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The consequences of introducing non-indigenous species: two case studies, the grey squirrel in Europe and the brushtail possum in New Zealand

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Summary

Two examples of the introduction of non-indigenous invasive species are reviewed: the grey squirrel in Europe (United Kingdom, Ireland and Italy) and the brushtail possum in New Zealand. Both have become very successful in their respective non-native habitats since their introductions in the mid-to-late 19th Century. Both species impact extensively on native biodiversity, environmental sustainability, forestry, and agriculture through a range of direct and indirect mechanisms. Management is currently mainly by lethal control, namely poisoning, trapping and shooting. Such methods of control are, however, increasingly contentious for both species, and alternative, non-lethal methods of population control, e.g. fertility control, are being developed. The case studies highlight many of the issues in invasive animal control; for example, prevention being better than control, lack of good understanding of impacts and the success of control measures on reducing impacts, interactive impacts on native biodiversity and ecosystems, the telling influence of public opinion on management options and, lastly, the need to better inform and educate the public.

Keywords

Brushtail possum – Grey squirrel – Invasive alien species – *Sciurus carolinensis* – Translocations – *Trichosurus vulpecula*.

A tale of introductions, damage and disease: the North American grey squirrel abroad

Background

The American grey squirrel (*Sciurus carolinensis* [26, 39]: Rodentia, Sciuridae) is a medium-sized tree squirrel (430 g to 720 g) native to the eastern United States and southern Canada. The grey squirrel typically inhabits dense broadleaved woods, but is also found in broadleaf/conifer mixes, pure conifer stands with nearby broadleaf woods, and urban parks, gardens and hedgerows (28). Grey squirrels feed predominantly on tree seeds, especially acorn, beech, chestnut and other large broadleaf seeds (28). Annual fluctuations in squirrel densities are linked to changes in tree seed supplies (27). Besides tree seeds, grey squirrels also eat fruit, flowers, buds, shoots, fungi and animal matter, particularly at times when seed crops are small (54).

Grey squirrels are polygamous. Up to two litters can be produced in a year, with the likelihood of a second litter determined by food availability and how early in the season the first litter is produced. The young are weaned at about ten weeks (88, 91). Dispersal mainly occurs in the autumn or spring, and is usually by juveniles or yearlings, and male-biased. Young females form female kin groups and are more likely to remain within their mother's home range (31). Juvenile survival is between 0% and 50%, with subsequent annual adult survival around 50% to 80%. The main mortality factors for grey squirrels are starvation and severe weather, with control or hunting, road casualties and predation, e.g. by foxes, goshawks and stoats, also important (28).

Translocations

The grey squirrel is one of the most 'travelled' tree squirrels worldwide, with numerous artificial translocations both within North America (e.g. California, Oregon and British Colombia), as well as overseas to the United Kingdom (UK), Ireland, Italy, Australia (failed) and South Africa (6, 38, 44, 52, 53, 72). Within Great Britain alone there were 33 recorded introductions and translocations of grey squirrels between 1876 and 1929 (52). A further introduction from the UK to Ireland occurred in 1911 (85). A systematic review of tree squirrel introductions, combined with a population viability analysis, indicated that tree squirrels are able to establish viable populations in new habitats with relatively few founders (93). Fifty-nine out of 74 (79.7%) grey squirrel introductions recorded worldwide were successful (5). In 20 out of 28 (71.4%) successful cases for which the number of founders was known, fewer than 10 individuals were released.

Grey squirrels are considered a serious forest pest species in some countries and are listed as one of the world's 100 worst invasive species (25, 46). The populations in Europe are of particular concern, as grey squirrels there continue to expand their range, are causing significant damage to crops and forests, and are replacing the native European red squirrel, *Sciurus vulgaris* (47). Populations in Italy are predicted to expand into Switzerland and France in the near future and from there to the rest of Europe and beyond (7, 48). This would represent a serious threat to native biodiversity and for the survival of the native red squirrel throughout its range. There is, thus, an urgent need for a co-ordinated European approach to grey squirrel management.

Impacts on the environment and biodiversity

Grey squirrels are considered a pest in their introduced range for several reasons: their impact on silviculture through damage to trees, specifically bark stripping, their impact on agricultural crops such as maize (Italy), their role in the decline of the native European red squirrel and their suggested impact on woodland bird communities (23, 28, 47, 73).

Bark stripping occurs in broadleaf woods typically in the spring. Significant damage, mostly in deciduous forests, occurs mainly between April and September when bark may be stripped from the base, stems or crowns of trees. Whilst small areas of damage may scar over, this may still lower the economic value and quality of the timber and allow disease organisms to enter the wood. Ring-barking behaviour on upper parts of the tree can weaken the branches and leave them susceptible to being snapped off by the wind. A large number of tree species are affected, although certain species are more susceptible to damage (e.g. beech and sycamore [40]). Pole-stage trees (age 10 to 40 years) are the most vulnerable (28, 51, 57). Forestry Commission data for the UK suggest that 5% of affected trees may die, with a significant proportion having reduced timber quality through stem deformation, introduced diseases or broken tree tops (51). Reasons for bark stripping remain unclear, but it is thought to be triggered by food shortage, or agonistic behaviour of young male squirrels (36). Damage reduces the value of amenity woodland as well as that of economic crops. If suitable grey squirrel habitat is present, damage can also occur to gardens, arable crops and orchards (28).

The spread of the grey squirrel in the UK, Ireland and Italy has been associated with a decline in the distribution of the native red squirrel. This is caused partly by competition between the two species for limited food resources. This competition is not interference-based (86), as red squirrels do not avoid greys, and in fact show greater core area overlap with greys than conspecifics (89). There is little evidence of niche partitioning in areas where the two species occur sympatrically, leading to direct resource competition when resources are limited (87). There is little impact on adult red squirrel residency or population turnover from this competition, but juvenile recruitment and body growth (88, 89), and breeding in female red squirrels (30), are reduced. Grey squirrels are also thought to pilfer scatter-hoarded food caches of red squirrels, leading to those reds with large core area overlaps with greys showing a reduced body mass in the spring (90).

Grey squirrels feed occasionally on birds' eggs and fledgling birds (54). There is some anecdotal evidence that bird nest predation can be reduced by grey squirrel population control. Grey squirrels may also compete for resources with seed-feeding birds such as finches (32).

Like all wild animals, grey squirrels are affected by disease as well as internal and external parasites (28, 47). Disease

monitoring is patchy and no systematic, comprehensive monitoring or screening of squirrel populations occurs. Grey squirrels act as a reservoir host to a poxvirus (squirrel poxvirus) that is asymptomatic in grey squirrels (71), but causes high mortality in red squirrels (29). Modelling studies and the mapping of observed cases have shown this disease to have a crucial role in the loss of red squirrels (68, 70, 79). Rates of decline can be 17 to 25 times higher in areas where the poxvirus is a factor (68). Serum samples from grey squirrels in the United States contain poxvirus antibodies, suggesting the disease was brought in with the introduced grey squirrel (50). Not all grey squirrel populations carry the virus (29). Grey squirrels have also tested positive for bovine tuberculosis (*Mycobacterium bovis*) infection; however, the potential risk of disease transmission from grey squirrels to cattle is considered to be very low (17).

Management

Grey squirrel populations in Europe are controlled to reduce economic damage to forests and detrimental impacts on native wildlife (32, 47). Whilst costs for grey squirrel management, which include equipment, bait, labour, etc., are relatively easy to measure, their impacts on timber production as well as on biodiversity and native species are much more difficult to quantify. In 2003, the damage to beech, sycamore and oak woodlands alone in the UK was estimated to be £10 million (1).

Grey squirrel control operations for timber protection and the conservation of native red squirrels in the UK are often considered together. However, they differ significantly in geographic location, timing, methodology and scale. Control for tree damage prevention aims to reduce local squirrel densities below levels at which damage occurs (< 5 ha^{-1}). Grey squirrel populations readily recover from culls, but the population can be reduced to coincide with the annual period of greatest damage (other population demographics, such as breeding, age profile and sex profile may be impacted for a longer period by culling) (41). The main methods used in the UK vary according to whether or not red squirrels are present: poisoning (using the anticoagulant Warfarin in special feeding hoppers) where red squirrels are absent, and cage trapping or shooting where they are present. This large-scale approach contrasts with grey squirrel control for red squirrel conservation, which aims to remove all grey squirrels throughout the year, in and around local designated red squirrel conservation areas (67). In Italy, grey squirrel eradication was attempted in 1997 in Piedmont, but it was stopped by a legal battle with animal rights activists, when after a three-year struggle in the courts, the eradication campaign collapsed (24). The species has since significantly expanded its range and eradication is no longer considered feasible.

A disastrous success: the common brushtail possum in New Zealand

Background

The common brushtail possum (*Trichosurus vulpecula* [38]: Diprotodontia, Phalangeridae), which can weigh between 1.3 kg and 3.5 kg, is an arboreal, hole-nesting, folivorous marsupial, endemic to mainland Australia, Tasmania, and some offshore islands (76). It has the widest distribution of any marsupial in Australia. Its preferred habitat is open forest and woodland, but it is found in a wide variety of vegetation types (37) and it has colonised urban areas successfully (65, 75). Possums are a highly adaptable species. Although leaves comprise most of the diet, a wide variety of other foods are eaten, including fruits, vegetables, flowers, fungi, insects, and small birds (14). They do not build nests but use available cover below, on, or above ground, especially tree hollows. They are seasonal breeders, giving birth to a single young in autumn (March to May). Some populations have a second period of births in spring (September to November) and, in tropical areas and some urban areas, young may be born year round (22). Possums are largely solitary, occupying home ranges of between 1 ha and 10 ha (15). These overlap extensively, both between and within sexes, only limited areas are defended, and social structure appears to be based primarily on dominance relationships between individuals with overlapping ranges (16). Natural dispersal involves primarily juvenile animals, predominantly males, which may move up to 42 km (average 5 km) from their natal areas (15).

Translocations

Although possums are found in zoos worldwide, and have been exported from New Zealand to Japan and France as pets, the only free-living, invasive populations are in New Zealand. Possums were introduced deliberately to establish a fur trade similar to that flourishing in Australia at the time. The first successful liberation was in 1858. Introductions continued in the second half of the 19th Century and early 20th Century, and about 200 to 300 individuals in total were imported from Victoria and New South Wales (42%) and Tasmania (58%), mostly between 1890 and 1900 (66, 92). Their spread was accelerated greatly by additional liberations of captive-bred progeny, people moving possums from one area to another, and protection afforded by their legal status (11). About half of the approximately 400 additional liberations were carried out by the acclimatisation societies and private individuals (in equal proportions) acting with official government approval, and the rest by private individuals

acting without official sanction (66). Today possums occupy more than 95% of New Zealand's land area, densities are habitat-dependent, range from < 1 to > 20 possums/ha, and their population has been estimated recently to be approximately 30 million (80). Possums in New Zealand have adapted to new diets and habitats, and have fewer parasites, predators and competitors than in Australia, and as a result the density of the possum population in New Zealand is between two and 20 times greater than in Australia (20).

Impacts on the environment and biodiversity

Possums are listed as one of the world's worst 100 invasive species (46), and in New Zealand are managed for three main reasons – they are agricultural pests, they are vectors for disease, and they threaten populations of native plants and animals through browsing damage, competition for resources, and predation. In Australia, possum browsing causes mostly minor damage to introduced and native forest plantations and crops, and possums are a widespread urban nuisance, damaging gardens and nesting in house roofs (2, 74). In New Zealand, possums are also an urban nuisance, but agricultural damage is much more severe, with an estimated US$20 million of economic losses annually to exotic forest plantations, plantings for erosion control, improved pastures, and a wide variety of arable and horticultural crops (3, 9, 13).

Possums in New Zealand, but not Australia, are the main wildlife host of bovine tuberculosis, which they transmit to domestic cattle and deer (12). The aim of New Zealand's tuberculosis control programme is to achieve official tuberculosis-free status by 2013. In the mid-1980s, about 1,600 cattle and deer herds were infected, but this has been reduced to fewer than 140 herds, with a significant part of the reduction due to extensive control of possums over more than six million hectares (78).

Browsing damage by possums to native vegetation, which results in extensive tree canopy defoliation and mortality, has been described in many areas of New Zealand (58, 61). It causes extensive tree canopy defoliation and mortality in the short term, but there is still uncertainty surrounding the possible long-term consequences (4). Such impacts have not been recorded in Australia. In New Zealand, selective browsing on particular native species and individual trees eliminates some species and favours others less palatable to possums, which may lead to gradual change in forest composition (61) and effects on ecosystem functioning (84). Possums also have negative impacts on native animals. They compete with native birds for seasonal resources, such as fruits, and for nest sites with hole-nesting birds (42, 45). They eat eggs, nestlings, and adults of a range of native bird species, and prey on rare and endangered invertebrates such as giant land snails (8, 69). These combined effects are sufficient to drive some species into decline (33, 34).

Management

The possum is the most significant mammal pest in New Zealand in terms of control expenditure (60), with about US$50 million spent annually, of which about US$30 million is spent on tuberculosis management. In addition, between one million and two million animals are harvested annually for their fur (83). Agencies involved in possum management include the Department of Conservation, local government, and the Animal Health Board (AHB), with national leadership and co-ordination provided by the Ministry of Agriculture and Forestry Biosecurity New Zealand. The Department of Conservation manages possums on New Zealand's national parks and protected lands (known collectively as 'the conservation estate'); local government is responsible for controlling possums within its geographical boundaries; and the AHB manages possums for the national strategy for bovine tuberculosis management. Many private landowners and community conservation groups also carry out possum control.

Large-scale possum control, particularly in less accessible areas, uses aerial poisoning with baits containing sodium fluoroacetate (1080 toxin), which routinely achieves a > 95% kill (56). Ground control is also extensive, using a mix of toxic baits in bait stations, and leghold and kill traps. The main toxins used for ground control are cyanide, 1080, cholecalciferol, and the anticoagulant brodifacoum (18). Shooting is often used by farmers, but is generally ineffective for population control. Non-lethal methods such as repellents and tree-guards are employed occasionally (55), and fences that are specifically designed to exclude possums and other pest mammals are being used increasingly to create pest-free reserves (more information about reserves and pest-proof fences is available at www.sanctuariesnz.org).

For tuberculosis management, the aim of control measures is to reduce and maintain possum density at the level at which, computer models suggest, and historical experience indicates, tuberculosis will die out naturally within five years; this is usually a post-control population of no more than one possum/ha (12). For biodiversity protection from possum browsing, post-control target possum densities (measured as the catch per 100 traps set for one night, expressed as a percentage) vary depending on desired outcomes – for example, from as low as 3% trap catch to preserve native mistletoe (77), between 7% and 9% trap catch to maintain Northern rata (*Metrosideros robusta*)

forest canopy (62), up to 10% trap catch to minimise browsing damage on kohekohe trees (*Dysoxylum spectabile*), and as much as 25% trap catch to maintain common hardwood canopy species (59). Protection of native animals from possum predation is more complex, and usually requires simultaneous control of a suite of invasive predators, including possums, rodents, and mustelids (33).

Social and environmental issues

Possum control, particularly aerial control with 1080 toxin, has become increasingly contentious (63, 65), despite a recent review and re-approval by New Zealand's Environmental Risk Management Authority (21). The 1080 debate covers a huge range of issues; for example, the toxin itself, its widespread aerial delivery, non-target risks to indigenous species and hunting resources, environmental contamination, job creation, community willingness to pay for alternatives, consultation and involvement in decision-making, and risks to the values of indigenous people (Maori). Some of these issues also arise when using other methods of possum control, for example, concerns have been expressed about brodifacoum residues in native birds (19) and the humaneness of traps (82). This has resulted in significant research into the relative humaneness of toxins and traps for possum control (43), so that management agencies can make informed choices about control options, and the banning or withdrawal of some toxins and control devices. A major research programme is also under way to develop fertility control and species-selective toxins for possum control (more information about the programme is available at: http:\\possumbiocontrol.agresearch.co.nz).

Recent reviews of pest management in New Zealand have highlighted the need for better definition of the desired outcomes of pest management and measurement of the actual outcomes (10, 35). Without robust evidence of benefit, the killing of large numbers of possums raises significant ethical concerns (81). When there is a high level of uncertainty about the outcome of managing wildlife-resource systems, agencies face ethical challenges (49). Warburton and Norton (81) suggest that the only defensible action in such situations is to apply a knowledge-based ethic that ensures future actions will be carried out with increased understanding.

Conclusions

Grey squirrels and brushtail possums are physically and biologically worlds apart, but there are some common lessons to be learned from the two case studies and these are likely to also hold true for other invasive mammal species. With hindsight it is clear that prevention is a better strategy than control, so priority should be given to early identification of an invasion and preventing pest establishment. Once this window is missed the focus is too often on numbers killed and an emphasis on attempting to eradicate the introduced population, when that opportunity has long passed. The focus should instead be upon the success of control measures in reducing the impacts of the invasive species, be it for the maintenance of biodiversity, human well-being, or economic benefit.

Brushtail possums and grey squirrels both cause problems through the interactions of their diseases and parasites with native organisms and livestock, and such problems may take a long time to identify and fully understand. Many aspects of the species' ecologies in their introduced ecosystem differ from those in their native ones and there is often little quantitative information about the social, environmental and economic impacts of pests. Finally, society's expectations are changing. There is an increasing need for more socially acceptable control tools, for example, species-selective bait applicators, species-selective toxins and fertility control. Public opinion can have a telling influence on management options and there is a need to inform, educate, and agree on common goals with the public when undertaking a management programme.

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Conséquences de l'introduction d'espèces non indigènes : deux études de cas, l'écureuil gris en Europe et le phalanger renard en Nouvelle-Zélande

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Résumé

Les auteurs font le point sur deux exemples d'introduction d'espèces envahissantes non indigènes : l'écureuil gris en Europe (Royaume-Uni, Irlande et Italie) et le phalanger renard en Nouvelle-Zélande. Après leur introduction, respectivement durant la deuxième moitié et la fin du XIX^{e} siècle, ces deux espèces ont colonisé avec succès leurs nouveaux habitats. L'impact de ces introductions sur la biodiversité, l'équilibre écologique, la sylviculture et l'agriculture est considérable et fait intervenir une série de mécanismes directs et indirects différents. Les efforts déployés pour maîtriser ce phénomène s'appuient actuellement sur des méthodes létales, en particulier l'empoisonnement, le piégeage et l'abattage des animaux capturés, et la chasse. Toutefois, ces méthodes de lutte étant de plus en plus controversées pour ces deux espèces, des méthodes non létales de gestion des populations sont progressivement mises en place, par exemple le contrôle de la fertilité. À partir de ces études de cas, les auteurs soulignent un certain nombre de questions liées au contrôle des populations animales envahissantes, par exemple : la prévention, préférable aux méthodes de lutte ; notre méconnaissance des différents impacts imputables aux invasions et de l'efficacité des méthodes de lutte employées pour limiter ces impacts ; l'interaction entre les impacts sur la biodiversité locale et ceux affectant les écosystèmes ; l'influence de l'opinion publique sur les options de gestion mises en place ; enfin, la nécessité de mieux informer le grand public et de le sensibiliser à ces questions.

Mots-clés

Écureuil gris – Espèce envahissante exotique – Phalanger renard – *Sciurus carolinensis* – Transfert – *Trichosurus vulpecula*.

Consecuencias de la introducción de especies no autóctonas: dos estudios de caso, la ardilla gris en Europa y el falangero de cola de pincel en Nueva Zelanda

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Resumen

Los autores describen dos ejemplos de introducción de especies exóticas invasoras, a saber, de la ardilla gris (*Sciurus aureogaster*) en Europa (Irlanda, Italia y Reino Unido) y del falangero de cola de pincel (*Trichosurus vulpecula*) en Nueva Zelanda. Tras su introducción, en la segunda mitad y fines del siglo XIX respectivamente, ambas especies colonizaron los nuevos hábitats. Pero su desplazamiento tuvo consecuencias considerables en la biodiversidad, el

equilibrio ecológico, la silvicultura y la agricultura que implicaron varios mecanismos directos e indirectos. Tradicionalmente, para controlar esos fenómenos se recurrió a la matanza de los animales, en particular con veneno, con trampas y el sacrificio posterior de los animales capturados, o mediante la caza. Pero las crecientes controversias que suscitan esos métodos de lucha contra ambas especies han conducido paulatinamente a utilizar métodos que no impliquen la matanza como, por ejemplo, el control de la fertilidad. Basándose en ambos estudios de caso, los autores destacan distintos aspectos del control de las poblaciones animales invasoras, como la prevención, preferible a los métodos de lucha; las lagunas de los conocimientos sobre las diferentes consecuencias de las invasiones, así como respecto de la eficacia de los métodos de lucha utilizados para limitarlas; las interacciones entre las repercusiones de las invasiones en la biodiversidad local y en los ecosistemas; la influencia de la opinión pública sobre los métodos de control utilizados y, por último, la necesidad de mejorar la información del público, así como de sensibilizarlo al respecto.

Palabras clave
Ardilla gris – Especie foránea invasora – Falangero de cola de pincel – Introducción – *Sciurus carolinensis* – *Trichosurus vulpecula*.

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