# Alien invasive vertebrates in ecosystems: pattern, process and the social dimension

Piran C. L. White<sup>A</sup>, Adriana E. S. Ford<sup>A</sup>, Mick N. Clout<sup>B</sup>, Richard M. Engeman<sup>C</sup>, Sugoto Roy<sup>D</sup> and Glen Saunders<sup>E</sup>

<sup>A</sup>Environment Department, University of York, Heslington, York, YO10 5DD, UK.

<sup>B</sup>Centre for Biodiversity & Biosecurity, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand.

<sup>C</sup>USDA/Wildlife Services, National Wildlife Research Center, 4101 LaPorte Ave, Fort Collins, CO 80521-2154, USA.

<sup>D</sup>Central Science Laboratory, Sand Hutton, York, YO41 1LZ, UK.

<sup>E</sup>Vertebrate Pest Research Unit, NSW Department of Primary Industries, Forest Road, Orange, NSW 2800, Australia.

<sup>F</sup>Corresponding author. Email: PCLW1@york.ac.uk

**Abstract.** The rate of biological invasions has increased dramatically over recent centuries. Alien invasive vertebrates have significant adverse effects on biodiversity, and island fauna are especially susceptible. Human-induced environmental change is likely to exacerbate these negative impacts of alien invasive species. However, invasion biology has advanced considerably over the last two decades, with improvement in understanding of the processes of establishment and spread. New developments in spatial modelling have elucidated the way in which behavioural processes at the individual level can drive population-level patterns such as spread. Combined with new genetic insights into the process of invasion, these advances may assist in the development of novel, better-targeted management strategies that provide new options in how to deal with the threat posed by invasive species. Decisions about whether to and how we should intervene are questions for all sectors of society, but research on the social and cultural impacts of invasive species is largely lacking. There are many opportunities for enhancing the social dimensions of invasive species research, and integrated assessments of the social, economic and environmental impacts of species provide one potential avenue. As part of this, there is also a need to increase stakeholder participation in the decision-making process regarding alien invasive species. These more holistic approaches are essential if we are to reduce the impact of alien invasive species to within acceptable limits in the face of rapid environmental change.

Additional keywords: alien species, biological invasion, climate change, ecosystem effects, invasive species.

#### Biological invasions: the historical context

Biological invasions are not a recent phenomenon. Over geological and historical time periods, species have shifted their ranges naturally in response to moving land masses, volcanic activity and changing environmental conditions (Vermeij 1991). For example, Hawaii, formed as a result of volcanic activity, had already been colonised by more than 1000 plants and 100 birds before the arrival of humans about 1700 years ago brought a more rapid influx of new invasive species (Brown and Sax 2004). Natural colonisations continue to occur today, with some species travelling considerable distance by utilising ocean currents and prevailing winds (Mack 2003; de Queiroz 2005). For example, since the late 1800s, the cattle egret has spread from Africa and Asia to Europe, North America and Australasia (Maddock and Geering 1994).

The colonisation of different parts of the world by humans over the last 50000 years has greatly increased the rate and pattern of species distributions through biological invasions. This acceleration has been illustrated by comparing known

© CSIRO 2008

modern rates of species invasion with historical rates, calculated by determining the rate of invasion required to account for indigenous species richness (Gaston *et al.* 2003). Species that have been valued by humans for food (both wild and domesticated), sport, companionship, aesthetic purposes or biological control, as well as commensal species that travel with humans, have been introduced as alien species (IUCN 2000) into areas of the world where they were previously absent. In many cases, their introduction into the new environment has been deliberate, although not all introduced species become established or have negative impacts.

The transportation of exotic species as pets, or for other entertainment or cultural purposes, can be traced back to ancient societies, including by the rulers of ancient Egypt and by ancient Greeks and Romans (Hughes 2003). These transportations may have had a more significant role in the loss of species from their native lands, particularly in the case of large mammals, than in the establishment of non-native species into new areas, although there are notable exceptions including the establishment of the domestic cat (*Felis catus*) in the Mediterranean, introduced from Egypt to Greece by the 5th century BC (Hughes 2003). In recent times, the increase in trade in exotic pets has contributed to the introduction of many aquarium fish species, and may be the most significant cause of introduction of non-native birds, reptiles and amphibians (Kraus 2003).

Vertebrate species that have typically been intentionally introduced into a new environment for food include cattle, sheep, goats, pigs, chickens and fish (Lockwood *et al.* 2007). Some fish species have also been introduced for sport, for example the rainbow trout (*Oncorhynchus mykiss*), native to western USA, which can now be found in every continent (Lever 1996). Along with game fish species, other smaller fish species, and even salamanders, have been introduced to new environments for use as fish bait (Fuller 2003). Other species that have been introduced for sport include game birds (such as ducks and pheasants) and various species of deer (Cervidae). For example 18 species of deer were introduced into Australia in the 19th and 20th centuries, although only six species have become established (Moriarty 2004).

Some vertebrate introductions occurred relatively early in human history, such as the arrival of the dingo (*Canis lupus dingo*) in Australia around 5000 years ago (Savolainen *et al.* 2004), but other ecosystems have experienced modification by introduced species only relatively recently. For example, New Zealand was first settled only about 850 years ago by Polynesian people, who brought with them the Pacific rat (*Rattus exulans*) and domestic dog (*Canis familiaris*) (Hogg *et al.* 2003). Some of these species originally introduced by humans are now commonly regarded as 'naturalised', and at least one (the brown hare, *Lepus europaeus*, in Britain) is currently the subject of a conservation action plan (Anon 1995*a*, 1995*b*).

More recently, the colonisation of the 'New World' by European settlers from the 1700s accelerated these changing patterns, and introductions were given further impetus by the acclimatisation movements that reached their zenith in the late 19th century (Lever 1977, 1985). As a result of these acclimatisation movements, European colonisation of New Zealand 200 years ago brought additional predatory mammals such as stoats, weasels, ferrets and hedgehogs, which have caused the extinction of many endemic birds and small mammals (Clout and Lowe 2000). Misguided attempts at biological control have also had serious impacts on native species, for example the Indian mongoose (Herpestes javanicus), which was released in the 19th and 20th centuries onto several oceanic islands in an attempt to control rat populations (Simberloff et al. 2000), various insectivorous birds released to control insect pests of crops (Lockwood et al. 2007) and cane toads (Bufo marinus), introduced into Australia in 1935 to control agricultural insect pests (Lever 2001).

In Australia, more than 80 introduced vertebrate species have established wild populations (Bomford and Hart 2002), with 60 of these during 1840–1860 alone (Myers 1986), and alien invasive species (alien species that have become established in natural or semi-natural ecosystems and threaten native biological diversity; IUCN, 2000) continue to have a severe impact on Australia's native fauna (Lunney *et al.* 2007). Alien invasive species are now recognised as one of the foremost causes of

species extinctions and population declines over historical time (Vitousek *et al.* 1997; Mack *et al.* 2000; Höijer *et al.* 2008), and fauna on islands or isolated continental land masses are particularly susceptible to the effects of alien invasive species, with the most significant impacts caused by introduced rats, cats, goats, rabbits and pigs (Courchamp *et al.* 2003; O'Dowd *et al.* 2003).

Although increasing awareness of the negative impacts of alien invasive species has led to regulatory responses and a reduction in intentional introductions of vertebrates, many of the adverse effects are increasing as these species continue to extend their ranges and as other environmental changes allow them to exert greater predation and competition pressure. A case in point is the cane toad in Australia, which is now spreading westwards across the continent at a much faster rate than several decades previously, probably partly as a result of changing environmental and habitat conditions (Phillips et al. 2007). The overall impact of humans on the biophysical environment is greater now than ever, and changes in climate in particular are occurring faster than previously recorded (IPCC, 2007). The ranges of alien invasive species may increase as climate change and increasing urbanisation and land clearance create habitats that favour some of them. Also, as natural ecosystems experience greater climate-induced stress, they will become more susceptible to the effects of other stressors such as alien invasive species (Mooney and Hobbs 2000; Höijer et al. 2008; Brook 2008, this issue). Thus, the impact of alien invasive vertebrate species is likely to be exacerbated by changing climate (Lafferty and Gerber 2002). Changing climate can also lead to nativespecies decline through increased spread of diseases, especially where the changing conditions favour alternative hosts or vectors of these diseases, thus increasing the survival of infectious agents (Kutz et al. 2005; Pounds et al. 2006; Bosch et al. 2007; Smith et al. 2007).

The study of invasion biology therefore remains an important endeavour, and the papers in this special issue high-light some of the areas where new research is leading to advances in knowledge and our ability to deal with the impacts of invasive species.

# Patterns and processes of invasion

The understanding of how invasive species establish themselves in new environments has moved on considerably in the last few decades (Kolar and Lodge 2001). The tens rule of Williamson (1996) proposes that 10% of imported species appear in the wild, that 10% of those introduced become established and that 10% of these become a pest (Williamson and Fitter 1996). As discussed by Clout and Russell (2008, this issue), it is now recognised that introduced vertebrates, and particularly mammals, have a much higher probability of establishing and spreading than the tens rule would suggest (Jeschke and Strayer 2005).

Establishment of introduced species is influenced by a number of factors, including competition and predation. Competition can hinder establishment by limiting the resources available for an invading species. Several different native species may be involved in utilising the resources required by the non-native species (Davis *et al.* 2000), thus raising questions over the role of species richness and species function in the establishment of invasives (Symstad 2000). Predation may hinder establishment through increasing the mortality rate of the

invader, whereas in other cases predation may facilitate establishment. This is particularly apparent for non-native herbivores, which often assist the establishment of exotic plants species through grazing pressure on native plants, for example introduced sheep on Tasmanian grasslands (Leonard and Kirkpatrick 2004). Host–parasite interactions can play a significant role in the success of introduced species, since invading species may be able to escape parasitism that they suffered in their native range, either through the failure of the parasite to be transported along with the invading species or the absence of other required life-cycle hosts in the new environment, whereas parasites native to the new environment may not be able to adapt to the invading species (Torchin *et al.* 2003).

Establishment of a set of introduced individuals (the 'propagules') may also be affected by propagule size (the number of individuals released) and propagule number (number of release events) (Lockwood *et al.* 2007), which has been illustrated by studies of bird introductions to New Zealand (Duncan 1997; Green 1997). Propagule health may also be a factor in establishment success, which in turn may be influenced by the locality from which they originated (Lockwood *et al.* 2007). Invasion success is also assisted by the availability of climatically suitable habitat and a high reproductive capacity (Clout and Russell 2008, this issue), and may be affected by other biological traits such as migratory tendency, geographical range, diet and habitat generalism and body mass.

Understanding of the process of spread has advanced significantly from the early, purely statistical models of Skellam (1951), towards more sophisticated approaches relying on indepth knowledge of species behaviour and responses to local environmental and habitat conditions (Phillips *et al.* 2008, this issue). These models can now make much more refined and robust predictions about risks of establishment and patterns of spread and can be used directly in an applied setting for conservation purposes.

The importance of understanding behavioural processes at the individual level for making predictions at the population level is emphasised by Russell et al. (2008, this issue). They stress that it may be dangerous to assume that behaviour is consistent between individuals across different population densities. Thus, dispersal behaviour of invading individuals will not necessarily be the same as those in an established high-density population. Russell et al. (2008) show that a single rat may choose to leave an island despite an apparent abundance of resources and with no other suitable islands apparently within its perceptual range. Such individual events run counter to generalised predictions of behaviour, yet they can be of great consequence for invasions, particularly if the animal moving is a pregnant female or if the movement of even one individual predator is of great concern to the last remaining wild-living population of a rare island endemic (Atkinson 1996). These observations have considerable implications for the maintenance of invasive-free status on islands following control.

The insights gained from some of the new, individual-based approaches can also highlight further complexities in conservation. For example, Gurnell *et al.* (2006) showed that management is context dependent, and that management of landscapes to reduce fragmentation and enhance the connectivity of native red squirrel (*Sciurus vulgaris*) populations in the UK may sometimes exacerbate the potential for negative interactions, such as diseases transmission and competition, with invasive grey squirrels (*Sciurus carolinensis*). This presents a real conservation dilemma between enhancing landscape connectivity, and therefore making broad conservation gains for many habitat-specialist species, but at the same time greatly increasing the level of threat to one species of high public value (White *et al.* 2001).

Research on the patterns and processes of invasion can therefore provide unexpected insights into the conservation of rare and endangered species. The potential benefits that the study of invasions can bring for conservation biology are also examined by Cassey *et al.* (2008, this issue), who focus on the implications for the translocation of native species. These authors highlight the role played by propagule pressure and suitable environments in invasion success, and argue that the most productive crossover in knowledge between conservation biology and invasion biology would come from studies of species that are experiencing threat in their native ranges yet are also being released as exotics outside this range.

Invasion biology can also gain much from other fields of research. Invasive species research is dominated by short-term impacts in recent historical time, but Searle (2008, this issue) argues that the study of 'natural' invasions in the past can be extremely useful for application to understanding new invasions. The study of genetics has only been incorporated within invasion biology relatively recently (Gleeson et al. 2006), but Searle (2008, this issue) suggests that it can give insights not only into the process of invasion, but also into revealing characteristics of invading organisms that might be useful in counteracting their spread. For example, in the stepping stone model of spread, genetic diversity will decrease from one location to the next, and populations of invasive species closer to the invasion front would therefore be expected to be less resilient to novel stressors in the environment, such as parasites and disease. In the future, it may be possible to use this understanding to assist in the development of more targeted control strategies for certain invasive species.

# Ecosystem impacts and the human dimension

The extent of ecological impacts caused by alien invasive species in an area is determined by the interactions between these species and the native species present. This may occur in a number of ways, which range from genetic through to individual, population, community, landscape and global impacts (Lockwood *et al.* 2007). Genetic impacts arise from the hybridisation of invasive and non-native species, and may lead to the loss of the native genotype. For example, the introduction of the mallard duck (*Anas platyrhynchos*) from the Northern Hemisphere into Australia and New Zealand has become a significant threat to already rare endemic ducks such as New Zealand's grey duck (*A. superciliosa superciliosa*) and Australia's black duck (*A. superciliosa rogersi*) owing to interbreeding (Lockwood *et al.* 2007).

Predation and direct competition between alien invasive species and native species are often the most immediately apparent impacts; the introduction of predators, competitors, parasites and diseases can result in impact on the individual scale, including changes in morphology or behaviour (Schlaepfer *et al.* 2005), which will often, in turn, lead to population-level impacts and, frequently, population decline. The loss of the endangered tuatara reptile (Sphenodon punctatus) from the mainland of New Zealand and many of the islands off the north coast owing to depredation, particularly of eggs and juveniles but also adults, as well as competition for limited food resources, by the introduced Pacific rat (Rattus exulans) is just one of many examples (Cree et al. 1995; Towns et al. 2007). Alien predators tend to have a much greater impact on prey populations compared with native predators (Salo et al. 2007), and in cases where introduced predators have negative impacts on a number of native species, entire ecological communities may become affected, sometimes leading to mass extinctions (Lockwood et al. 2007). For example, the introduction of the Nile perch (Lates niloticus) into Lake Victoria (East Africa) in the 1960s played a significant role, along with eutrophication, in the extinction of many endemic cichlid fish species (Verschuren et al. 2002; Goudswaard et al. 2002). However, the effects of predation and competition may also be indirect and complex (Glen and Dickman 2005; Salo et al. 2007). As discussed by Clout and Russell (2008, this issue), it is now known that the successful management of alien invasive predators can sometimes lead to mesopredator release (Courchamp et al. 2003) or competitor release (Caut et al. 2007), reducing the benefits gained from the control, and sometimes exacerbating the problems faced by endangered native species, albeit from another predator.

It is also becoming increasingly apparent that alien invasive species can cause disruptions to ecosystem functioning and services. Examples of predation by alien invasive species on seabirds affecting nutrient flow on islands are discussed by Clout and Russell (2008, this issue). Dolman and Wäber (2008, this issue) provide an example of competition between invasive muntjac and native roe deer in English woodland. Roe deer have an important role as seed dispersers in the landscape (Eycott et al. 2007), but roe can be displaced by muntjac in dense woodlands (Hemami et al. 2004, 2005). Muntjac are much less effective at seed dispersal than roe (Eycott et al. 2007), so this may have impacts on woodland regeneration and diversity. On oceanic islands, ecosystems are often simple, with a few species fulfilling multiple roles. They can recover well from climatic perturbations such as cyclones and hurricanes, because generally, the species on them are relict, early colonist species, which have become adapted to be able to persist at low population sizes (Cronk 1997). This simplicity, however, means they are vulnerable to invasion and as some species become extinct there is often a cascade of extinction of species reliant on them, totally altering ecosystem function and services (Fowler and Lindström 2002).

In many areas of ecology, there is increasing recognition that management of ecosystems and the drivers affecting them requires the recognition of humans as a dominant force within the system (Rapport *et al.* 1999; Hannon 1992; Mageau *et al.* 1995; Xu and Mage 2001). This perspective also pervades recent global and national strategies and reports such as the Convention on Biological Diversity (www.cbd.int), the Millennium Ecosystem Assessment (www.millenniumassessment. org/en/index.aspx), and 'The State of the Nation's Ecosystems' programme in the USA (www.heinzctr.org/ecosystems; Meyerson *et al.* 2008, this issue). Although the importance of the social and cultural dimensions is well-recognised by those managing alien invasive species on the ground, it has been slow to enter the mindsets of researchers in invasion biology or those concerned with the development of invasive species policy.

The notion of invasive, and especially 'alien' species, provokes a strong negative response in many people (Gobster 2005). This appears to be due to an in-built suspicion or fear of the unknown, combined with a desire to protect something that is perceived, albeit incorrectly in many cases, as pristine and undamaged. Negative attitudes to alien invasive species pervade society and are also held widely among scientists and conservationists. There have been calls for more objectivity in the assessment of invasive species against a background of 'natural' flux in species distributions over time, for example by Brown and Sax (2004). Based on the evidence of responses to dramatic environmental changes in the past, Brown and Sax (2004) stressed the resilience of ecosystems to external stresses, yet they still considered that human-assisted invasions have had and will continue to have significant impacts on biodiversity. Human opinions of alien invasive species also vary globally. Perceptions in some parts of the world, for example Australia and New Zealand, may be more adverse to alien species, with a much more protectionist attitude towards native fauna and flora, than in other areas, such as the UK and other parts of Europe. This may be the result of a combination of cultural differences, the extent of recognised biodiversity loss owing to invasive species and the timescale on which these losses are taking place.

For some sections of society, certain alien invasive species may be viewed positively, especially larger herbivores such as deer and feral pigs, which provide a source of revenue through sport, hunting and tourism (Gordon et al. 2004). For these species in particular, some people argue that they should be viewed in terms of the social and economic benefits that they bring, rather than simply as an alien organism that must be eradicated (Hall and Gill 2005). Nonetheless, while the recreational benefits derived from such species can be accumulated through a variety of monetary metrics, the species' harm to the environment and native species is more difficult to quantify monetarily, and most empirical economic assessments of invasive species have therefore been limited to the calculation of direct financial costs and benefits associated with damage and control (Born et al. 2005; Olson 2006). Recent efforts have examined methods for placing societal monetary values on rare species and habitats (Engeman et al. 2004a), and these valuation techniques have been applied to swine damage in Florida where their impacts in even small areas can equate to large sums of money and high benefit-cost ratios for swine control (Engeman et al. 2003, 2004b, 2007). Although it is fraught with difficulties, the calculation of empirical monetary benefits derived from alien invasive species management is particularly appealing to land managers and governmental authorities, since it allows the development of fiscal arguments likely to be well received by the public.

The establishment of alien invasive species does not always lead to a decline in species richness. Although there have been many losses of individual species and a decrease in species richness globally as a result, many of the changes have led to local increases in species richness (Brown and Sax 2004). For example, even in New Zealand, where the impacts of alien invasive species have been particularly severe, the species richness of many islands has increased substantially since European colonisation (Sax and Gaines 2003), although several endemic species have become extinct. Furthermore, it is often those species that are specialised or low in abundance prior to the arrival of invasive species that become extinct owing to interactions with the invaders, since such species are already extinction prone (McKinney and Lockwood 1999). For already rare and threatened species, alien invasive species are just one more pressure contributing to their decline, along with other factors such as habitat loss and fragmentation, exploitation and pollution (Gurevitch and Padilla 2004). Nevertheless, the higher conservation value bestowed by society to endemic and threatened species, particularly the 'charismatic megavertebrates' (Loomis and White 1996; White et al. 1997, 2001), warrants the management of alien invasive species even in environments where local species richness has increased.

Although species richness may increase locally following the arrival of alien invasive species, the key concern of society is probably, first and foremost, the loss of charismatic individual species at the local level. This is combined with a deep-seated but less tangible unease with the increasing homogenisation of the species pool globally (Brown 1995; McKinney and Lockwood 1999). The increasing distribution of the most successful species, such as Norway rats (Rattus norvegicus) and foxes (Vulpes vulpes), has parallels with the globalisation of human culture, with the most economically successful cultures invading smaller cultures, speeding their demise and becoming increasingly dominant throughout the world. Some of the hostility felt by society towards alien invasive species may therefore reflect the unease of many people regarding the socio-economic, cultural and environmental effects of globalisation, as described by Ehrenfeld (2005).

There would be clear benefits from establishing more objective measures for assessing the impacts and management of alien invasive species. However, for many invasive species, the necessary data to underpin these assessments are lacking (Gren 2008). Andersen (2008, this issue) highlights the potential contribution of risk assessment for invasive species impacts, combining problem formulation with the analysis of exposure and effects. However, he also stresses that each stage of the risk assessment process requires an in-depth knowledge of the system, including, where possible, quantified functional relationships such as the interactions between species density and direct or indirect ecological impacts. Detailed risk assessment methods already exist for many invasive plant species through the European Plant Protection Organisation (EPPO) (http://www.eppo.org/, verified April 2008), and some of the techniques are now being applied to vertebrates invasives (Copp et al. 2005).

The problem of limited data availability on invasive species is also highlighted by Meyerson *et al.* (2008, this issue). Alien invasive species are used as an indicator of biodiversity conservation status in a growing number of countries, including USA (Meyerson *et al.* 2008, this issue) and the UK (http://statistics.defra.gov.uk/esg/indicators/, verified April 2008). However, much of the monitoring work on species distributions is usually done locally and outside the context of a larger, national or even regional monitoring programme. As a result, the information tends to be fragmentary and of variable quality, and the impacts of invasive species on a national scale are frequently poorly understood. In the absence of coordinated monitoring programmes, indicators related to invasive species are inevitably crude measures (Meyerson *et al.* 2008, this issue) and are not well-suited for detailed trend assessment over time, which is important if biodiversity conservation policies are to be evaluated. More and better-coordinated surveillance programmes are required if we are to prevent new invasions and detect new arrivals before they can become established (Böhm *et al.* 2006).

For some alien invasive species, there is a diverse range of stakeholder groups holding different views and interests, and this can also hinder progress towards achieving objectivity and consensus for management. One way in which these can be considered together is within an assessment such as the triple bottom line (Elkington 1998), where social, economic and environmental impacts are considered together. This approach has been used in Australia to highlight the most damaging invasive species (McLeod 2004). However, it was used in that context in an essentially qualitative manner, with the social, economic and environmental impacts considered independently, which means it is difficult to incorporate it into a monitoring programme and to draw comparisons between species.

Andersen (2008, this issue) stresses the importance of participatory approaches in developing risk assessment models. The combination of expert and stakeholder knowledge is an area with rich potential for application to many areas of humanwildlife interactions (Martin *et al.* 2005; Fazey *et al.* 2006), something that has been advocated for alien invasive species management at high levels of government legislation (Wittenberg and Cock 2001), but this approach is rarely integrated within formal research (Dougill *et al.* 2006) and has not been used extensively to date in research on strategic assessments of invasive species.

Recently, the interest in ecosystem-level analysis has led to renewed interest in holistic indicators of ecosystem status. Holistic indices that integrate social, economic and environmental impacts have been applied for assessing ecosystem health (Aguilar 1999; Robertson et al. 2003; Raffaelli et al. 2005) and these may provide a means of progressing the 'triple bottom line concept' further in a way that is more amenable to invasive species management. The production of a single index is advantageous in enabling comparisons and evaluating progress. This is also the method's weakness, in terms of the assumptions inherent in combining across the social, economic and environmental categories. However, this also provides a mechanism for enhancing stakeholder participation, since the weightings accorded to the different components of the index can be discussed and agreed on by the stakeholder groups, and the sensitivity of the index to changes in the weightings of these components can also be quantified. The application of this type of holistic approach could make a useful contribution to policy decisions regarding invasive species management.

# Conclusions and recommendations for future research

The papers in this special issue draw together some of the key principles and current knowledge for managing the impacts of alien invasive species. There have been considerable advances in terms of the understanding of species spread, assisted by the development of new, more sophisticated modelling techniques. Models based on behavioural processes at the individual level, coupled with an application of genetic technology, hold considerable promise for enhancing our ability to predict species spread, and may also provide insights into novel ways of managing their impacts or reducing populations. There has also been a growing realisation that invasion biology should not be viewed as an isolated area of study, but that it can contribute to enhancing our understanding of conservation biology as a whole.

We are in an era of unprecedented environmental change, and the adverse impacts of alien invasive species on native biodiversity are expected to increase with climate change. For example, recent research has confirmed that climate change, by increasing the spread of the chytrid fungus (Batrachochytrium dendrobatidis), is a factor behind global declines in amphibian populations (Pounds et al. 2006). Further impacts on biodiversity from environmentally induced changes in host-parasite dynamics are likely to occur increasingly in the future. Advances in scientific understanding of invasion biology, such as those described in this special issue, will help us to intervene more effectively to limit the impacts of invasive species. However, they will not help us to decide when we should intervene. This and many other questions surrounding alien invasive species are not scientific ones. Scientists can investigate causes and consequences of invasions, and quantify their impacts. But decisions as to what impacts are desirable or not, and whether or not and how invasive species should be managed are questions for society. Intervention in some cases may need to be rapid, but a mechanism may not be in place to implement a rapid intervention. Management actions are usually the responsibility of government agencies; but unless resources and pre-emptive plans are in place, then an effectively timely intervention is unlikely to take place, even if it would be an expression of the public will.

There are many opportunities for enhancing the social dimensions of alien invasive species research, and integrated assessments of the social, economic and environmental impacts of species provide one way in which these can be advanced. The absence of a research paper on the social impacts and consequences of invasive species from this issue reflects the lack of formal investigation of these issues to date, and therefore the need for expansion in this area. There is also a need to increase stakeholder participation in the decision-making process regarding invasive species. With environmental change and globalisation of trade, the pressure from new introduced species and the impacts of already established invasive species will only amplify. Increasingly, we will need to make hard decisions about when to intervene or when to leave alone. Active engagement with stakeholder groups will be an important part of this deliberation process, and is essential if we are to capture the greatest value to society from alien invasive species management.

#### Acknowledgements

We are grateful to Camilla Myers for all her help and enthusiasm in putting together this Special Issue, and to all the authors and reviewers for their contributions. The Special Issue arose partly out of a symposium run by The Mammal Society (UK) in London in November 2006. We thank The Mammal Society, Defra, the Invasive Animals CRC and the Zoological Society of London for their support for the symposium.

### References

- Aguilar, B. J. (1999). Applications of ecosystem health for the sustainability of managed systems in Cost Rica. *Ecosystem Health* 5, 36–48. doi:10.1046/j.1526-0992.1999.09905.x
- Andersen, M. C. (2008). The roles of risk assessment in the control of invasive vertebrates. *Wildlife Research* 35, 242–248. doi:10.1071/WR07107
- Anon. (1995*a*). 'Biodiversity: the UK Steering Group Report, Volume 1: Meeting the Rio Challenge.' (HMSO: London.)
- Anon. (1995b). 'Biodiversity: the UK Steering Group Report, Volume 2: Action Plans.' (HMSO: London.)
- Atkinson, I. A. E. (1996). Introductions of wildlife as a cause of species extinctions. *Wildlife Biology* 2, 135–141.
- Böhm, M., White, P. C. L., Daniels, M. J., Allcroft, D., Munro, R., and Hutchings, M. R. (2006). The health of wild red and sika deer in Scotland: an analysis of key endoparasites and recommendations for monitoring disease. *Veterinary Journal* **171**, 287–294. doi:10.1016/ j.tvjl.2004.10.020
- Bomford, M., and Hart, Q. (2002). Non-indigenous vertebrates in Australia. In 'Biological Invasions: Environmental and Economic Costs of Alien Plant, Animal and Microbe Invasions'. (Ed. D. Pimental.) pp. 25–44. (CRC Press: New York.)
- Born, W., Rauschmayer, F., and Bräuer, I. (2005). Economic evaluation of biological invasions – a survey. *Ecological Economics* 55, 321–336.
- Bosch, J., Carrascal, L. M., Duran, L., Walker, S., and Fisher, M. C. (2007). Climate change and outbreaks of amphibian chytridiomycosis in a montane area of Central Spain; is there a link? *Proceedings of the Royal Society of London, Series B* 274, 253–260. doi:10.1098/rspb.2006.3713
- Brook, B. W. (2008). Synergies between climate change, extinctions and invasions. *Wildlife Research* 35, 249–252. doi:10.1071/WR07116
- Brown, J. H. (1995). 'Macroecology.' (University of Chicago Press: Chicago, IL.)
- Brown, J. H., and Sax, D. F. (2004). An essay on some topics concerning invasive species. *Austral Ecology* 29, 530–536. doi:10.1111/j.1442-9993.2004.01340.x
- Cassey, P., Blackburn, T. M., Duncan, R. P., and Lockwood, J. L. (2008). Lessons from exotic species as a possible information source for managing translocations of birds. *Wildlife Research* 35, 193–201. doi:10.1071/WR07109
- Caut, S., Casanovas, J., Virgos, E., Lozano, J., Witmer, G., and Courchamp, F. (2007). Rats dying for mice: modeling the competition release effect. *Austral Ecology* **32**, 858–868. doi:10.1111/j.1442-9993.2007.01770.x
- Clout, M. N., and Lowe, S. J. (2000). Invasive species and environmental changes in New Zealand. In 'Invasive Species in a Changing World'. (Eds H. A. Mooney and R. J. Hobbs.) pp. 369–383. (Island Press: Washington, DC.)
- Clout, M. N., and Russell, J. C. (2008). The invasion ecology of mammals: a global perspective. *Wildlife Research* 35, 180–184. doi:10.1071/ WR07091
- Copp, G. H., Garthwaite, R., and Gozlan, R. E. (2005). Risk identification and assessment of non-native freshwater fishes: a summary of concepts and perspectives on protocols for the UK. *Journal of Applied Ichthyology* 21(4), 371–373. doi:10.1111/j.1439-0426.2005.00692.x
- Courchamp, F., Chapuis, J.-L., and Pascal, M. (2003). Mammals invaders on islands: impact, control and control impact. *Biological Reviews of the Cambridge Philosophical Society* 78, 347–383. doi:10.1017/ S1464793102006061
- Cree, A., Daugherty, C. H., and Hay, J. H. (1995). Reproduction of a rare reptile, the tuatara *Sphenodon punctatus*, on rat-free and rat-inhabited islands in New Zealand. *Conservation Biology* 9, 373–383. doi:10.1046/ j.1523-1739.1995.9020373.x
- Cronk, Q. C. B. (1997). Islands: stability, diversity, conservation. Biodiversity and Conservation 6, 477–493. doi:10.1023/A:10183729 10025

- Davis, M. A., Grime, J. P., and Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88(3), 528–534. doi:10.1046/j.1365-2745.2000.00473.x
- De Queiroz, A. (2005). The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology & Evolution* 20, 68–73. doi:10.1016/ j.tree.2004.11.006
- Dolman, P. M., and Wäber, K. (2008). Ecosystem and competition impacts of introduced deer. Wildlife Research 35, 202–214. doi:10.1071/ WR07114
- Dougill, A. J., Fraser, E. D. G., Holden, J., Hubacek, K., Prell, C., Reed, M. S., Stagl, S., and Stringer, L. C. (2006). Learning from doing participatory rural research: lessons from the Peak District National Park. *Journal of Agricultural Economics* 57, 259–275. doi:10.1111/ j.1477-9552.2006.00051.x
- Duncan, R. P. (1997). The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. *American Naturalist* 149, 903–915. doi:10.1086/286029
- Ehrenfeld, D. (2005). The environmental limits to globalization. Conservation Biology 19, 318–326. doi:10.1111/j.1523-1739.2005. 00324.x
- Elkington, J. (1998). 'Cannibals with Forks: the Triple Bottom Line of 21st Century Business.' (New Society Publishers: Gabriola Island, BC.)
- Engeman, R. M., Smith, H. T., Shwiff, S. A., Constantin, B. U., Nelson, M., Griffin, D., and Woolard, J. (2003). Prevalence and economic value of feral swine damage to native habitat in three Florida state parks. *Environmental Conservation* **30**, 319–324. doi:10.1017/ S0376892903 00033X
- Engeman, R. M., Shwiff, S. A., Smith, H. T., and Constantin, B. U. (2004*a*). Monetary valuation of rare species and imperiled habitats as a basis for economically evaluating conservation approaches. *Endangered Species Update* 21, 66–73.
- Engeman, R. M., Smith, H. T., Severson, R., Severson, M. A., Woolard, J., Shwiff, S. A., Constantin, B. U., and Griffin, D. (2004b). Damage reduction estimates and benefit-cost values for feral swine control from the last remnant of a basin marsh system in Florida. *Environmental Conservation* 31, 207–211. doi:10.1017/S0376892904001572
- Engeman, R. M., Stevens, A., Allen, J., Dunlap, J., Daniel, M., Teague, D., and Constantin, B. (2007). Feral swine management for conservation of an imperiled wetland habitat: Florida's vanishing seepage slopes. *Biological Conservation* 134, 440–446. doi:10.1016/j.biocon. 2006.08.033
- Eycott, A. E., Watkinson, A. R., Hemami, M.-R., and Dolman, P. M. (2007). The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. *Oecologia* 154, 107–118. doi:10.1007/s00442-007-0812-1
- Fazey, I., Fazey, J. A., Salisbury, J. G., Lindenmayer, D. B., and Dovers, S. (2006). The nature and role of experiential knowledge for environmental conservation. *Environmental Conservation* 33, 1–10. doi:10.1017/ S037689290600275X
- Fowler, S., and Lindström, J. (2002). Extinctions in simple and complex communities *Oikos* 99(3), 511–517. doi:10.1034/j.1600-0706.2002. 11757.x
- Fuller, P. L. (2003). Freshwater aquatic vertebrate introductions in the United States: patterns and pathways. In 'Invasive Species: Vectors and Management Strategies'. (Eds G. M. Ruiz and J. T. Carlton.) pp. 123–151. (Island Press: Washington, DC.)
- Gaston, K. J., Jones, A. G., Hanel, C., and Chown, S. L. (2003). Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 270, 1091–1098. doi:10.1098/rspb.2003.2332
- Gleeson, D., Harman, H., and Armstrong, T. (2006). Genetics of invasive species in New Zealand. In 'Biological Invasions in New Zealand'. (Eds R. B. Allen and W. G. Lee.) *Ecological Studies* 186, 103–118.
- Glen, A. S., and Dickman, C. R. (2005). Complex interactions among mammalian carnivores in Australia, and their implications for wildlife

management. *Biological Reviews of the Cambridge Philosophical* Society **80**, 387–401. doi:10.1017/S1464793105006718

- Gobster, P. H. (2005). Invasive species as ecological threat: is restoration an alternative to fear-based resource management? *Ecological Research* 23, 261–270. doi:10.3368/er.23.4.261
- Gordon, I. J., Hester, A. J., and Festa-Bianchet, M. (2004). The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* **41**, 1021–1031. doi:10.1111/j.0021-8901.2004.00985.x
- Goudswaard, P. C., Witte, F., and Katunzi, E. F. B. (2002). The tilapiine fish stock of Lake Victoria before and after the Nile perch upsurge. *Journal* of Fish Biology 60, 838–856. doi:10.1111/j.1095-8649.2002.tb02413.x
- Green, R. E. (1997). The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *Journal of Animal Ecology* 66, 25–35. doi:10.2307/5961
- Gren, I.-M. (2008). Economics of invasive species management choices of targets and policies. *Boreal Environment Research* 13, 17–32.
- Gurevitch, J., and Padilla, D. K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* 19, 470–474. doi:10.1016/j.tree.2004.07.005
- Gurnell, J., Rushton, S. P., Lurz, P. W. W., Sainsbury, A. W., Nettleton, P., Shirley, M. D. F., Bruemmer, C., and Geddes, N. (2006). Squirrel poxvirus: landscape scale strategies for managing disease threat. *Biological Conservation* 131, 287–295. doi:10.1016/j.biocon. 2006.04.009
- Hall, G. P., and Gill, K. P. (2005). Management of wild deer in Australia. *The Journal of Wildlife Management* 69, 837–844. doi:10.2193/0022-541X(2005)069[0837:MOWDIA]2.0.CO;2
- Hannon, B. (1992). Measures of economic and ecological health. In 'Ecosystem Health: New Goals for Environmental Management'. (Eds R. Constanza, B. G. Norton and B. J. Haskell.) pp. 207–222. (Island Press: Washington, DC.)
- Hemami, M. R., Watkinson, A. R., and Dolman, P. M. (2004). Habitat selection by sympatric muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a lowland commercial pine forest. *Forest Ecology and Management* 194, 49–60. doi:10.1016/j.foreco.2004.01.049
- Hemami, M. R., Watkinson, A. R., and Dolman, P. M. (2005). Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus* capreolus in a lowland pine forest. *Forest Ecology and Management* **215**, 224–238. doi:10.1016/ j.foreco.2005.05.013
- Hogg, A. G., Higham, T. F. G., Lowe, D. J., Palmer, J. G., Reimer, P. J., and Newnham, R. M. (2003). A wiggle-match date for Polynesian settlement of New Zealand. *Antiquity* 77, 116–125.
- Höijer, L., Korpimäki, E., Leppäkoski, E., Niemelä, P., Nordström, M., and Salo, P. (2008). Alien species – environment, biorisks, future. *Boreal Environment Research* 13, 1–2.
- Hughes, J. D. (2003). Europe as consumer of exotic biodiversity: Greek and Roman times. *Landscape Research* 28(1), 21–31. doi:10.1080/0142639 0306535
- IPCC (2007). 'Summary for Policymakers. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.' (Cambridge University Press: Cambridge.)
- IUCN (2000). 'IUCN Guidelines for the Prevention of Biodiversity Loss caused by Alien Invasive Species.' Information Paper from the Fifth Meeting of the Conference of the Parties to the Convention on Biological Diversity, approved by the 51st Meeting of Council, February 2000. (IUCN: Gland..)
- Jeschke, D. M., and Strayer, D. L. (2005). Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 7198–7202. doi:10.1073/pnas.0501271102

- Kolar, C. S., and Lodge, D. (2001). Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* 16, 199–204. doi:10.1016/ S0169-5347(01)02101-2
- Kraus, F. (2003). Invasion pathways for terrestrial vertebrates. In 'Invasive Species: Vectors and Management Strategies'. (Eds G. M. Ruiz and J. T. Carlton.) pp. 68–92. (Island Press: Washington, DC.)
- Kutz, S. J., Hoberg, E. P., Polley, L., and Jenkins, E. J. (2005). Global warming is changing the dynamics of Arctic host-parasite systems. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 272, 2571–2576. doi:10.1098/rspb.2005.3285
- Lafferty, K. D., and Gerber, L. R. (2002). Good medicine for conservation biology: the intersection of epidemiology and conservation theory. *Conservation Biology* 16, 593–604. doi:10.1046/j.1523-1739.2002. 00446.x
- Leonard, S. W. J., and Kirkpatrick, J. B. (2004). Effects of grazing management and environmental factors on native grassland and grassy woodland, Northern Midlands, Tasmania. *Australian Journal of Botany* 52, 529–542. doi:10.1071/BT03106
- Lever, C. (1977). 'The Naturalized Animals of the British Isles.' (Hutchinson & Co.: London.)
- Lever, C. (1985). 'Naturalized Mammals of the World.' (Longman: London.)
- Lever, C. (1996). 'Naturalized Fishes of the World.' (Academic Press: London.)
- Lever, C. (2001). 'The Cane Toad. The History and Ecology of a Successful Colonist.' (Westbury Academic and Scientific Publishing: Otley, UK.)
- Lockwood, J. L., Hoopes, M. F., and Marchetti, M. P. (2007). 'Invasion Ecology.' (Blackwell Publishing: Oxford.)
- Loomis, J. B., and White, D. S. (1996). Economic benefits of rare and endangered species: summary and meta-analysis. *Ecological Economics* 18, 197–206. doi:10.1016/0921-8009(96)00029-8
- Lunney, D., Eby, P., Hutchings, P., and Burgin, S. (2007). 'Pest or Guest: the Zoology of Overabundance.' (Royal Zoological Society of New South Wales: Mosman.)
- Mack, R. N. (2003). Global plant dispersals, naturalization, and invasion: pathways, modes, and circumstances. In 'Invasive Species: Vectors and Management Strategies'. (Eds G. M. Ruiz and J. T. Carlton.) pp. 3–30. (Island Press: Washington, DC.)
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., and Bazzaz, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10, 689–710. doi:10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2
- Maddock, M., and Geering, D. (1994). Range expansion and migration of the cattle egret. *The Ostrich* 65, 191–203.
- Mageau, M., Constanza, R., and Ulanowicz, R. (1995). The development and initial testing of a quantitative assessment of ecosystem health. *Ecosystem Health* 1, 201–213.
- Martin, T. G., Kuhnert, P. M., Mengersen, K., and Possingham, H. P. (2005). The power of expert opinion in ecological models using Bayesian methods: Impact of grazing on birds. *Ecological Applications* 15, 266–280. doi:10.1890/03-5400
- McKinney, M. L., and Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends* in Ecology & Evolution 14, 450–453. doi:10.1016/S0169-5347(99) 01679-1
- McLeod, R. (2004). 'Counting the Cost: Impact of Invasive Animals in Australia, 2004.' (Pest Animal Control CRC: Canberra.)
- Meyerson, L. A., Engeman, R., and O'Malley, R. (2008). Tracking nonnative vertebrate species: indicator design for the United States of America. *Wildlife Research* 35, 235–241. doi:10.1071/WR07098
- Mooney, H. A., and Hobbs, R. J. (2000). 'Invasive Species in a Changing World.' (Island Press: Washington, DC.)
- Moriarty, A. (2004). The liberation, distribution, abundance and management of wild deer in Australia. *Wildlife Research* **31**, 291–299. doi:10.1071/WR02100

- Myers, K. (1986). Introduced vertebrates in Australia with emphasis on the mammals. In 'Ecology of Biological Invasions: An Australian Perspective'. (Eds R. H. Groves and J. J. Burdon.) pp. 120–136. (Australian Academy of Science: Canberra.)
- O'Dowd, D. J., Green, P. T., and Lake, P. S. (2003). Invasional 'meltdown' on an oceanic island. *Ecology Letters* 6, 812–817. doi:10.1046/j.1461-0248.2003.00512.x
- Olson, L. (2006). The economics of terrestrial invasive species: a review of the literature. Agricultural and Resource Economics Review 35, 178–194.
- Phillips, B. L., Brown, G. P., Greenlees, M., Webb, J. K., and Shine, R. (2007). Rapid expansion of the cane toad (*Bufo marinus*) invasion front in tropical Australia. *Austral Ecology* **32**, 169–176. doi:10.1111/j.1442-9993.2007.01664.x
- Phillips, B. L., Chipperfield, J. D., and Kearney, M. R. (2008). The toad ahead: challenges of modelling the range and spread of an invasive species. *Wildlife Research* 35, 222–234. doi:10.1071/WR07101
- Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., and Fogden, M. P. L., *et al.* (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167. doi:10.1038/nature04246
- Raffaelli, D., White, P. C. L., Perrings, C. A., Smart, J. S., and Renwick, A. (2005). 'The Future of Healthy Ecosystems.' Report to Defra. (University of York: York.)
- Rapport, D. J., Bohm, G., Buckingham, D., Cairns, J., Jr, and Costanza, R., et al. (1999). Ecosystem Health: the concept, the ISEH, and the important tasks ahead. *Ecosystem Health* 5, 82–90. doi:10.1046/j.1526-0992.1999.09913.x
- Robertson, M. P., Villet, M. H., Fairbanks, D. H. K., Henderson, L., and Higgins, S. I., *et al.* (2003). A proposed prioritization system for the management of invasive alien plants in South Africa. *South African Journal of Science* **99**, 1–7.
- Russell, J. C., Beaven, B. M., McKay, J. W. B., Towns, D. R., and Clout, M. N. (2008). Testing island biosecurity systems for invasive rats. *Wildlife Research* 35, 215–221. doi:10.1071/WR07032
- Salo, P., Korpimäki, E., Banks, P. B., Nordström, M., and Dickman, C. R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 274, 1237–1243. doi:10.1098/rspb.2006.0444
- Savolainen, P., Leitner, T., Wilton, A. N., Matisoo-Smith, E., and Lundeberg, J. (2004). A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of* the National Academy of Sciences101, 12387–12390.
- Sax, D. F., and Gaines, S. D. (2003). Species diversity: from global decreases to local increases. *Trends in Ecology & Evolution* 18, 561–566. doi:10.1016/S0169-5347(03)00224-6
- Schlaepfer, M. A., Sherman, P. W., Blossey, B., and Runge, M. C. (2005). Introduced species as evolutionary traps. *Ecology Letters* 8, 241–246. doi:10.1111/j.1461-0248.2005.00730.x
- Searle, J. B. (2008). The genetics of mammalian invasions: a review. Wildlife Research 35, 185–192. doi:10.1071/WR07123
- Simberloff, D., Dayan, C., Jones, C., and Ogura, G. (2000). Character displacement and release in the small Indian mongoose, *Herpestes javani*cus. Ecology 81, 2086–2099.
- Skellam, J. G. (1951). Random dispersal in theoretical populations. *Biometrika* 38, 196–218.
- Smith, K. F., Sax, D. F., Gaines, S. D., Guernier, V., and Guegan, J. F. (2007). Globalization of human infectious disease. *Ecology* 88, 1903–1910. doi:10.1890/06-1052.1
- Symstad, A. J. (2000). A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81, 99–109.
- Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J., and Kuris, A. M. (2003). Introduced species and their missing parasites. *Nature* 421, 628–630. doi:10.1038/nature01346

- Towns, D. R., Parrish, G. R., Tyrell, C. L., Ussher, G. T., Cree, A., Newman, D. G., Whitaker, A. H., and Westbrooke, I. (2007). Responses of tuatara (*Sphenodon punctatus*) to removal of introduced Pacific rats from islands. *Conservation Biology* 21, 1021–1031. doi:10.1111/j.1523-1739.2007.00742.x
- Vermeij, G. J. (1991). When biotas meet: understanding biotic interchange. Science 253, 1099–1104. doi:10.1126/science.253.5024.1099
- Verschuren, D., Johnson, T. C., Kling, H. J., Edgington, D. N., Leavitt, P. R., Brown, E. T., Talbot, M. R., and Hecky, R. E. (2002). History and timing of human impact on Lake Victoria, East Africa. *Proceedings of the Royal Society Series B* 269, 289–294. doi:10.1098/rspb.2001.1850
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science* 277, 494–499. doi:10.1126/science.277.5325.494
- White, P. C. L., Gregory, K. W., Lindley, P. J., and Richards, G. (1997). Economic values of threatened mammals in Britain: a case study of the otter *Lutra lutra* and the water vole *Arvicola terrestris*. *Biological Conservation* 82, 345–354. doi:10.1016/S0006-3207(97)00036-0

- White, P. C. L., Bennett, A. C., and Hayes, E. J. V. (2001). The use of willingness-to-pay approaches in mammal conservation. *Mammal Review* 31, 151–167. doi:10.1046/j.1365-2907.2001.00083.x
- Williamson, M. (1996). 'Biological Invasions.' (Chapman & Hall: London.) Williamson, M., and Fitter, A. (1996). The varying success of invaders.
- Ecology 77, 1661–1666. doi:10.2307/2265769 Wittenberg, R., and Cock, M. J. W., Eds (2001). 'Invasive Alien Species:
- A Toolkit of Best Prevention and Management Practises.' (CAB International: Wallingford, Oxford.) Xu, W., and Mage, J. A. (2001). A review of concepts and criteria for assess-
- Xu, w., and Mage, J. A. (2001). A review of concepts and criteria for assessing agroecosystem health including a preliminary case study of southern Ontario. Agriculture Ecosystems & Environment 83, 215–233. doi:10.1016/S0167-8809(00)00159-6

Manuscript received 15 April 2008, accepted 15 April 2008