

# Impacts and management of invasive burrowing herbivores in grasslands

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**Abstract.** Maintenance of the productivity of the world's grasslands is critical for livestock production, biodiversity conservation and ecosystem services. Using case studies from Australasia, North America and China, we identify general principles of managing invasive native and introduced herbivores. Management aims to achieve optimised livestock production while conserving biodiversity and ecosystem services, which are often intangible. We identify similarities and differences in the ecologies and impacts of European wild rabbits, Californian ground squirrel and plateau zokors, discuss management tools and strategies, and the ecological, social and cultural factors affecting management. The ecosystem engineering characteristics of these species that make them important for ecosystem function in grasslands are perversely the selfsame ones that bring them into conflict with livestock producers. All three species create habitat patches through their burrowing and foraging behaviours, but changes in vegetation floristics and structure, increased soil exposure and decreased litter negatively affect grassland and livestock production when the animals are superabundant. Management is therefore complex and we recommend an adaptive approach that is founded on the scientific knowledge of the local agri-ecosystem, economic principles and social inclusion to increase knowledge and iteratively improve management.

**Keywords:** Rabbits, ground squirrels, zokors, invasive, adaptive management.

## Introduction

Grasslands constitute 40.5% of the world's terrestrial ecosystems and are critical for livestock production, biodiversity and environmental services (Suttie *et al.* 2005a). The forecast growth rate for human population over the next half century is 1.2% per year on the 7 billion reached in 2011 (US Census in Chavas 2011). This places an imperative to improve production efficiency for all primary industries, including grassland-based meat and fibre production. Reduction in losses caused by invasive animals, both native and introduced, will be important in improving efficiency of livestock production systems around the world.

Degradation of grassland ecosystems, by factors including herbivorous invasive species, impacts upon their production almost everywhere (Suttie *et al.* 2005b). However, despite the importance of grasslands for food production, most research on the impacts of invasive herbivores has been conducted on those animals that cause damage to high value and intensive food crops (*e.g.* rodents, Jacob and Tkadlec 2010; Stenseth *et al.* 2003) and their storage, or to forestry (*e.g.* ungulates and macropods: Jorritsma *et al.* 1999; Reimoser *et al.* 1999; Bulinski and McArthur 1999; Di Stefano *et al.* 2007). A recent review (Davidson *et al.* 2012) concentrated on losses of ecosystem

services and biodiversity responses to declines in burrowing, herbivorous mammals but neglected the adverse effects some have on agriculture.

Here, we briefly review general principles of invasive animal management, the ecological characteristics of invasive herbivores pertaining to their impacts on grazing systems and their management, and technical and social factors that affect management. We address the management of invasive burrowing herbivores through specific case studies, one each from Australasia, North America and China. The case study animals are all colonial, burrowing, herbivorous small mammals, but one is introduced and the others are native. They are used to demonstrate generalities of management, while identifying crucial differences that must be considered when devising strategies that work for the people involved and their local agri-ecosystems.

## Principles of invasive animal management

### *Adaptive management*

Adaptive management (Walters and Hilborn 1978) is a process whereby the knowledge required for implementing efficacious and efficient strategies to achieve production and conservation goals is collected and iteratively improved using scientific methods. Because knowledge about an ecosystem of interest is usually deficient and often in-

sufficient to confidently predict the outcomes of management strategies, the adaptive management strategy is best for applying current knowledge whilst incorporating capacity for gaining and including new knowledge (Braysher 1993; Gunderson 1999).

The process of adaptive management includes the following key steps: (1) defining the issue including the people, current knowledge, species involved and their biology, ecology and impacts; (2) setting measurable objectives with a timeframe; (3) devising a plan incorporating either active or passive experimentation to assess strategies; (4) monitoring all the relevant parameters including operational costs and changes in impacts, and denoting responsibilities and reporting frameworks; and (5) using the monitoring data to iteratively improve management through gained knowledge. Although many adaptive management programs have begun with high hopes but failed to deliver (Allan and Curtis 2005), there are many examples of successful implementation including management of large ungulate systems in Kruger National Park in South Africa (Parr *et al.* 2009) and free-ranging dog management in eastern Australia (Fleming *et al.* 2006; Chapple *et al.* 2011). Successful adaptive management, including that of invasive fossorial and semi-fossorial mammals, requires sufficient definition of the issue using all the available knowledge and identification of key knowledge deficits that require work within the framework.

#### Ecological factors

Ecological principles are being applied more and more in the adaptive framework to make management of invasive rodents and European wild rabbits (*Oryctolagus cuniculus*) more effective, cost-beneficial, and ecologically and economically sustainable (Williams *et al.* 1995; Caughley *et al.* 1998). A detailed understanding of biology enables the identification of stress points in animal life cycles that can be targeted for more efficacious control or for enhancing survival for conservation.

Some knowledge of ecological variables including home range size and use, sociality and group size, rates of population increase, densities and dynamics, diet selectivity, patterns of breeding and their triggers, mortality factors and recolonisation characteristics is also required for strategic management plans. All these factors need quantification if management strategies are to be effective in reducing damage to grasslands and livestock production. Semi-fossorial mammals can have important functions either beneficially through facilitation of other species (*e.g.* vizcachas *Lagostomus maximus* and hairy armadillos *Chaetophractus villosus* facilitating burrowing owl *Athene cunicularia* populations by providing nest sites; Machicote *et al.* 2004) or adversely through their component of total grazing pressure (*e.g.* rabbits, red kangaroos *Macropus rufus* and cattle in semi-arid rangelands; Low and Low 1975) and alteration of vegetation community structure (*e.g.* Bird *et al.* 2012).

Understanding predator–prey interactions and interactions among herbivores also allows the prediction of the consequences of management strategies that should be considered before management is commenced. For example, European wild rabbits are seen as a keystone species in

southern Europe (Delibes-Mateos *et al.* 2007) and declining wild rabbit abundance is a process threatening Iberian lynx (*Lynx pardinus*) and Iberian imperial eagle (*Aquila adalberti*) with extinction in Spain (Moreno *et al.* 2004; Cabezas-Díaz *et al.* 2009). Rabbit decline is, in turn, threatened by loss of habitat, hunting by humans (Angulo and Villafuerte 2004) and disease (Cabezas-Díaz *et al.* 2009).

#### Economic factors

Of primary concern to livestock production are the financial losses caused by invasive semi-fossorial herbivores, and the costs of control and land rehabilitation, including weed removal, repasturing and soil restoration. Losses to livestock production are sometimes subtle, and often synergistic. For example, plateau zokor (*Myospalax baileyi*) population increases in Qinghai-Tibet have been associated with sheep overgrazing, leading to gradually reduced carrying capacity of sheep and long term land degradation, which benefited plateau zokor populations (Fan Nainchang *et al.* 1999). In Australia, much of the semi-arid rangelands in the Western Division of NSW degraded by overgrazing by sheep and rabbits between 1890 and 1910 did not recover carrying capacity and floristic diversity until after Rabbit Haemorrhagic Disease Virus (RHDV) had substantially reduced rabbit populations after 1995 (Denham and Auld 2004).

The underlying premise for economic evaluation of damage and management strategies is an understanding of the relationship between the density of the invasive species and the damage it causes (Hone 1994). The shape of density–damage functions (or their inverse, density–yield functions; Hone 2007) determines what analyses are applicable, and underpin comparisons of control techniques and strategies to optimise production or conservation gains. The simplest of density–damage curves is a monotonically increasing regression, where an increase in pest density is matched with a constant incremental increase in damage (Hone 1994). However, it is difficult to generalise density–damage functions across ecosystems because local productivity will alter the shape and slope of the curve.

#### Social factors

The successful management of animal populations, invasive species and their impacts is dependent on understanding social factors surrounding the issue (Gunderson 1999; Stenseth *et al.* 2003; Chapple *et al.* 2011). In Australasia for example, rabbits were introduced for the benefit of humans and, indeed, were initially protected in Victoria (Coman 1999). Rabbits were important food sources during the Great Depression and so provided a public good for some (Rolls 1984), whereas others regarded them as vermin.

Societal attitudes change, but they influence what can be done to manage damaging vertebrates (Fall and Jackson 1998). There is often conflict between elements of society that are adversely affected by invasive species and those that are not. It is important that management of animals, particularly when management involves their killing, falls within the prevailing “social licence” (Prno and Slocombe 2012). In adaptive management of invasive species all stakeholders that are directly affected must be included in

the planning and actions. Without such inclusivity and ownership, management programs are doomed to failure in the long term.

## Invasive herbivores and grasslands

### *Characteristics of invasive herbivores of grasslands*

Invasive animals can be naturally occurring native species or species introduced into new ecosystems by humans. The success of invasive animals is often facilitated by anthropogenic landscape changes that encourage them or disadvantage their competitors. Invasive herbivores can be large (for example feral ungulates and overabundant macropods), medium sized such as the lagomorphs and larger rodents, or small like the more ubiquitous mice and rats. Damage seems to be unrelated to size and is usually associated with overabundance.

The primary common characteristic of invasive animals is that they are able to respond to introduction or human disturbance of ecosystems by establishing, becoming abundant, and expanding their range (Williamson 1996). Often, these species have few competitors or predators in their new or modified ecosystem. Ehrlich (1989) reiterated the importance of a human connection in successful invasions, and indicated that, in general, successful invaders have large native ranges where they are naturally abundant, have a broad diet, short generation times, genetic variability (and hence phenotypic plasticity and ability to function across a wide range of physical conditions), and are reproductively *r*-selected or able to switch between *r* and *k* life strategies. The combination of reproductive strategy and short generation time enables rapid population increase, and diet plasticity enables ready acclimatisation to novel foods and rapid increase when environmental conditions are optimum.

### *General impacts*

Many of the world's grasslands are shaped and maintained by burrowing mammals (Davidson *et al.* 2012) and this is often seen as a positive or ecosystem service (Kotliar *et al.* 1999). These services include nutrient recycling through burrowing activities, providing shelter and refuge for other fauna including threatened species (*e.g.* Grillet *et al.* 2010), and providing food for predators, some of which are endangered (Davidson *et al.* 2012). Ecosystem services, for example the ground water and riverflows sourced by annual snowmelt in California and the Tibetan Plateau, are mostly intangible but essential for healthy and productive ecosystems.

Where these animals also cause damage to human production activities or amenity, human-wildlife conflict is inevitable and consensus between people who favour or disfavour them is difficult to achieve (Stenseth *et al.* 2003). Negative impacts include competition with livestock and other herbivores, overgrazing, weed infestation, erosion, increased runoff and downstream siltation, and land degradation. All these lead to reduced productivity and often are associated with reduced natural biodiversity. Invasive animals are often an important source of protein for the resident people, which, although often ignored in cost-benefit analyses, is a direct positive impact that has value.

## Case Studies

We use three case studies from around the world to highlight the generalities of invasive herbivore management, and identify site- and species-specific differences that are crucial to devising management strategies that work for the people involved and their local agri-ecosystems.

### *Case study 1: Ecology, impacts and management of European wild rabbits in Australasia*

#### Study region, biology and ecology

Grazing of grasslands constitutes 55% of Australian land use and >80% of this is of native vegetation (State of the Environment Committee 2011). Prior to European migration and settlement, grasslands were home to a varied fauna, including small semi-fossorial herbivores such as the Greater and Lesser bilbies (*Macrotis lagotis* and *M. lucu-rra*), the latter becoming extinct last century. In New Zealand, grasslands now make up about 60% of the land mass (Percival *et al.* 2000), and most are anthropogenic through clearing and burning activities of Maori and European settlers. There are also indigenous tussock grasslands (Mark and McLennan 2005).

The European wild rabbit is a grey-brown burrowing leporid between 1.0 and 2.25 kg (adult weight), with long erect ears, long hind legs and claws. It forages above ground, mostly on short grasses and herbs. It is native to the Iberian peninsula, south western France and north western Africa, where it is considered near threatened (Smith and Boyer 2008) and a keystone species (Delibes-Mateos *et al.* 2011). Rabbits construct large and often deep (3 m) colonial warrens, usually comprising about 2 to 10 adults, which provide nests and protection from predators and climatic extremes. Females are highly fecund, producing about 5 litters of up to 5 young in a year after age 4 months (Tablado *et al.* 2009). They are active all year and can breed at any time of the year given suitable conditions (Williams *et al.* 1995).

Since their successful introduction into Tasmania by 1822 and into Victoria in 1859 (Coman 1999), rabbits have spread rapidly and occupied most grassland ecosystems in Australia below the Tropic of Capricorn. Rabbits occur in 56% of New Zealand and are considered critical pests of South Island semi-arid grasslands (Parkes *et al.* 2002). It is likely that the success of rabbits in Australia and New Zealand was facilitated by the prior introduction of sheep (Williamson 1996; Mark and McLennan 2005) and active spread by humans (Rolls 1984). Although rabbits are widespread in Australian and New Zealand habitats, they prefer grasslands on loamy soils in Mediterranean climates. They are rarely found on heavy soils with high clay content because these are unsuitable for burrowing (Williams *et al.* 1995).

#### Impacts on grasslands

Apart from minor harvest of pelts and fur for hat-making and some use as meat, European wild rabbits in Australasian grasslands have no economic benefit. Their foraging and burrowing activities negatively affect agricultural and environmental values. Although they provide food for predators including Wedge-tailed eagles (*Aquila audax*) and introduced wild dogs (*Canis lupus spp*), feral ferrets (*Mus-*

*tela putorius furo*), feral cats and European red foxes (*Vulpes vulpes*), they are not considered a keystone herbivore in Australasia.

Prior to the advent of effective biological control in Australia in the 1960s (rabbit myxoma virus) and in both countries in the late 1990s (rabbit haemorrhagic disease) (Cooke and Fenner 2003), rabbits spread rapidly and formed plagues in grasslands (Rolls 1984; Mark and McLennan 2005). High rabbit densities are associated with floristic and structural changes to vegetation (Croft *et al.* 2002), lower livestock carrying capacity, reduced wool production, lower lambing percentages, lower weight gain, more frequent breaks in the wool, earlier stock deaths during droughts and slower recovery after droughts (Williams *et al.* 1995; Bomford and Hart 2002). Gong *et al.* (2009) estimated the annual loss of economic surplus caused by rabbits to Australia was \$AU206 million in 2008 values.

Despite much work on their impacts, biology and control (Williams *et al.* 1995), little is understood about the relationship between rabbit density and damage or yields. In central western NSW, the density–damage function for rabbits on pasture height has been shown to be strongly positive and linear (Croft *et al.* 2002) but the impacts on wool production were not so straight forward, with an implied density threshold below which rabbits are not detrimental to production (Fleming *et al.* 2002). Full economic studies of rabbit damage have not been published for anywhere else in Australasia. The relationships between rabbit densities and grassland environmental variables such as soil exposure, litter deposition rates, flora recruitment and survival, and fauna have seldom been determined (Williams *et al.* 1995; Croft *et al.* 2002). In their region of origin, rabbits burrows are beneficial to burrowing lizard populations (Grillet *et al.* 2010).

#### Management tools and strategies

Traditional physical methods of control include trapping and shooting, which are usually only successful at the local level and when rabbit population densities are low or focal, and private and government exclusion fencing such as the south east Queensland rabbit exclusion zone. Destruction of habitat, including the removal of brush and deep ripping of warrens, is effective for reducing rabbit populations and slowing reinvasion after poisoning and biological control (Mutze 1991; McPhee and Butler 2010). Compound 1080 (sodium fluoroacetate) and pindone (an anticoagulant) are the most frequently used broadscale poisons for rabbit control and are usually distributed on carrot bait (Brown 2012).

The use of biological agents for control of wild rabbits in Australasia have been notably successful (Barlow *et al.* 2002; Saunders *et al.* 2002). Considerable research effort preceded the general Australian release of myxoma virus in the 1950s (Fenner and Ratcliffe 1965), but it was never officially released or established in New Zealand (Parkes *et al.* 2002). RHDV escaped from the trial quarantine facility at Wardang Island, South Australia in October 1995 and rapidly spread through Southern Australia over the following 2 years. At that time, the disease which was illegally released in the South Island of New Zealand and actively spread by farmers, took hold showing high prevalence and death rates (Parkes *et al.* 2002). In 2004, the economic benefit of research investment of RHDV to Australia,

assuming a 50% rabbit population reduction, was between 5.9 and 32.4:1 (Vere *et al.* 2004), which is likely conservative (Saunders *et al.* 2002). The economic benefit to Australia of biological control since myxomatosis was introduced 60 years ago is estimated at \$AU70 billion (Cooke *et al.* 2013).

It is not the tools one uses but how they are applied that has greatest impact on the management of invasive animals, and over the last 25 years considerable effort has been applied to strategic management of rabbits (see Braysher 1993; Williams *et al.* 1995; Braysher and Saunders 2003; Brown 2012). However, land managers of Australian and New Zealand grasslands must guard against complacency and apathy in response to the success of biological control agents.

#### Factors affecting management

Although biological control agents have been very successful in managing rabbit numbers and impacts, in Australia the myxoma virus and rabbits have evolved such that efficacy of field strains to cause death is now about 50% and incidence may be only 5–7% of rabbits (Mutze *et al.* 2010). Similar evolution of resistance to RHDV has been observed (Mutze *et al.* 2008) and cross resistance is provided by antibodies to a naturally occurring rabbit calicivirus RCV-A1 (Strive *et al.* 2010).

An underlying limitation to active rabbit management is the subtleness and indirectness of much rabbit damage. Except during droughts and where the reduced pasture, invasive plants and dead shrubs are apparent around large warrens in semi-arid rangelands, the impacts of rabbits are often inconspicuous. It is also possible that low densities of rabbits are beneficial to some production systems (*e.g.* wool production, Fleming *et al.* 2002), at which time producers have no incentive to control rabbits. The economic framework for rabbit control is often not clear because of the difficulties in measuring the benefits of control. However, a strategic approach that accounts for livestock production system differences, seasonal factors, social factors and rabbit ecology will usually avoid the necessity for crisis management (Williams *et al.* 1995).

#### *Case study 2: Ecology, impacts and management of California ground squirrels in USA*

##### Study region, brief biology and ecology

California's grasslands, an important resource for range livestock production, are unique due to the region's Mediterranean climate (*i.e.* adaptation to rainfall during the coldest months) and the predominance of annual species (Stromberg *et al.* 2007). They are distributed over approximately 100,000 km<sup>2</sup> occurring as open grasslands or as the understorey of oak woodlands and savannahs (Heady *et al.* 1992). These ecosystems support a high biodiversity, including several plant species listed as rare or endangered (Skinner and Pavlik 1994) and several endemic rodents such as the Fresno kangaroo rat (*Dipodomys nitratoides exilis*), Tipton kangaroo rat (*D. n. nitratoides*), giant kangaroo rat (*D. ingens*), California ground squirrel (*Otospermophilus beecheyi*) and San Joaquin pocket mouse (*Perognathus inornatus*) (Goldingay *et al.* 1997).

The California ground squirrel is a burrowing rodent of

about 885 g (adult weight), with a body length of 30 cm and a 15 cm tail. It has mottled grey and brown fur with a lighter buff or greyish yellow underside, and a white ring around each eye (Kays and Wilson 2009). It is widely distributed throughout its native range in western North America, occurring in urban and agricultural areas as well as native grasslands, oak woodlands and savannah habitats. The California ground squirrel prefers open habitats with high visibility, and rarely occurs in areas of heavy tree or brush growth (Grinnell and Dixon 1918; Fehmi *et al.* 2005). It lives in colonies containing up to 20 animals (Marsh 1994) in complex burrow systems for nesting, caching food, hibernating, and sheltering from inclement weather and predators. Burrow systems have multiple entrances and can be as long as 42 m and as deep as 1.7 m (Grinnell and Dixon 1918, Berentsen and Salmon 2001). During the day, ground squirrels are active aboveground, retreating to their burrows in the late afternoon. In winter months most ground squirrels hibernate, and in summer periods of high temperatures some squirrels will aestivate (Fitch 1948).

California ground squirrels are primarily herbivorous, and their diet changes with the season (Fitch 1948). They usually forage within a 70 m radius of their burrows (Boellstorff and Owings 1995), although they have been observed to travel to bait stations placed up to 100 m away (Whisson and Salmon 2009). After emerging from winter hibernation, they feed almost exclusively on green grasses and herbaceous plants and a single litter, averaging 8 young, is produced in spring. Time of breeding varies throughout the species' range with breeding occurring earlier in the southern, warmer areas. When annual plants begin to dry and produce seed, squirrels switch to feeding on seeds, grains, and nuts, and also begin to store food underground.

#### Impacts on grasslands

The value of California ground squirrels impacts in grasslands is poorly understood although likely to be significant. Ground squirrels are ecosystem engineers, creating a mosaic of disturbance patches in grasslands as a result of their grazing on vegetation, trampling of trails, mound building, and burrowing. Their burrow systems are used as shelter or nest sites by other species, including some of conservation concern (*e.g.* burrowing owl, *Athene cunicularia*, Dechant *et al.* 2003; California tiger salamander, *Ambystoma californiense*, Loredó-Prendeville *et al.* 1994). Carnivores such as the San Joaquin kit fox (*Vulpes macrotis mutica*), coyote (*Canis latrans*) and American badger (*Taxidea taxus*) commonly modify California ground squirrel burrows for their own dens. Furthermore, California ground squirrels provide an important prey source to a large suite of predators including raptors, mammalian carnivores and snakes (Fitch 1948; Kuenzi *et al.* 1998).

However, California ground squirrels are also considered a major pest in rangelands used for livestock production, and have long been the subject of extensive management programs (Marsh 1998). Since ground squirrels favour open areas with high visibility, livestock grazing appears to result in higher ground squirrel densities (Marsh 1998), although the relationship between grazing intensity, squirrel densities and rangeland biomass is un-

clear (Fehmi *et al.* 2005). Ground squirrels are thought to compete with livestock for food and their burrowing and trampling activities also damage vegetation, and burrow openings are a hazard to livestock (Marsh 1998). Full economic evaluations of California ground squirrel control and damage have not been undertaken. However, Grinnell and Dixon (1918) estimated that during spring months, 200 ground squirrels consume the same amount of range forage as a 450 kg steer and Howard *et al.* (1959) observed higher weight gains in heifers when ground squirrels were controlled. Marsh (1998) suggested that ground squirrel competition for range forage may be particularly detrimental in years of below-average rainfall.

#### Management tools and strategies

Most management strategies rely on lethal control measures including pesticides, burrow fumigation and trapping (Whisson and Salmon 2009). Bait containing rodenticide may be broadcast (by aerial or mechanical spreader) onto rangeland pastures, or hand- or mechanically-spread or delivered in bait stations near active burrow systems (Salmon *et al.* 2007; Whisson and Salmon 2009).

Ripping burrows to minimise reinvasion, as is commonly undertaken for rabbits in Australasia, is also effective but costly (Salmon *et al.* 1987). Habitat manipulation to increase vegetation cover and reduce the suitability of a location to ground squirrels may be useful in some situations (Ordeñana *et al.* 2012) but is generally impractical and ineffective in grasslands (Fitzgerald and Marsh 1986).

#### Factors affecting management

The effectiveness of ground squirrel management is generally limited by lack of understanding of the relationship between ground squirrel densities, rangeland biomass and grazing intensity, the timing of control actions, the rapid rebound of populations after control, and the potential for treated areas to be reinvaded. The timing of control actions relative to the biology of ground squirrels and environmental conditions is critical to their success.

Fumigation is most effective in spring when moist soil helps seal gasses in the burrow system, and because it removes breeding squirrels. Baiting is only effective in summer and autumn when squirrels are feeding on seeds. However, squirrels entering aestivation during periods of hot temperatures can limit the effectiveness of summer bait applications. Baiting can also be problematic in autumn when ground squirrels are caching seed; bait applications may need to be increased at this time.

As with all the case study species, the appropriate scale for management operations is an important consideration. California ground squirrels rapidly invade treated areas such that large areas must be treated for effective long term control (Salmon *et al.* 1987; Salmon *et al.* 2007). As for the zokor below, social factors have influenced the toxins available for ground squirrel control. For almost 35 years until the 1980s when 1080 was withdrawn from registration as a rodenticide in California, compound 1080 on grain bait was used in annual squirrel control programs (Marsh 1998). Since the 1980s, there has been more reliance on zinc phosphide and the first-generation anticoagulants.

### Case study 3: Ecology, impacts and management of plateau zokor in China

#### Study region, brief biology and ecology

The Tibetan Plateau, which includes the Tibet Autonomous Region, much of Qinghai Province and extends into western Gansu and Sichuan Provinces, is the highest grazing land on earth. The 2.5 million km<sup>2</sup> plateau is called the “Water Tower of China” because of its rich water resources, and plays a very important role in downstream ecosystems. The alpine meadow grasslands, which cover 56% of the plateau, have a wealth of faunal biodiversity, including more than 30 native rodents (Hua *et al.* 2008).

The plateau zokor is a mostly subterranean-dwelling rodent native to the alpine (2800-4000 m ASL) croplands, meadows and shrublands of the Tibetan Plateau in south western China. Sub-adult zokors are covered with grey velvety fur that changes to earthy yellow as they become adults, which weigh between 173-490 g and are 160-235 mm long from snout to vent (Han Chunxuan *et al.* 2005). Reflecting their subterranean existence, zokor’s external ears are reduced, their eyes are small and their front claws are stocky and strong for digging. They have a large, robust nose pad that enables them to easily push soil around underground. Zokors are pulse breeders, producing a litter of 1-4 in spring–summer. The zokor does not hibernate but is less active in winter. Like rabbits and Californian ground squirrels, zokors prefer soft soil with enough moisture to enable formation of stable tunnels and burrows. The tunnel systems of zokors are complex, including one or two deep nests, foraging tunnels about 7-12 cm in diameter, 6-20 cm below the surface, food storage tunnels, travel tunnels between foraging tunnels and vertical connectors between nests and other tunnels (Fan and Gu 1981; Fan *et al.* 1999).

#### Impacts on grasslands

Zokor and other rodent damage to grasslands is a serious ecological, economic and social issue on the Tibetan Plateau. In 2010, 1.28 million ha (50%) of the total grassland area in the Gannan Tibet Autonomous Prefecture of Gansu Province was degraded, leading to loss of grassland productivity, soil erosion and social instability as livestock numbers and production become reduced. Zokors tunnel to forage on roots and subterranean stems during plant growing seasons and their excavations form mounds covering plants with soil and resulting in plant death. In some seriously zokor-damaged grasslands, the soil organic matter is buried and deeper sub-soils are pushed to the surface, changing areas of grassland to bare soil, which is easily eroded (Sun *et al.* 2011).

The most common plants on zokor mounds are weedy successional annuals, including *Elsholtzia* spp. and *Hypocoum* spp. When the population density of zokors is above the local carrying capacity, they become pests of pastures. Under laboratory feeding conditions, their daily intake accounts for 53.6% of their body weight (Zhang and Zhou 1994). Each zokor stores 20-30 kg hay and roots in their tunnels for winter food, which reduces grassland livestock production (Peng Meike 2007). Zokor mounds reduce the available livestock grazing area: in severely damaged area, a density of 351-540 zokor mounds/ha can be built over two months (Han *et al.* 2005), and the average area of each

zokor mound is 0.19 m<sup>2</sup>. Although positive and linear density–damage functions have been developed for crop damage caused by the larger Chinese zokor (*M. fontanieri*) (Zhang *et al.* 1999), no such equations have been established for damage to grasslands by the plateau zokor.

However, the zokor is also a very important component of grassland biodiversity and plays an important role in the ecosystem function of alpine meadows on the Tibetan Plateau. Although sometimes detrimental, the diggings of the zokor are also important for soil turnover and plant biodiversity. Zokor foraging behaviour spreads plant seeds and rhizomatous roots, which aids plant dispersal. The complex underground tunnels provide nests for birds, store soil moisture and benefit soil microbiology (Zhang *et al.* 2003), but sometimes become traps for horses and yaks, which can break through the top of the tunnels and suffer damage to their legs and feet.

#### Management tools and strategies

Special hunting bows and traps are used to kill zokor. Although this approach is target-specific and leaves no residue, it is a labour intensive and specialist activity. Rodenticides, like bromadiolone and Botulin type C, are commonly used. However, these pesticides also kill some birds and other animals. The more ecological approach is to build tall scaffolds for attracting predatory birds, such as the upland buzzard (*Buteo hemilasius*) and Eurasian eagle-owls (*Bubo bubo*), to control surface rodents. Although Cui *et al.* (2003) found that zokors were a secondary food resource of the two raptors, the scaffolds also prove useful for controlling zokors, but this method requires economic assessment. Similar methods have proven useful for the control of invasive rodents in Australian field crops (Kay *et al.* 1994).

#### Factors affecting management

Many studies have shown that livestock grazing pressure and the population density of zokors are directly related (*e.g.* Han *et al.* 1999; Zhang and Liu 1999). Heavy grazing pressure reduces the proportion of edible forage for livestock and increases the proportion of rhizomatous weeds, which are preferred foods of zokors. However, to reduce grazing pressure, which discourages degradation and zokor abundance and allows grassland rehabilitation, farmers must sacrifice some of their income source. Consequently, farmers are antipathetic towards zokors and regulations that limit grazing and rest pastures.

Social factors impact upon management practices and require investment for better acceptance of zokor management strategies. Farmers whose pasture is damaged by zokors prefer to use rodenticides to reduce the local zokor populations. This short term management approach, necessitated by their imperative to reduce losses to their livestock production, is detrimental to soil and grassland management in the long term.

Although the relationships between livestock numbers and plateau zokor density, and the relationship between zokor mound density and damage to grassland productivity are known, more research on rehabilitation of zokor damaged lands is required to improve grassland management and sustainability. Full economic evaluation of zokor control strategies are required to offset farmers’ antipathy and

enable them to improve their grassland resource.

## Discussion and Conclusions

Our three case studies are useful in demonstrating the commonalities of ecological roles that burrowing mammals exhibit in diverse grasslands. Whereas the zokor and California ground squirrel are invasive native animals and have corresponding conservation imperatives for ecosystem services as well as negative production issues, rabbits in Australia and New Zealand are highly invasive and most impacts are negative. As shown by our case studies, overgrazing by livestock and burrowing herbivores are often synergistic and self-reinforcing. That is, overgrazing with livestock degrades the grassland and provides conditions that encourage invasion or expansion of populations of burrowing mammals. In turn, their burrowing, grazing and browsing activities reduce livestock carrying capacity, which results in further overstocking as people try to retain previously achievable economic stocking rates, leading to a cycle of grassland degradation.

Grasslands will become increasingly important for providing food for the growing human population. It is therefore an imperative that production from these systems is optimised and their degradation stopped and reversed. Where burrowing mammals are part of the land degradation spiral, their effective management will be critical. Reduction in populations of these invasive small mammals and simultaneous active land reclamation are therefore required. Regardless of the suite of control methods chosen for a particular invasive mammal, application in an adaptive framework is more likely to achieve ecologically, socially and economically sustainable production from affected grasslands.

Our case studies all suffer from insufficient knowledge to determine and recommend the most cost-effective management options, and fundamental economic research is lacking for invasive mammals in these grassland ecosystems (Hone 2007). Research is required to determine the costs and benefits of new and existing strategies for managing invasive burrowing mammals in grasslands. Admittedly, such research is often difficult to undertake, particularly in grazing systems where damage is often subtle and insidious, and needs to be repeated in different ecosystems to reflect underlying productivity and livestock systems. However, without such research it is impossible to determine break-even points and the levels of investment required to achieve cost-effective management. Social factors affecting the adoption of best strategies also require investigation. The strategies to rehabilitate degraded grasslands in the presence of native herbivores and livestock still require investigation and this could be done efficiently in an adaptive management framework.

## Acknowledgements

We are grateful to Tarnya Cox and Annette Brown for comments that improved the document.

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