provide a more comprehensive framework for dealing with invasive species[145]. So far a frustrating limitation to control schemes has been the lack of powers of access to private land that might harbour invasives.

UK legislation relevant to invasive mammals hinges principally on Section 14 of The Wildlife and Countryside Act (WCA) (1981). This makes it illegal to allow any animal which is not ordinarily resident in Great Britain, or which is listed on Schedule 9, to escape into the wild, or to be released into the wild. Offences under section 14 carry a maximum penalty of a £5 000 fine (£40 000 in Scotland) and/or six months imprisonment. Schedule 9 of the WCA is currently under review in Scotland, and Defra intends to review it for England and Wales shortly. The Nature Conservation (Scotland) Act 2004 increases control of WCA Schedule 9 species to include hybrids, and Section 13 provides a new power to Ministers to restrict trade and transport and possession of listed species.

Section 50 of the Natural Environment and Rural Communities (NERC) Act (2006) allows authorities to ban the sale of invasive non-native species known to cause damage, in England and Wales, and Section 51 issues the codes of practice which can be used in a court of law to demonstrate that the defendant failed to take the necessary precautions (or show due diligence) to prevent damage caused by release of non-native species.

The Scottish Government is currently reviewing the consultation exercise on its intended Wildlife and Natural Environment Bill that includes legislation to prevent release, and powers to control, invasive non-native species. It also recommends increased protection against such species through secondary legislation.

The Destructive Imported Animals Act (1932) restricts the import and keeping of certain mammals including muskrat, coypu, grey squirrel, mink, arctic fox and 'non-indigenous' rabbits. The Dangerous Wild Animals Act (1976) regulates the keeping of dangerous animals as pets by private individuals. Licences are granted if the local authority is satisfied that it would not be contrary to public interest on the grounds of safety or nuisance, that the applicant is a suitable person, and that the animal is kept in adequate and secure accommodation. The local authority is entitled to specify where and how an animal is kept. The Countryside and Rights of Way Act (2000) adds Section 19ZA of the WCA giving wildlife inspectors the power to enter any premises (except dwellings) to ascertain whether an offence has been committed, and section 19ZB gives police officers and wildlife inspectors the power to obtain a blood or tissue sample from a specimen to be used for analysis (including DNA analysis) to determine the identity or ancestry of the specimen. Dangerous captive species are regulated by the Zoos Licensing Act (1981) and pet animal trade is licensed by the Pet Animals Act (1951).

The European Strategy on Invasive Alien Species was developed in 2003 under the Bern Convention. Current legislation for the control of non-native species is under The Convention on the Conservation of European Wildlife and Natural Habitats Article 11(2)(b). Article 22 of the Directive on the Conservation of natural habitats and of wild fauna and flora (EC Habitats Directive) requires member states to 'ensure that the *deliberate* introduction into the wild of any species which is not native to their territory is regulated so as not to prejudice natural habitats within their natural range or the wild native fauna and flora and, if they consider it necessary, prohibit such introduction.' Despite the focus of the CBD, and the added provisions of numerous international agreements, international standards regarding invasive animals remain incomplete and inconsistent (as is true also for plants), especially for those that are not pests of plants under the International Plant Protection Convention (IPPC)[147]. The IPPC has been in force since 1952, to prevent the spread of plant pests and has 111 governments as Contracting Parties. It was extensively revised in 1997 in order to ensure, amongst other things, that internationally traded food is safe; and to prevent the spread of animal and plant diseases[164]. While this does not specifically consider the problem of invasive animals, the general provisions in relation to risk assessment and determination of the appropriate levels of sanitary protection can be used as a fall back position where no other legislation applies[147]. Furthermore, the IPPC has pioneered thinking about risk analysis for invasives, and ideas developed for plants can be applied more broadly. The Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES)[165] legislation may also be a useful instrument for the control of invasive animals. Originally conceived to ensure that international trade of wild animals and plants did not threaten their survival in the wild[165], this legislation is used to prevent movement of endangered mammal species but could be adapted to prevent movement of putative invasive species (and already has provision under Article 4(6)(d) to regulate the sale and import of species which present a threat to native species). A major strength of CITES legislation is that it has teeth – including the power of confiscation[147].

Dave Bevan

Dave Bevan

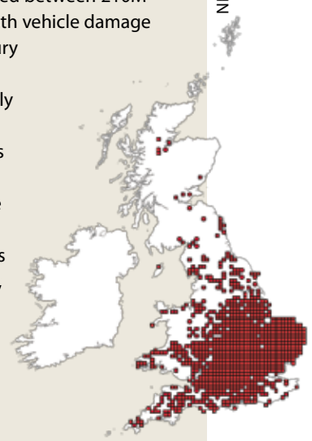
Muntjac *(Muntiacus reevesi)*

Muntjac are native to China and Taiwan[166]. The first wild population of muntjac in the UK was released from Woburn Park in Bedfordshire in 1901[166]. Further deliberate introductions occurred in the 1930s and 1940s in southern counties including Oxfordshire, Warwickshire and the Norfolk/Suffolk borders[166]. At an annual rate of increase of 8.2% muntjac have been expanding their distribution the most rapidly of all introduced and native deer[135].

Muntjac mainly occur in woodland and scrub[9] but are versatile, avoiding only marginal uplands[166]. Their main food is browse, supplemented seasonally with fruits and grasses or herbs. Muntjac do little harm to agriculture[144], but do damage coppiced woodlands and woodland ground flora[167],where they may induce an increase in unpalatable species such as grasses and sedges, with knock-on effects on invertebrates. These impacts may be positive, for example for those Lepidoptera which use grasses[168], or negative, such as the removal of honeysuckle leaves that provide egg-laying sites for the white admiral[169]. Their impact on woodland may also have negative repercussions for woodland songbirds[170] and some gardeners consider them pests[166].

Muntjac habitat use is similar to that of other deer, particularly roe, which also eat bramble[171]. Chapman *et al.* (1993)[172] found that roe deer numbers declined in forests where muntjac had increased. Hemami (2003)[139] noted that the body weight and fertility of roe deer decreased during the previous two decades at the same time that muntjac numbers rose. There is similar evidence for Chinese water deer, which also eat bramble in autumn and winter[136,173]. One hypothesis is that muntjac are limited by winter food, as may generally be the case for British deer.

Like other deer, muntjac can be managed by preventing access (by using fences, repellents or tree guards) or by lethal control[174]. As muntjac have no defined breeding season there are welfare issues associated with shooting females which may have young at foot, though they are increasingly sought after by US and European hunters. Road traffic accidents involve up to 74 000 deer each year[138], with muntjac contributing around 22%, almost exclusively in England. The economic impact of these is estimated between £10M and £16M in both vehicle damage and human injury costs per year, though generally DVCs involving muntjac are less likely to cause serious damage or injury than similar collisions with other deer, due to their comparatively small size.






HIGHLAND CLEARANCES

The Highlands of Scotland enshrine wilderness in Britain but also, less happily, are the stage for some of the most troubling problems with invasive mammals. Here, we highlight two cases – hedgehogs and wildcats - which further exacerbate the scientific and ethical dilemmas.

HEDGEHOGS

Amongst Britain's internationally recognised biodiversity assets, and responsibilities, are the breeding sites of wading birds on North Uist, Benbecula and South Uist (collectively, the Uists) in the Outer Hebrides. Many of the nesting areas are Sites of Special Scientific Interest (Wildlife and Countryside Act) and include about 7 000 hectares of Special Protection Areas (SPA, EC Birds Directive). A survey in 1983[175] estimated that these islands supported 17 000 pairs of nesting waders, including 25% of the total UK breeding population of dunlin and ringed plover; along with snipe, redshank, lapwing and oystercatcher. Originally, Uists' birds had been spared the attention of mammalian predators, although latterly there may have been impacts of feral ferrets (that probably exterminated ptarmigan on Harris) brought to the outer Hebrides in the early 1900s to control the rabbits imported during the 17th century; they were joined by brown rats possibly in the 19th century; and American mink, first reported on Lewis in 1969[38]. 1974 saw the foolish introduction of four hedgehogs – reputedly with the aim that they would control garden slugs[176] (hedgehogs had previously been transported around several Hebridean and Orkney islands). The Uist hogs multiplied, spreading 1-2km pa – leading to an estimated 6 500 on South Uist and Benbecula by 2000[177], whereupon their numbers stabilized – seemingly limited for the next decade by density-independent factors such as harsh winters[178]. An estimated 350 had colonized North Uist by 2005. Exactly how many hogs there are, or have been, in the Uists is hard to say. Estimates have fluctuated from a pessimistic 10 000 in 2003[179], to, most recently, c.2 750 (+/- 800) adults and subadults producing about 3 000 young pa on South Uist in 2007[180]. Debate over the precise numbers shouldn't detract from the obvious point that there's quite a few of them where there shouldn't have been any. Further, Jackson concludes that warming climate is making life easier for the hogs, and thus worsened the problem of egg losses.[180]

Impact and intervention

Hedgehog egg predation coincided with a decline in wader nesting success[177] and nest abundance[178] (although H. Warwick (pers. comm.) speculates that egg-eating is learnt by only some hogs). Ten years with hogs saw a 39% decrease in nesting overall, compared with a 9% increase in areas without them. Lapwing and redshank were worst affected, and hogs accounted for an estimated 36-64% of nest failures[177]. The effect was locally mitigated (by a factor of 2.4) by experimentally removing hogs[181]. What was to be done, with a legal obligation to protect the waders, but a vociferous public (including, awkwardly for the RSPB, many of their million members) adamantly against the dispatching of hedgehogs, whose numbers are in decline on the mainland? Amidst tension between bird and hog advocates, the Uist Wader Project[175] was tasked by Scottish Natural Heritage (SNH) with 'reducing the hedgehog population across the Uists to a level that allows the waders to recover *fully*' (a remit latterly rephrased to retain the possibility that this might not require complete removal of the hogs).

Hog removal began on North Uist on 7th April 2003, was extended to Benbecula in 2004, whilst South Uist was postponed. The hogs were either live-trapped or intercepted by torchlight in the pre- and post-breeding season, with a break from June to mid-Sept, according to 'requirements for animal welfare' set out by Scottish SPCA. Initially, SNH arranged their dispatch by lethal injection, killing 658 animals between 2003-2006, while the Uist Hedgehog Rescue[182] (UHR, a coalition of Advocates for Animals, British Hedgehog Preservation Society, Hessilhead Wildlife Rescue Trust and International Animal Rescue), reported that they had translocated a further 756, mostly from South Uist (to avoid SNH killing them). Then, fresh evidence[183,184] of the ability of translocated hedgehogs from the Uists to survive release into the wild[183,184] caused the SSPCA to change its advice, so in March 2007 SNH replaced the killing of the hogs with enforced transportation to the mainland. By October 2008, 440 hogs had been translocated. In 2009 there were 58 000 trap checks and 110 captures[175]. Overall 958 were removed from Benbecula over four years, significantly reducing their numbers over approx 55km^2, whereas removing 165 over five years has effectively cleared the 50 km^2 that was invaded on North Uist.

What happens to released animals?

What swung policy from killing to translocation? The two published accounts of fates of translocated Uist hogs make tantalizing reading[183,184]. In April 2005, 20 Hebridean hogs were released at Eglington Country Park, Irvine (which had no signs of badgers). Depending on the assumptions made, between 67% and 80% of radio-tracked transportees survived the month[183], but it was unknown how this compared with local hogs, or those that remained on the Hebrides. Some of these questions were answered by a team from Bristol[184], comparing five groups of 20 hogs each. These including transportees from the Uists which were, or were not, given a month in well-fed captivity prior to release in Bristolean gardens, and were compared with the local hogs amongst which they were released, and another local control group. Importantly, the Uist transportees that had been cosseted for a month had a survival rate (81.8%) almost as high as the locals (94.7%) (in contrast 19 of the 20 hogs released without this interlude were dead when the study ended after seven weeks). Both studies were short, but their conclusions are supported by the fates of 832 hogs from rescue sanctuaries on Jersey and liberated there, which lasted at least 10.8 months on average, comparable to home-bred hogs'[185,179]. It raises an interesting ecological puzzle if hedgehogs not only live below carrying capacity but can successfully assimilate immigrants at no cost to the residents (although that cost might not bite during a month or two in spring). Intriguingly, the resident Bristolean hogs that received Hebridean incomers survived marginally better than their neighbours! Demographers will appreciate that this issue turns partly on the relative roles of density dependent and independent factors. Considering the scrutiny focused on the rights and wrongs (not to mention the effort) of translocating Uists' hogs, that these animals are not monitored – muddying the long-term distinction between death and integration – is extraordinary. If the incomers eventually starve, their transportation would have constituted an expensive, and arguably crueller, way of killing them; if they integrate, then a question in community ecology is why was there space for them. If extra mortality is shared by residents and immigrants, then the equation includes the additional suffering experienced by those transported hogs that die, plus the marginal difference in suffering associated with the deaths experienced by the residents because of the immigrants. However, these 'ifs' remain unknown, although we are far from the first to think them worth investigating[186].

Has it worked?

In 2007 the BTOs Breeding Wader Survey of the three affected SPAs found breeding ringed plover numbers had declined by 3-6% since 2000, dunlin had declined marginally within the SPAs, and more so across the islands as a whole; whereas redshanks have done the opposite, and oystercatchers increased in South Uist (where hogs are not yet controlled) and decreased in North Uist (where they are). A SNH synthesis[187] of six species monitored in four survey areas between 2000-07, reveals ten population increases and 14 decreases, and, despite these variable results, concludes *'it is clear that wader productivity is being affected by hedgehog predation'* [178]. Hedgehogs were associated with a 7.5% daily nest failure rate for redshank, 5% for dunlin, 4.9% for snipe[177], but it's hard to know how much better things are because of current hog removal, or how much worse they'd have been without it. An interesting parallel concerns the hogs introduced to North Ronaldsay, Orkney, in 1972, whose arrival coincided suspiciously with a decline in breeding success of, in particular, Arctic terns. However, when the hogs died out the terns' breeding remained poor, raising a question over the original suspicion of cause and effect (a possibility is that collapse of sand eel populations reduced tern food, and so also reduced kleptoparasitic opportunities for the Arctic skuas which turned instead to waders).[188]


Laurie Campbell

Management options

In 2007, a SNH-commissioned model[187] confirmed the observed reality – hogs can be winkled out of the Uists, but at various costs in money, labour and animal welfare. H. Warwick (pers. comm.) tells us that it has cost c.£950 per hedgehog killed and closer to £850 per hog translocated. So what are the options? Aside from doing nothing (and, to the extent that hogs are damaging birds, failing to protect the SPA network, while worsening the Government's and SNH's stated objective of halting the decline in biodiversity by 2010), a minimalist option would target control solely to protect the SPAs. More ambitious goals would be to eradicate hogs from Benbecula and North Uist, or throughout South Uist too. Each scenario raises complications – e.g. retaining the breeding season moratorium while attempting to eradicate hogs from Benbecula and North Uist would require more staff over more years. Ultimately, costs of killing hogs might best be expressed in terms of extra waders thereby produced.

In the absence of the moratorium, full-time staff members would be more efficient than seasonals, and would also avoid interim recolonization, allowing trapping in wader hotspots outside the breeding season. However, current welfare concerns would necessitate avoiding or accommodating lactating females with young. This raises some questions about offseting concern for populations of waders against that for individual hogs. How weighty in the balance are the additional deaths of suckling hogs (and how is their sentience affected by their tendency to enter torpor when chilled, as when their mother is killed by a car)? Apparently the answer is different for the




invasive Hebridean mink being killed without closed season. Incidentally, if the closed season is removed, the model suggests that hogs could be eradicated from the Uists by fewer fieldworkers in less time than with the moratorium: how might these numerical differences be expressed in terms of total numbers of hedgehogs experiencing death, suffering or bereavement (is it better to spread a lower individual quota of suffering amongst more individuals?) and, by the way, is it humanity's business how much (and how many) parent plovers experience distress at the loss of their broods to a predatory species inflicted upon them by humans? Phew! Our purpose is not to deride any particular view, but merely to illustrate how complex is the cascade of complications!

To thicken the brew of incommensurables, are the Uists an inadvertent ark: Carter and Bright (2003)[179] raise the interesting dilemma that '*the hedgehog has probably undergone a significant decline at least in some regions elsewhere in the UK, so culling thousands of them in the name of conserving bird species whose conservation status is probably similar seems inappropriate*'. Of course, trades-off in the conservation of different species are commonplace[19], and the fact that the Uists are within the UK doesn't make hedgehogs in those islands any less invasive; but since their genes hail from the mainland they would be good candidates for replenishment, if (though unlikely) that is what proves necessary to restore mainland hedgehogs.

What next?

On 23 February 2010, SNH supported the Uist Wader Project recommendations to extend trapping throughout the year and to introduce the use of sniffer dogs to locate hedgehogs. Trapping will concentrate on areas of high hog density. From late May, and when hogs are in late pregnancy or lactating, removal will focus on areas with low hog density, and will involve collaboration with SSPCA and UHR, liberating lactating females (perhaps with radio-transmitters for later removal). Of the outputs of intervention, a change in wader breeding success may be more relevant than the number of hogs removed, and SNH plans field studies of wader productivity in 2010, to explore any relationship between removing hogs and wader breeding performance. In early 2011, SNH will assess the animal welfare consequences of year-round trapping and sniffer-dogs, and the financial implications of, and public benefits associated with, future investment in hog removal.

SCOTTISH WILDCATS

It is a matter of definition whether domestic mammals are considered as invasives, but amongst the varied threats to Scottish wildcats, domestic cats are paramount[43] and since people brought them into existence and into Britain, it seems appropriate to consider them alongside wild invasives.

Following the demise of lynx by early mediaeval times, the Scottish wildcat is the only remaining indigenous felid in Britain and following the losses of wolf (1743) and bear (c.1 000-2 000 years ago), only the wildcat survives as an icon of Highland wilderness. Domestic cats are often assumed to have reached Britain courtesy of the Romans c.2 000 years ago, but archaeologists have found their bones at Iron Age (3 200 – 2 586 years ago) and Late Iron Age (2 400 – 2 100 years ago) sites[189].

Domestic cats, variously independent of people, pose two insidious threats to Scottish wildcats. First, wildcats are commonly infected with viruses transmitted by domestic cats, including the feline leukemia virus. The second threat was first articulated in 1790 when Hodgson and Bewick wrote '*The domestic Cat, if suffered to escape into the woods, becomes wild, and lives on small birds and such other game as it can find there; it likewise breeds with the wild one*'.

The subspecies of wildcat, *Felis silvestris silvestris*, of which the Scottish wildcat is a representative, is a sister taxon to *F. s. lybica* from which domestic cats were domesticated in a single, but prolonged, domestication event, from at least five wildcat matrilines in the Fertile Crescent 9-10 000 years ago[190]. With only a few genes distinguishing them, it's not surprising that Scottish wildcats and domestics interbreed. Introgression between the two now threatens the cryptic extinction of the wildcat, not just in Scotland, but worldwide (introgression is the flow of genes from one species into the gene pool of another by repeated backcrossing of interspecific hybrids with one of its parent species). Introgression results in individuals with a complex mixture of parental genes and, consequentially, morphological and behavioural characteristics. The difficulty of distinguishing 'genuine' wildcats from hybrids on morphological cues thwarted earlier surveys[191,192]), a fact which in itself is evidence of introgression, and the problem of telling the ersatz cross-breed from the genuine (pre-Iron Age) wildcats is complicated by the fact that this hybridization was probably occurring long before the type specimen of '*Felis grampia*' was collected in 1904. Indeed, Daniels *et al.'s* (1998) morphological analysis of 333 'wild-living' cats revealed two non-exclusive and overlapping categories differing in limb bone length, skull size and intestinal length: Group I cats were most different to domestics, and generally approximated traditional wildcat pelage; whereas Group II cats were similar to domestics. Microsatellite analysis of 230 'wild-living' cats confirmed that some individuals possessed both domestic and furthest-from-domestic (putatively wildcat) genes[194] and Driscoll *et al*. (2007)[190] discovered widespread introgression throughout the wildcat's range, ensuring that wildcat conservation is beset by complex scientific, legal and ethical issues alongside daunting practical ones[195,43].

Wildcat diagnostics

The problem is that near identical morphologies makes distinguishing wildcats and the common feral mackerel tabby a challenge even to experts and, harder still, differentiating a wildcat from a hybrid whose diagnostic features are blurred by introgression. This frustrates conservationists, trying to foster wildcats, and gamekeepers, trying to eradicate feral domestics and hybrids. Wildcats are protected, inter alia, under Schedules 5 and 6 of Britain's Wildlife and Countryside Act 1981 and Annex IVa of the European Habitats Directive 1992, whereas ferals and hybrids are legitimate targets as perceived (although largely unquantified) pests of the grouse moor. Since no specimens of pre-Iron Age wildcat are to hand for reference, a pragmatic solution could be to define as a wildcat those cats whose characteristics are furthest from those of the domestic cat. This straightforward approach is thwarted because each of the different characteristics, whether morphological or genetic, identifies a somewhat different non-domestic cat grouping[43]. Probabilistic distinctions based on morphology, skull shape and size along the continuum from closest-to to furthest-from domestic may provide statistical satisfaction[196], but can't be applied through a rifle sight while squinting into a squall. However, a pragmatic and practical diagnosis can be based on seven key pelage characteristics. Based on a score of 1, 2 or 3 for each characteristic, wildcats are defined as those having a 7PS score of 19 or greater, and no scores of 1, unless there is evidence to the contrary[197]. Furthermore, wildcats and domestics can be distinguished genetically using a combination of mitochondrial DNA, microsatellite genotyping[190] and Y-chromosome data (Driscoll unpub. data). Mitochondrial DNA is passed through the maternal side and Y-chromosome data through the paternal side thus revealing whether hybridization is occurring and, if so, how.

Defining the diagnostic characteristics of a wildcat lures conservationists into academic aspects of taxonomy and systematics with far-reaching legal ramifications[43]. For example, a proposal to add the wildcat/domestic cat hybrid to the Wildlife and Countryside Act 1981 was rejected, so hybrids have no legal protection although the wildcat genes they carry may be valuable to conservation.

What to do?

Saving the Scottish wildcat from cryptic extinction at the paws of invasive domestics requires immediate action to protect individuals and to restore viable populations. The Wildlife and Countryside Act 1981 legally protects only strictly-defined wildcats, but Macdonald et al. (2004)[195] recommend a Code of Practice for Wildcat Conservation (CPWC) which, although lacking legal teeth, should be supported by an education programme. For protection of individuals on the hill, it would be convenient if Scottish wildcats could be conserved simply by protecting specimens meeting strictly defined criteria; but it's implausible that a) there'd be enough of such cats left and b) that practical people could diagnose them under field conditions. The more strictly the Scottish wildcat is defined, the rarer it will be, and therefore, paradoxically, the biodiversity locked up in the bodies of cats that just failed to qualify will be all the more important – put tritely, the tricky question is whether a hybrid individual should be shot because of its coat colour or treasured for its genes. In practice, the CPWC might spare any cat


Laurie Campbell

with a distinct striped tabby coat pattern and a thick ringed tail with a black blunt tip, which never occurs in the pelage group closest to the domestic cat; yet an estimated 50% of the Scottish wild-living cats would meet this relaxed definition, increasing the genetic and morphological resource potentially useful to restore the Scottish wildcat population[197]. At the population level, regulations could define a wildcat by where it lives as opposed to what it looks like, having first identified the wildcat hotspot areas. Nobody knows what blend of individual- versus population-based approach will work best, and experiments should test this.

Staunching the invasive flow of domestic-cat genes into wildcat populations is a prerequisite to conserving wildcats. The options – all of them controversial and bedevilled by ethical awkwardnesses – include shooting or trapping unapproachable, feral domestics (a proportion of which will be wearing a domestic coat over valuable wild genes), and neutering those semi-dependent domestics most likely to seed further hybrids. Unfortunately, the processes involved in feralization, and the most likely routes to hybridization, are largely unknown; so targetting a neutering campaign is difficult. This too demands research, experimentation and monitoring. Prevention is better than cure (in Germany, domestic cats may be killed if they are more than 300m from human habitation) so a campaign for responsible cat ownership is essential. Kilshaw et al. (2008)[198] proposed a combination of intensive neutering of feral cats, subsidised neutering of local domestic pet cats, education of domestic cat owners, changes in game keepering to prevent accidental mortality of the wildcat and education of game keepers to ensure correct identification of wildcats to be carried out in and around areas of suitable wildcat habitat.




ISSUES

Few issues rival policy towards non-native species – and especially invasive mammals – in their capacity to bring conservationists into the realms of paradox, inconsistency and unintended consequences.

Take the case of habitat fragmentation, which along with invasive species, is a component of Jared Diamond's infamous '*Evil Quartet*' of biodiversity blights. Conservation theory sets out the ubiquitous dangers of habitat loss, fragmentation and degradation, leading rightly to calls for policy to enhance landscape connectivity and to create wildlife corridors in order to maintain metapopulations and sustain genetic viability. The urgency of these calls becomes more strident as the need escalates to adapt to climate change and the shifting distributions of species. However, non-native species can stand the mantra – that connectivity is inherently a conservation good – on its head. In the wetlands of the Lovat River basin in Belarus, water voles appeared to survive best in small, isolated ponds – probably because these were less frequently visited by invasive American mink than were the big, connected water bodies[199]. Similarly, our team is collaborating with Scottish Natural Heritage in investigating the benefits of creating corridors for red squirrels to pass between small woodlands in the Highlands whilst being attentive to the paradox that these corridors may one day facilitate the spread of grey squirrels and thus the demise of the reds.

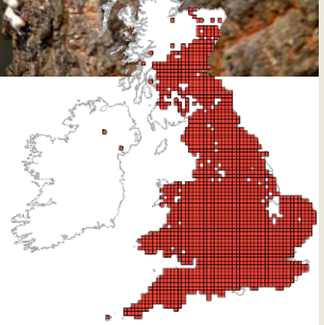
A different dilemma in connecting habitats, at a different scale, is that climate change, probably largely caused by human activities, is facilitating the passage to Britain of new colonists. Cattle egrets and small red-eyed damsel flies are beautiful, but should we regard them as undesirable non-natives brought here by carbon pollution, and should we rejoice if vagrants from the Continent, such as Kuhl's and Savi's pipistrelles, hitherto only occasionally blown through our islands, join a new generation of climate pioneers? Of course a simple answer would be that if a species arrives without the direct assistance of man then it is a natural colonizer and de facto a new native. But does this hold true if the mixing effects of the changing climate with non-natives arriving out of their normal range promotes more establishment? In 1986 spider crabs from the northern hemisphere took root in Antarctic waters, perhaps because they are warming[127]. A more important question is whether they have negative impacts on UK biodiversity and if so, can we do something about them?

When is control ethical?

So, when is it justified to control, which generally means to kill, non-native mammals? Actually, this is just a subset of the general question of when is it appropriate to control any wildlife. We suggest that the answers to three questions should be 'yes' in order for control to be a justified option. First, does the stakeholder suffer loss to the 'pest'; second, does action taken reduce that loss; and third, is it cost-effective? When does control of invasive species pass this test? This is a surprisingly tricky question. It would be comforting to join Darwin's contemporary, philosopher Herbert Spencer, in conciliatory liberalism: '*Every man is free to do that which he wills, provided he infringes not the equal freedom of any other man*'[200]. However, the awkward reality is that the grey squirrel or muntjac, perceived by some woodland managers as blights, may delight the walkers who glimpse them in that same woodland. What, for that matter, of the 'equal freedoms' of fur-trappers, sport hunters, animal rightists, photographers, or anybody else who holds an opinion?

Although the arguments are made easier where a non-native damages economic interests, public health or some other aspect of human well-being, a fundamental objection to the presence of non-natives is that they represent a departure from the natural processes of evolution and community assembly. This permeation of the barriers that formerly partitioned the world's fauna and flora tends to nudge nature towards a man-made uniformity, a time in history evocatively named the Homogocene era by Gordon Orians[201]. People shifting species around the world may be judged as unnatural. Putting aside the question of what point, in history, does one stop considering mankind as part of nature, how valuable is the naturalness of these processes? This question may be partly answered in scientific terms – do the invasive species diminish the resilience, or alter the diversity, of the natural communities that would have existed had introductions not arrived? Part of that answer might even be given a monetary value, but a big part of the answer will be philisophical. Valuing nature is difficult, partly because so many relevant measures are incommensurable (thwarting the compendious cost-benefit analysis that would take account of all the factors), and partly because if the analysis is based solely on economic elements (in a sort of crude utilitarianism), the point about value is missed. Worse, value links inescapably to knowledge – those not educated to appreciate the beauty of natural processes are unlikely to value them.

Conservation interventions should be based on scientific evidence, but policy extends beyond science into judgment. Decisions about killing mammals can be informed by animal welfare science[202], but judgments on the importance of the suffering involved are amongst the most difficult, and bedevilled by unintended consequences: it seems kinder to control a pest by contraception than by killing, but in the US immunocontraceptives designed for white-tailed deer interfere with males' weight gain and antler development and females' cycles in ways that may be perceived perversely to cause more suffering than would a quick death[203]. While conservationists, focusing on populations, generally believe that welfare considerations do not trump all others, the suffering involved in removing a non-native is surely a weighty factor in the cost-benefit analysis[204]. In this respect, non-native mammals may be qualitatively different from other non-native taxa, but are no different to native mammals. Firstly, the ethics of inflicting pain on a mammal differ from those of doing so to a Colorado beetle or New Zealand flatworm. Secondly, remembering another of Herbert Spencer's epithets that '*Opinion is ultimately determined by the feelings, and not by the intellect*'[205], mammals are deemed cute, even cuddly, in ways other species aren't. While conservation advocates are generally eager to capitalise on this, they may lament inconsistencies in public attitudes, exhibiting a certain double standard themselves. Cuddliness is a factor: there has been no protest at the eradication of brown tree snakes in Guam or cane toads in Australia[206], or American bullfrogs in the UK, but mark the press reaction to the perceived open season on London's ring-necked parakeets. In reality the general licence from Natural England that grants automatic permission to landowners to control mink and ring-necked parakeets is valid only where they cause significant damage to crops, have a significant, negative impact on native wildlife, or raise issues affecting public health and safety (as is the case for edible dormice)[112]. The Tiggywinkle factor that causes people to like hedgehogs (seemingly more than the similarly insectivorous moles that were until recently legally poisoned using strychnine) ensures a widespread abhorrence at the prospect of killing them. Yet, on South Uist, these introduced hedgehogs have been responsible, since surveys conducted in 1983, for halving populations of dunlin, ringed plover



Grey squirrel *(Sciurus carolinensis)*

Native to North America, grey squirrels have been present in the UK since 1828, with 30 separate introductions between 1892 and 1929 from Loch Long in Scotland to Kent[26]. They spread dramatically from 1930 to 1945[213], and today occur throughout much of England, Wales and lowland Scotland and are still expanding their range[214].

Arguably Britain's most notorious invasive mammal, greys have devastated the native red squirrel, which can be excluded from broadleaved woodland within five years of their arrival[215]. The larger grey, with its greater ability to digest and detoxify acorns, has a competitive advantage[216]. With a few exceptions, the species may co-exist for 40 years or more, where the mix of conifer and broadleaved woodland favours reds especially, as in Scotland, where disease is not yet a factor[217,218]. However, in 1996 the squirrel poxvirus (SQPV) was discovered in England, carried by greys but with a much higher mortality rate in reds[96,213]. When SQPV is present, the replacement of red squirrels by greys is twenty times faster[219] and it could reach red squirrel strongholds in Scotland within 25 years[220].

Red squirrels were formerly perceived as a pest of forestry, a role now taken and expanded by greys, particularly in broadleaved woodlands. Bark stripping can kill 5% of damaged trees[221], causing economic damage or preventing regeneration of native woodland[222]. There are also concerns, as yet unproven, that nest predation by grey squirrels damages populations of native woodland birds[223,224]. Recent analysis of the *Breeding Bird Survey* data[225] suggests that squirrels are unlikely to have driven observed declines in woodland birds. However, in areas where squirrel numbers are high, for some species (especially common blackbird and Eurasian collared dove), squirrel abundance appears related to nest failure.

Grey squirrels are killed in an attempt to prevent damage to forestry and to protect reds. This is most effectively done using poison – warfarin – (where there are neither reds nor pine martens) and live-trapping (with humane despatch)[221]. A national eradication campaign has been deemed unfeasible on the grounds of scale, expense and public opinion[146]. A trapping plan to prevent greys from colonising Thetford forest was estimated to cost £300 000 per year[226]. The Grey Squirrels (Prohibition of Importation and Keeping) Order 1937 makes it an offence under the Destructive Imported Animals Act 1932 to import greys into Britain or to turn loose any captives. In the light of affection for greys amongst the public, Natural England's Non-Native Species Strategy currently takes the conciliatory approach of licensing the release of live-trapped greys where reds are not present and into areas not deemed red squirrel habitat.

Immunocontraception may offer scientific scope, with public acceptability, as a future means of controlling grey squirrels[227]. As the invasion by greys of remaining red squirrel refuges in England, such as Kielder Forest, becomes ever likelier, efforts to kill greys are focused strategically[228]. Ironically sitka spruce, itself a non-native introduced from the coast of Northwest America, is relatively poor habitat for greys and therefore may provide a refuge for reds, albeit at much lower population densities than they can achieve in broadleaf woodlands[229].

and redshank that comprised, at that time, 25%, 25% and 10% respectively of Britain's breeding stock[175,182]. The transportation of 1 000 hogs to the mainland beguilingly seems a kinder, if expensive, approach; but the pros-and-cons, from the standpoints of both the hedgehogs and their prey, raises questions in ecological science, economics and ethics (see pages 20-22). Double standards are rife: these same Hebridean islands are also populated by American mink but almost nobody laments their eradication, beautiful and fascinating though they are. The brutal truth is that people like (that is, value) some species more than others (for example, gorillas over nematodes), and conservation purists would be foolish to pretend otherwise[207]. So, to return to the question of when is it legitimate to kill individuals of a non-native species, the answer is that it depends on the balance of judgment.

Public opinion

Whether influenced by science or sentiment, the consequences of public perception of non-natives are far-reaching. In Britain, the negative impacts of grey squirrels are well researched and widely known, but most householders remain neutral or even positive towards them[208]. In Italy, the opportunity to prevent their early spread was thwarted by legal action brought by animal protestors concerned about young squirrels left to starve when their mothers are killed[209]. Consequently, an opportunity to apply the principle of prevention being better than cure was lost, and grey squirrels have now spread so widely in Italy that removing them will be expensive, perhaps impossible, and involve killing many more of them[210]. An important statutory challenge is to explain the issues well enough to enable the public to make informed and balanced decisions.

Shifting values and regulated freedoms

The last half century has seen radical evolution in the theory and practice of nature conservation[207]. Initially, the focus was protecting species, often principally to satisfy dedicated enthusiasts. But values change. In the 1950s while conservationists in Britain rejoiced in introducing muntjac, their colonial counterparts sought to exterminate African wild dogs as wanton killers. Now the demise of wild dogs prompts despair, while many contemporary conservationists in Britain would favour the control of muntjac. Latterly, the human dimension has become paramount, the benefits of wildlife to human wellbeing are central to policy; and an emphasis on the importance of ecosystems at least rivals that on species. The new, scientifically, ethically and politically literate inter-disciplinarity complicates the dilemmas caused by introduced species. The introduced beavers on Navarine Island in the Beagle Straits[211], are simultaneously a source of meat and facilitators for the spread of exotic fish beloved by anglers (but not by conservationists). They also damage roads, fell trees, cause erosion and sedimentation: some love them, others hate them. On the same island, a different balance of factors bears on the equally invasive mink[212].

Policy and regulation inevitably restrict freedoms, in this context the freedom to choose an exotic pet: as garden centres add to the risk of invasive plants, so the exotic pet trade does in regard to animals. It is probably fun to keep American bullfrogs in an aquarium, but in 1996 their first sinister gulpings were heard in the wild in East Sussex. The impact of these invaders on native amphibian communities is unknown, but they carry chytrid fungi that threaten amphibians worldwide[36], so there is no room for complacency when one female can lay 30 000 eggs and disperse over several kilometres. Some 9 000 bullfrogs had been winkled out of Sussex by 2004, and their subsequent appearance in Essex in 2006 was rapidly knocked back to five individuals in 2008[37]. So, the fun of keeping a bullfrog is offset against the problems caused by their escape, a balance that the UK's Invasive Non-Native Species Framework Strategy[145] strikes through a risk-based emphasis on prevention that attempts light-touch regulation, fostering partnership agreements from trade organisations and wider public education.

Dave Bevan

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Policy and pragmatism

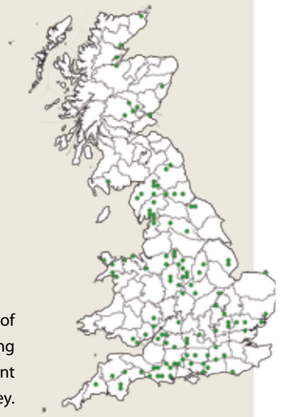
The mesh of often contradictory considerations regarding non-native species denies conservation policy-makers easy answers: when considering Britain's introduced mammals, they cannot rely entirely on utilitarian arguments, or expect any single scientific argument to do the job alone. Take heart from Goedel's mathematical proof that no theory can be both complete and consistent: it seems consistency is similarly elusive in conservation policy. As Macdonald et al. (2006)[207] put it '*Conservationists will thus find themselves striving to protect species for motives that may differ between two ends of a spectrum: at one end prudence, to protect the biodiversity we need, and at the other end preference, to protect the biodiversity they like*'. In the context of non-natives, this pragmatism might advocate eradication where it is worthwhile and feasible. Invoking their alien status as justification for killing, even persecuting, individuals in ways that offer no prospect of limiting their impact is as tawdry in the context of non-natives as is inflicting suffering and squandering resources in any other context. In this morass of complications, Natural England's policy on invasives is pragmatic, aiming to prevent any releases that have an impact on native wildlife, but taking account of people's enjoyment of some non-native species in the attempt to strike a balance between preventing harm and allowing limited releases of individual animals (for example those which have been cared for and rehabilitated), where these are likely to have a limited impact[145]. Insofar as pointless persecution is inappropriate, the Canute-like aspect of battling several of Britain's invasive mammals makes it increasingly hard to justify killing grey squirrels in much of suburban England solely on the grounds of their non-nativeness, and perhaps even harder for muntjac: it's a pity they were brought here, and regrettable that they damage woodland flora and alter the balance of the deer community, but we confess to taking delight in seeing them.

Ferret *(Mustela furo)*

The ferret, probably domesticated from the European polecat, is mentioned by Aristotle in the 4th century BC. Thompson (1951)[230] suggested that ferrets were introduced to Britain sometime between the 11th and 14th centuries to hunt rabbits. Despite their being frequently observed, the status of feral ferrets in the UK is poorly known; however, they are well established on various Hebridean islands, including notably Mull, North Uist, Lewis, Bute, Arran, as well as the Isle of Man and Shetland. Indeed, islands with abundant rabbit populations and few carnivores seem the best sites for ferrets[231]. An unknown proportion of sightings are of representatives of a 'standing crop' of escapees and deliberately released captive ferrets[230].

Ferrets are a conservation concern because they hybridize with native polecats, producing viable offspring[232]. This threat was particularly worrisome when polecats were at the start of their recovery in the 1950s and still rare. Polecat-ferret hybrids are widely distributed across the UK except for parts of Scotland, Wales and the Marches. The main areas of overlap with polecats are Northwest England, North Wales, the North Midlands, East Midlands, Southeast Wales and central Southern England[233]. Around 50% of polecat-ferrets are 'dark', and easily confused with true polecats. Unfortunately the genetic mixing is such that it is not possible to discriminate conclusively whether an animal is a ferret, hybrid or polecat. Molecular evidence suggests that polecats from the Welsh borders are probably more similar to original polecats, whilst there is a gradient towards 'ferretiness' to the east[234]. Domestication has deliberately reduced hunting skills in ferrets, so that rabbits would be bolted rather than caught; which makes domesticated mustelids less adapted to the wild than their feral progenitors (an idea also mooted with respect to American mink). Polecats appear dominant over ferrets in the wild, leading to the suggestion that based on current evidence there is no case for selective culling of ferrets or polecat-ferrets to maintain the genetic integrity of polecats in Britain[233]. Nonetheless measures to reduce the numbers of escapes and losses of fertile ferrets into the wild would help reduce the risk of hybridization, particularly as many ferret-keepers favour the dark form.

Further concerns are raised by experience in New Zealand where, in the absence of large predators, feral ferrets seriously impact native wildlife[235], may spread tuberculosis to cattle[236] and may be difficult to trap especially in winter[237]. Fortunately, ferrets failed to become established in Australia[83].



Records of polecat-ferrets during 2004-2006 Vincent Wildlife Trust survey.

The Vincent Wildlife Trust

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Fallow deer *(Dama dama)*
The fallow deer is generally considered native in Britain, but in fact, having died out during the Last Glacial they were reintroduced by the Normans in the early Middle Ages for hunting[238]. Fallow currently occur patchily across the UK, perhaps reflecting the distribution of ancient deer parks. Fallow are bulk feeders, taking cover in deciduous and mixed woodland, where they also browse trees and shrubs, whilst grazing in nearby fields[238]. Although the average annual expansion of their range between 1972-2002 was 1.8%, this disguises large regional differences and a much faster expansion in Scotland and central England[135].

The fallow deer is the species most associated with arable damage in southern England. These deer also cause some harm to orchards and grasslands[143]. Culls for management or sport take 14-24% of the population annually[239]. Fallow account for more DVCs (37%) than all other deer species in England and Scotland combined, causing an estimated economic impact of up to £25M including approximately 4 000 accidents involving significant damage[138].

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A lesson from history: coypu *(Myocastor coypus)*
The coypu, or nutria, is a large semi-aquatic rodent introduced into Britain from South America for fur-farming in the 1920s. Fifty or so coypu farms were established, mainly in southern England but most had closed by 1939 due to the outbreak of war and a fall in the value of fur. Escapees established in southern England: by 1940 colonies thrived in Suffolk and Norfolk[240]; by the late 1950s 100 000 to 200 000 populated East Anglia[241].

Apart from not being part of the British ecosystem, coypu were a pest of crops, and their burrowing undermined river banks and dykes. Their foraging on aquatic plants converted reed beds to open water, reduced the supply of Norfolk reed thatch, and impacted the invertebrate community and threatened marshland birds.

A two-year government campaign initiated in 1960 killed 97 000 animals but neither eradicated them nor stopped their expansion. 40 000 more were killed between 1962-5[241], and harsh winters of 1962-69 reduced their population by 80%; mild winters in the early seventies, however, facilitated a recovery until, in 1981 a campaign was instigated by the then Ministry of Agriculture, Fisheries and Food (MAFF)[242]. MAFF succeeded in eradicating the coypu from Britain by 1989, culling animals over 12 000km^2, at a cost of £2.5M[243,38]. This success owed much to the central involvement of science and adaptive responses to interim analyses and, crucially, the courageous use of a final bonus scheme to incentivise trappers to complete the eradication (thereby avoiding the temptation inherent in bounty schemes to sustain a harvest).

Coypu numbers continue to grow in France, Italy and Germany, but their eradication in Britain illustrates how a strong scientific base and ingenious use of financial instruments can repel an invasion.

Like coypu, the North American muskrat (*Ondatra zibethicus*) valued for its pelt, mushquash, escaped from British fur farms in the 1920s, and established in the Tay Basin, Shropshire, Sussex and Surrey by 1930[38]. Their damage to banks of canals stimulated a successful MAFF eradication campaign from 1932-1937[243]. In contrast to the selective live-trapping of coypu[67], muskrats were killed using (now illegal) leg-hold traps, causing thousands of non-target deaths[244].




People's Trust for Endangered Species

The People's Trust for Endangered Species (PTES) strives to ensure a future for endangered wildlife worldwide. The critical state of some of the mammals on our doorstep in the UK led us to focus on this group of animals as one of our top priorities. Our special campaign fund for native mammals has already distributed over £800 000 to conserve priority species and habitats, over 35 young interns have been helped to pursue careers in mammal conservation, and our mammal monitoring surveys are collecting vital information. Our achievements are many but the challenge to conserve UK mammals continues apace.

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people's trust for endangered species mammals

WildCRU

The mission of the Wildlife Conservation Research Unit (WildCRU) is to achieve practical solutions to conservation problems through original scientific research.

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WILDCRU Wildlife Conservation Research Unit

The state of Britain's mammals ***a focus on invasive species*** is the eighth update following the publication of Britian's mammals: a challenge for conservation, in April 2000. For copies of this report and of previous updates visit www.ptes.org or call 020 7498 4533.

Acknowledgements for distribution maps

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