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Review

The paradox of keystone species persecuted as pests: A call for the conservation of abundant small mammals in their native range

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ABSTRACT

Small mammals, such as European rabbits (*Oryctolagus cuniculus*), plateau pikas (*Ochotona curzoniae*) and prairie dogs (*Cynomys* spp.), traditionally have been perceived as pests and targeted for control within their native ranges, where they perform essential ecosystem roles and are considered keystone species. These species can reach high densities, and have been subjected to eradication campaigns because of their putative negative impact on natural habitats and agriculture and their competition with livestock for forage. Eradication programmes have been a main factor causing sharp declines of these species in their natural ranges. Paradoxically, they are keystone species where they are abundant enough to be perceived as pests. The term "pest" is usually a social perception that is rarely supported by scientific data, whereas there is considerable scientific evidence of the key ecological roles played by these species. We call for the conservation of these species and present a conceptual model regarding the management of their populations. Where they occur at high numbers, and hence their effects on biodiversity are still of crucial importance, the persecution of these species should be avoided and their natural habitats preserved. In areas with high conservation value, but where these species occur at low densities, management efforts should aim to increase their density. In areas of high commercial value, managers ideally should consider changing prioritization of the area to high conservation value by purchasing the land or obtaining conservation easements. In situations with high commercial value and demonstrable low conservation concern, small mammals could be reduced humanely.

Contents

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1. Introduction

There is increasing evidence of a global decline in biodiversity. Although many factors are responsible for this decline, the root cause seems to be increasing pressure from human activities (Mace et al., 2005). Thus, there is a need to identify the drivers leading to conflicts between human activities and the conservation of biodiversity, and to promote the judicious management of these conflicts (Young et al., 2005; White et al., 2009; Dickman, 2010; McShane et al., 2011).

Invasive species constitute severe threats to biodiversity in many ecosystems, and these are often referred to as "pests" (Mooney and Hobbs, 2000). However, traditionally land managers and farmers have also considered several native species as pests in their native ecosystems (see below; but also Singleton et al., 1999, 2003). A crucial difference between native and invasive species is that native species may have evolved to perform key roles in ecological systems, and thus they can be important from a conservation point of view. Designating species that play major roles in ecosystems as pests frequently creates conflicts between conservationists and agriculturalists regarding the way in which the land should be managed (Smith et al., 2006; Miller et al., 2007). Several species of small mammals are especially well-known in this context. These include European rabbits (*Oryctolagus cuniculus*; Angulo and Villafuerte, 2003; Ward, 2005; Delibes-Mateos et al., 2008), plateau pikas (*Ochotona curzoniae*; Smith and Foggin, 1999) and prairie dogs (*Cynomys* spp.; Hoogland, 2006; Miller et al., 2007; Slobodchikoff et al., 2009).

Here we present a conceptual model portraying the conditions under which these species may be considered keystones or pests, the situations that lead to each designation, and the role of different management strategies (eradication programmes for pests and conservation actions for keystone species) in their respective ecosystems (Fig. 1). In addition, we identify different management models to address the conservation of these important species.

2. Methods

We focus on the well-studied cases of European rabbits, plateau pikas and prairie dogs, because they are functionally similar in

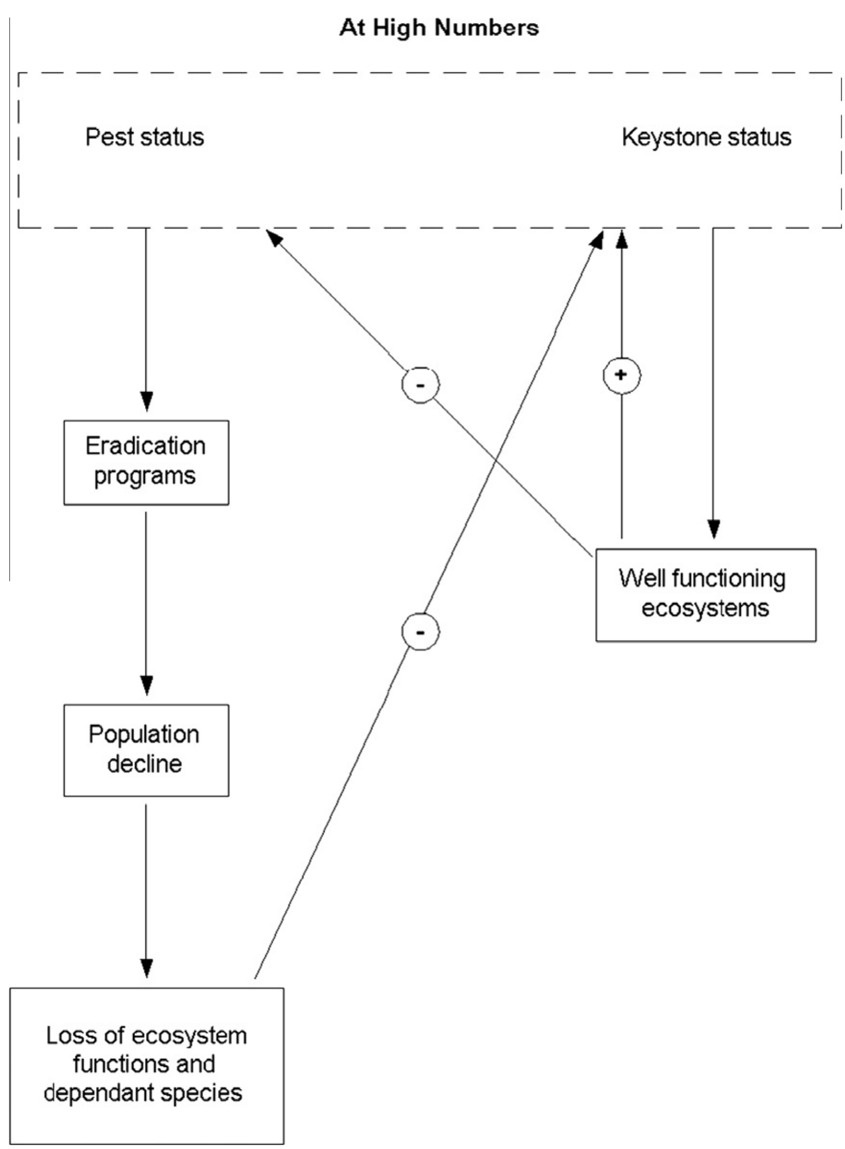

Fig. 1. A model showing the case of species of small mammals that, at high densities, can act as keystone species and simultaneously be perceived as agricultural pests. These species play major roles in the functioning of ecosystems, which provides them with keystone status but, when attributed pest status, eradication programmes have been developed, causing sharp declines of these species. Population declines of keystone species have caused the loss of ecosystem functions and dependant species, which moves these species away from the keystone status. The signs "+" and "−" indicate that keystone or pest status may be enhanced or reduced, respectively.

three very different ecosystems (Mediterranean ecosystems in southwestern Europe, high altitude grasslands on the Tibetan Plateau, and prairie grassland ecosystems in North America, respectively). Our central question concerns whether these species act as keystone species and/or as pests, as well as the situation that led to each status. To address this question we searched comprehensively to identify studies showing the potential economic impact and the supporting ecological roles of each of these species.

First, we conducted an in-depth review of published scientific papers that report potential economic impacts caused by European rabbits, plateau pikas and prairie dogs. Relevant studies were identified by conducting a search in the ISI Web of Knowledge. We searched terms that stemmed from the following words, in the following combinations: (1) (rabbit OR *Oryctolagus*) AND (pest OR damage) AND (Iberian Peninsula OR Spain OR Portugal); (2) (plateau pika OR *O. curzoniae*) AND (pest OR damage); (3) (prairie dog OR *Cynomys*) AND (pest OR damage). Additionally, we searched for information on this topic in relevant reference books. As it is important that searches of this nature are sufficiently rigorous and broad so as to identify a representative sample of relevant studies (Pullin and Stewart, 2005), we also consulted experts in the field of European rabbit, plateau pika, and prairie dog damage in their native ecosystems to identify other possible sources of information.

Second, as diverse literature reviews on the key ecological roles played by European rabbits, plateau pikas and prairie dogs already exist (e.g. Kotliar et al., 1999, 2006; Smith and Foggin, 1999; Delibes-Mateos et al., 2008), we did not execute another exhaustive review on this topic. Alternatively, we conducted a semi-structured review in which the ecological roles played by these small mammals were predefined and compiled evidence, by species, for each of these ecological roles: keystone species (influence upon vertebrate species richness, invertebrate species richness, plant species richness and endangered species); and ecosystem services provided (improved soil organic content, improved soil moisture content, minimisation of erosion and enhanced water infiltration, role as an allogenic engineer due to burrowing activity, increased available nitrogen and improved nutrient cycling, enhancement of plant growth and biomass, seed dispersal and stabilization of the vegetative community; Table 1).

3. Small mammals as pests

The model (Fig. 1) starts with the assumption that these small mammals can reach high densities locally (e.g. population densities of 300–350/ha have been recorded in the case of plateau pikas; Smith and Foggin, 1999; Pech et al., 2007). Landowners, farmers and managers usually believe that these small mammals have a negative impact on agriculture, damage natural habitats, and compete for forage that could otherwise be utilised by livestock.

In the Iberian Peninsula, for example, rabbits are considered to be a pest, not only in agricultural areas, but also in traditional

Table 1
Evidence, by category, of the keystone roles and ecosystem services provided by European rabbits, plateau pikas and prairie dogs in their native ecosystems.

Service	Response effect	European rabbit	Plateau pika	Prairie dog
Keystone species	Increased vertebrate species richness	Delibes-Mateos et al. (2007), Gálvez-Bravo et al. (2009) and Jaksic and Delibes (1987)	Arthur et al. (2008), Badingqiuying (2008), Lai and Smith (2003), Li (1989), Lu et al. (2009), Ma (1995), Prejevalski (1876), Schaller (1998) and Zeng and Lu (2009)	Kotliar et al. (1999), Lomolino and Smith (2003) and Reading (2009)
	Increased invertebrate species richness	Galante and Cartagena (1999), Sánchez-Piñero and Ávila (1991) and Verdú and Galante (2002, 2004)		Bangert and Slobodchikoff (2004, 2006) and Slobodchikoff et al. (2009)
	Increased plant species richness	Gálvez (2008)	Bagchi et al. (2006) and Hogan (2010)	Ceballos et al. (1999), Coppock et al. (1983), Fahnestock and Detling (2002), Kotliar et al. (1999), Slobodchikoff et al. (1988, 2009) and Whicker and Detling (1988)
	Important prey for endangered species	Delibes and Hiraldo (1981), Delibes-Mateos et al. (2008), Ferrer and Negro (2004), Jaksic and Delibes (1987) and Palomares et al. (2001)	Badingqiuying (2008), Li et al. (2004a,b), Liu et al. (2010a,b), Schaller (1998) and Xu et al. (2006)	Campbell et al. (1987), Kotliar et al. (1999) and Lomolino and Smith (2003)
Ecosystem service	provided	Improved soil organic content		Li and Zhang (2006)
	Improved soil moisture content		Li and Zhang (2006)	Archer and Detling (1986)
	Minimises erosion; enhanced water infiltration		Hogan (2010) and Smith et al. (2010)	Detling (1998), Kotliar et al. (1999) and Outwater (1996)
	Allogenic engineer; burrows increase habitat for other species	Blázquez and Villafuerte (1990), Gálvez-Bravo et al. (2009), Palomares and Delibes (1993) and Revilla et al. (2001)	Arthur et al. (2008), Hogan (2010), Lai and Smith (2003), Lu et al. (2009) and Zeng and Lu (2009)	Bangert and Slobodchikoff (2000), Kotliar et al. (1999), Shipley and Reading (2006) and VanNimwegen et al. (2008)
	Increased available nitrogen/ improved nutrient cycling	Willot et al. (2000)	Liu et al. (2010a,b) and Xu (2008)	Coppock et al. (1983), Holland and Detling (1990) and Whicker and Detling (1988)
	Enhanced plant growth/ biomass	Petterson (2001) and Willot et al. (2000)		Coppock et al. (1983), Ingham and Detling (1984) and Uresk (1985)
	Active dispersal of seeds; improved seed germination rate and success (2006*)	Cerván-Carmona and Pardo-Navarro (1997), Dellafiore et al. (2006, 2009), Malo and Suárez (1995), Malo et al. (1995, 2000), Muñoz Reinoso (1993), Soriguer (1986) and Verdú et al. (2009)		Fahenstock et al. (2003)
	Stabilized vegetative community	Gálvez et al. (2008), García-Fuentes et al. (2006), Gómez-Sal et al. (1999) and Rueda (2006)	Jiang and Xia (1985, 1987)	Coppock et al. (1983), Davidson et al. (2010) and Whicker and Detling (1988)

agro-forestry landscapes, which provide some of the best rabbit habitat. Although damage to crops in areas where rabbits have been introduced is known to be very important (e.g. in Great Britain rabbits caused between € 115 and 150 million in damage to agricultural crops in 1986; Mills, 1986), information regarding the magnitude of potential damage on the Iberian Peninsula is scarce. In a recent study, Barrio et al. (2010) observed that in some agricultural areas of southern Spain where rabbits reach high densities, grapevine harvest was significantly lower from vines damaged by rabbits, and these yielded an average of 22.5% fewer grapes than undamaged vines. Nevertheless, Barrio (2010) observed in the same study area that average grapevine yield did not differ significantly between fenced plots (i.e. without rabbits) and unfenced plots (i.e. with rabbits), which suggests that the net effect of rabbit damage on vines is at least uncertain. According to Barrio et al. (2010), plant diversity had a significant negative effect on the extent of the damage caused by rabbits to vines; thus, the impoverishment of plant communities due to agricultural intensification may have reduced the availability of food for rabbits, forcing them to consume agricultural crops. Nevertheless, Ward (2005) suggested that current rabbit damage to crops, such as the situation described above, is exceptional and largely driven by droughts that reduce natural food sources, and therefore that farmers seem to exaggerate the impact of supposed "rabbit plagues," failing to recognise that rabbits used to be much more abundant several decades ago.

Similarly, plateau pikas are perceived as pests because they are thought to compete with livestock for scarce food resources and contribute to rangeland degradation. However, these relationships between livestock and pikas have rarely been documented (Smith and Foggin, 1999; Pech et al., 2007), and some authors have even suggested that pikas may provide a beneficial service to livestock. The clearest statements as to why plateau pikas should have pest status are given by Fan et al. (1999), Limbach et al. (2000), Van Wageningen and Sa (2001), Zhang et al. (2003) and Zhou et al. (2005). For example, Fan et al. (1999) claim that pikas "dig and destroy vegetation causing many serious problems such as soil erosion, and reductions in livestock carrying capacity and ecosystem diversity," and Limbach et al. (2000) state that the burrowing activity of pikas "exacerbates erosion by loosening the *Kobresia* sod and killing its roots" thus forming "paths of preferential flow of snowmelt, runoff, and storm waters, thereby exacerbating these erosive forces," and that "the plateau pika competes with livestock for aboveground biomass during the summer growing." These statements, as well as similar claims repeated in the other publications, are not supported with any data or references. In contrast, experimental work on the relationship between the burrowing activity of pikas and the hydrological regime on the plateau has demonstrated that infiltration rates are higher within active pika colonies, thus reducing potential erosion from torrential summer monsoon rains (Hogan, 2010; Smith et al., 2010). Ecosystem diversity is clearly not compromised by the presence of the native plateau pika; instead many co-dependent species are lost regionally following the poisoning of pikas (Table 1). The claim that pikas reduce the carrying capacity of livestock generally involves extrapolation of the metabolic need (thus forage consumed) of a plateau pika times pika density times a target area (Fan et al., 1999; Van Wageningen and Sa, 2001). This calculation is accompanied by the number of sheep or yak that could be supported by the resulting amount of forage consumed by pikas, under the (unstated) assumption of total competition between livestock and pikas. However, there appears to be little competitive overlap between pikas and livestock when both are found at low or moderate densities (Jiang and Xia, 1985, 1987). Additionally, Tibetan pastoralism has existed sustainably alongside pikas on the plateau for approximately 4500 (Li et al., 2003) to 8800 years (Meihe et al., 2009).

On the other hand, at high densities pikas may compete with livestock (yak, sheep; Jiang and Xia, 1985, 1987). Ironically, several studies demonstrate that pikas are found at their highest densities only on land that has already been seriously degraded or overgrazed (Holzner and Kriechbaum, 2001; Zhang et al., 2003). Thus, high pika densities may indicate that rangelands are in poor condition, rather than being the actual cause of the degradation (Smith and Foggin, 1999; Holzner and Kriechbaum, 2001). Plateau pikas are believed to impact rangeland habitat negatively through facilitating the origin of "black sands," small depressions with steep edges and larger areas primarily devoid of vegetation (Ekvall, 1968; Ma et al., 2000; Shang and Long, 2005). Once more, however, no scientific work confirms this hypothesis (Smith and Foggin, 1999), and black sand areas may equally originate from overgrazing or climate change (Ma et al., 2000; Shang and Long, 2005). Finally, Wei et al. (2007) show that the proportion of low-quality forage was higher in regions dominated by pika burrows than undisturbed sites. In contrast, Schaller (1998) suggested that, by eating poisonous herbs, pikas may slow the spread of plants not palatable to livestock, and thus improve the condition of grasses and sedges preferred by livestock.

The potential role of pikas in causing rangeland degradation is closely linked with the issue of overgrazing by livestock, perhaps complicated by recent global warming. Indeed, most of the sources (as above) that advocate pikas as pests and lobby for their control (poisoning), also nuance the relationship between overgrazing and pikas. Fan et al. (1999) state "overgrazing by livestock leads to grassland degeneration which results in rodent [pika] infestation and further grassland degeneration. Human activities, especially cultivation and livestock grazing, play an important role in this vicious cycle." Zhang et al. (2003) claim "overgrazing is the major factor causing serious rodent [pika] infestations." And Zhou et al. (2005) conclude "The principal factors causing grassland degradation are thought to be long-term overgrazing and the destruction by rodents [pikas] that follows, and climate warming, which accelerates the grassland degradation process." An additional complication is that the variable in question, rangeland degradation, is rarely defined in the Chinese literature (but see Zhou et al., 2005), and a recent comprehensive analysis indicates that many estimates of degradation have been exaggerated (Harris, 2010). The most thorough analysis of this situation, using controlled experiments and livestock exclosures, showed that there was no apparent increase in forage production in areas where plateau pikas had been controlled (Pech et al., 2007). This study concluded "It was not evident that control programmes are warranted or that they will improve the livelihoods of Tibetan herders" (Pech et al., 2007). Finally, the time span over which the plateau pika has been controlled (roughly four decades; Fan et al., 1999) coincides with a marked decline in weights of livestock (yak by 10–15 kg; sheep by 3–4 kg; QPCB, 1994), rather than an increase – an indication that the cost of control has not led to demonstrable benefits in animal husbandry on the Tibetan Plateau.

As with pikas, prairie dogs are often perceived as pests, because many ranchers, farmers and range managers believe that prairie dogs compete for forage with cattle and contribute to rangeland degradation (Vermeire et al., 2004; Hoogland, 2006; Slobodchikoff et al., 2009). In the published literature this perception seems to have arisen with a statement by Merriam (1902) that prairie dogs ate between 50% and 75% of the forage that could be used by livestock and that 256 prairie dogs ate as much forage as a single cow. However, no data were presented to support this statement. Surprisingly, few studies have examined competition between prairie dogs and cattle. Hansen and Gold (1977) studied the dietary overlap between prairie dogs and cattle and concluded that overlap ranged from a low of 42% in winter to a high of 69% in summer, but gave no indication of how this overlap might affect the weight gain of the cattle. O'Meilia et al. (1982) studied the weight gain of cattle foraging in pastures occupied by prairie dogs vs. pastures that did not have prairie dogs, and found no significant differences in weight gain or loss between the two conditions. A detailed economic study in the Conata Basin, South Dakota, by Collins et al. (1984) contrasted the net gain in forage for livestock from poisoning prairie dogs with the cost of control and determined that control was not economically feasible; annual maintenance costs were greater than the annual value of forage gained. A simulation study by Uresk and Paulson (1988), based on dietary overlap between prairie dogs and cattle and projections of forage production, suggested that there might be a 3.2–10% reduction in the number of cattle that could be supported on a 2100 ha pasture if the grazing area was occupied by 40 ha of prairie dogs. Finally, a study by Derner et al. (2006) suggested that monetary losses due to decreased cattle weights might range from 5% in grazing areas where prairie dogs occupied 20% of the habitat, to 14% in grazing areas where prairie dogs occupied 60% of the habitat.

Similar to pikas, there appears to be evidence that prairie dogs tend to colonise degraded or overgrazed habitats, rather than creating degraded conditions (Knowles, 1986a,b). Densities of prairie dogs seem to be affected by the distribution of food resources in their habitat. In relatively undisturbed grasslands, where food resources are evenly distributed, prairie dog densities tend to be lower, whereas in disturbed habitats, where food is patchily distributed, such as in overgrazed grasslands, prairie dog densities tend to be higher (Travis et al., 1995). There is also some evidence that prairie dogs can help restore native vegetation in degraded habitats. Prairie dogs clip vegetation both for their forage and also to facilitate detection of approaching predators. Native vegetation tends to resprout much more readily than introduced weeds, leading to the possibility that over time degraded habitats can be restored to more native conditions through the activity of the prairie dogs (Slobodchikoff et al., 1988). Finally, prairie dogs can even increase forage quality as a result of their activities, thus mitigating any potential competition with livestock (Coppock et al., 1983).

While acknowledging that conditions vary across the range of prairie dogs in North America, several meta-analyses of these studies have concluded that, while poisoning prairie dogs may lead to additional forage for cattle, the resulting increase in body mass of cattle is rarely sufficient to offset the cost of poisoning (Detling, 2006; Miller et al., 2007; Slobodchikoff et al., 2009). Additional keystone species and ecosystem services benefits of healthy prairie dog colonies further skews the benefit/cost analysis against poisoning (Miller et al., 2007; Slobodchikoff et al., 2009).

4. Control measures

Due to the pest status of these small mammals, they have been targeted for control during the past few decades. Eradication programmes for small mammal populations usually include shooting, trapping, digging up warrens, and/or poisoning as control strategies. For example, recreational shooting of prairie dogs has been estimated to kill two million animals per year (Reeve and Vosburgh, 2006). Poisoning, however, has been the primary agent for controlling plateau pikas (beginning in the early 1960s; Smith et al., 1990; Fan et al., 1999) and prairie dogs (since the early 1900s; Forrest and Luchsinger, 2006).

Largely as a result of these eradication programmes, plateau pikas and prairie dogs have been reduced significantly throughout their natural ranges (Smith and Foggin, 1999; Forrest and Luchsinger, 2006; Miller et al., 2007). Fan et al. (1999) documented that over 208,000 km^2 was poisoned to reduce or eliminate plateau pika populations in Qinghai province alone in the first three decades of treatment. More recently, bolstered by a huge input of funding (7.5 billion yuan = US\$966 million at the time of funding; Ma, 2006), pikas have been poisoned with grain laced with type C botulinum toxin over an estimated 320,000 km^2 in Qinghai – centered on the Sanjiangyuan National Nature Reserve. It is increasingly difficult to find healthy populations of plateau pikas in the region (Smith et al., 2006).

At the beginning of the 1900s, prairie dog colonies covered between 40 and 100 million ha in western North America, but they range over only about 600,000 ha at present; at least a 98% decline in the area they formerly occupied (Miller et al., 1994, 2007; Slobodchikoff et al., 2009). Strychnine-soaked grain reduced Colorado's prairie dog population between 1902 and 1912 by an estimated 91% (Clark, 1989). An 85% reduction in prairie dog numbers was achieved in Montana after a treatment with zinc phosphide (Knowles, 1986a,b).

With regard to the European rabbit, disease (which also has affected prairie dogs through sylvatic plague; Wuerthner, 1997; Cully et al., 2006) has been cited as a main cause of population declines. On the Iberian Peninsula the main rabbit decline apparently has been caused by the myxoma virus, which arrived in the area following its release in France in an attempt to control rabbits to protect crops (Fenner and Ross, 1994). Populations of European rabbits declined by about 70% in Spain between 1973 and 1993 (Virgós et al., 2007), and an even greater decline may have occurred since the arrival of myxomatosis in the 1950s (perhaps over 90%, as occurred in other regions; Armour and Thompson, 1955). These deliberate attempts to control rabbits through disease are exacerbated by on-going habitat loss and hunting (Angulo and Villafuerte, 2003; Delibes-Mateos et al., 2010).

5. Species status

Overall, population reductions resulting from control programmes have been so severe that some of these small mammals have been classified within a threatened category in national red lists. Thus, the European rabbit has been classified as 'near threatened' and 'vulnerable' in Portugal and Spain, respectively (Cabral et al., 2005; Villafuerte and Delibes-Mateos, 2007). The Utah prairie dog (*Cynomys parvidens*) has been listed as a federally threatened species, and the Mexican prairie dog (*C. mexicanus*) as endangered, under the US Endangered Species Act (USFWS, 2010). Some species also appear on international Red Lists: the European rabbit, as treated in its native range, is classified as Near Threatened, and the Mexican prairie dog (*C. mexicanus*) is classified as Endangered (IUCN, 2010; *C. pardivens* is treated as a subspecies of the white-tailed prairie dog, *C. leucurus*, in the IUCN Red List and is therefore not listed there). Whereas the plateau pika is still too wide-spread and numerous to be red-listed, 24 of the 30 species of *Ochotona* occur in China (Smith and Xie, 2008), and some of these, as well as other small mammals, are at risk and could be jeopardised by the wide-scale poisoning directed at the plateau pika.

6. Small mammals as keystone species

The keystone species concept is increasingly important in community ecology and conservation biology. According to Power et al. (1996), a keystone species is one that has: (1) large effects on community structure and function; and (2) these effects are disproportionately large relative to abundance. The second criterion can potentially exclude species that have large effects because of numerical dominance, such as European rabbits, plateau pikas or prairie dogs. However, Kotliar (2000) proposed that a third criterion be incorporated into the definition: keystone species perform roles not performed by other species and processes. In this perspective, these three species have been labelled as keystone species (Kotliar et al., 1999, 2006; Smith and Foggin, 1999; Delibes-Mateos et al., 2007, 2008; see Table 1). Not only do they fulfil most of the functions of a keystone species (sensu Mills et al., 1993), but through habitat modification due to burrowing, they also act as allogenic engineers (Jones et al., 1997; Dickman, 1999).

By definition, the elimination or major reduction of a keystone species from an ecosystem would have a greater than average effect on other species' populations or ecosystem processes (Power et al., 1996). In fact, declines in the numbers of European rabbits, plateau pikas and prairie dogs have caused serious negative impacts for the preservation and conservation of native biodiversity on prairie/grassland ecosystems of Mediterranean areas of southwestern Europe, the Tibetan Plateau and western North America, respectively (Table 1). These species serve as prey for a large number of predators (e.g. >40 species prey on rabbits in the Mediterranean ecosystem of southwestern Europe; Table 1), including threatened predators such as the Iberian lynx (*Lynx pardinus*) and the Spanish imperial eagle (*Aquila adalberti*). Predator populations have been noted to decline following rabbit declines (Fernández, 1993). The lynx and eagle are apparently so specialised on European rabbits that they have difficulty persisting where these prey have declined substantially or disappeared (Palomares et al., 2001; Ferrer and Negro, 2004; Delibes-Mateos et al., 2007). On the Tibetan Plateau the brown bear (*Ursus arctos*), Pallas's cat (*Felis manul*), Tibetan fox (*Vulpes ferrilata*), steppe polecat (*Mustela eversmanii*), upland buzzard (*Buteo hemilasius*), and saker falcon (*Falco cherrug*) feed primarily on plateau pikas (Schaller, 1998; Smith and Foggin, 1999; Li et al., 2004a,b; Xu et al., 2006; Badingqiuying, 2008). Where poisoning has occurred, avian and mammalian carnivores are largely absent (Smith and Foggin, 1999; Smith et al., 2006; Badingqiuying, 2008). Additionally, the poisoning of pikas has led to an escalation of human–bear conflict, with bears increasingly destroying houses of Tibetan nomads in search of food (Worthy and Foggin, 2008). In western North America the endangered black-footed ferret (*Mustela nigripes*) is dependent on prairie dogs, and therefore persists only in the few areas where they maintain high numbers (Campbell et al., 1987; Kotliar et al., 1999).

The European rabbit, plateau pika and prairie dog also conspicuously alter landscapes and provide foraging, shelter and nesting habitats for a diverse array of species (Table 1). Their burrows provide nest sites and shelter for many species of vertebrates and invertebrates. European rabbit warrens have a positive influence on density and diversity of lizards (Gálvez-Bravo et al., 2009), as well as a large number of amphibians, other reptiles, mammals and birds (reviewed in Delibes-Mateos et al., 2008). Seven species of Tibetan Plateau endemic passerines nest primarily in pika burrows (Hume's groundpecker, *Pseudopodoces humilis*; two genera of snow finch, *Montifringilla, Pyrgilauda*); where pikas have been poisoned and their burrows have collapsed, these species largely disappear (Smith and Foggin, 1999; Lai and Smith, 2003). Additionally, two amphibians (*Bufo raddei*; *Nanorana pleskei*) and two lizards (*Eremias multiocellata*; *Phrynocepalus vlangalii*) also rely heavily on the presence of pika burrows (Smith and Foggin, 1999; Hogan, 2010). In North America, Kotliar et al. (1999) argued that nine species clearly depended on prairie dogs for survival and reproduction, 20 species opportunistically benefited from prairie dogs, and another 117 species had a natural history that suggested a benefit from associating with prairie dogs (see also Lomolino and Smith, 2003). This list has since been extended to 247 vertebrate species that have either an obligate or casual association with prairie dogs (Reading, 2009).

European rabbits, plateau pikas and prairie dogs promote increased plant species richness compared with areas where they have been poisoned by creating mosaics of disturbance due to burrowing (Table 1). The selective pattern of grazing by European rabbits promotes maintenance of open scrubland (Gómez-Sal et al., 1999; Gálvez et al., 2008), which is their preferred habitat (Moreno and Villafuerte, 1995). Additionally, rabbits are known to serve as active seed dispersers for at least 72 species of plants from 23 different families (Delibes-Mateos et al., 2008). Bagchi et al. (2006) and Hogan (2010) determined that plant species richness was significantly higher in the vicinity of active plateau pika colonies, compared with areas where pikas were absent due to prior poisoning. Bagchi et al. (2006) concluded that eradicating pikas can lead to a loss of vegetative diversity on the alpine meadow ecosystem and that this "is not a solution for the degradation problem." Prairie dogs are known to influence plant cover and composition, and ultimately they act as stabilizers of the grassland ecosystem in which they live (Davidson et al., 2010). In addition, their presence increases the local species richness of native plants (Slobodchikoff et al., 1988, 2009).

Finally, these species also affect ecosystem processes, including soil disturbance, nutrient cycling rates and hydrological processes, and hence contribute positively to ecosystem-level dynamics (Table 1; Kotliar et al., 1999; Smith and Foggin, 1999; Willot et al., 2000; Hogan, 2010). For example, Xu (2008) concluded that the burrowing of plateau pikas enhanced the nitrogen cycle, and thus that the pika benefits the restoration of the alpine meadow plant community.

7. Should native small mammals be considered keystone species or pests?

The combined direct and indirect impacts of European rabbits, plateau pikas and prairie dogs have a pronounced effect on ecosystem processes and patterns, even though their numbers are only a fraction of historic levels. In fact, it has become evident that these species are keystone species because the declines in their numbers in recent decades has allowed the study of corresponding responses in community dynamics and ecosystem processes (e.g. Cully, 1991; Lai and Smith, 2003; Fig. 1). However, the impacts of these small mammals on landscape structure and dynamics must have been significantly higher prior to the dramatic declines in their populations. Although information is scarce regarding the effect of these small mammals on biodiversity prior to their decline, it is noteworthy that they currently play key roles in areas where their populations are large enough to support other species or ecosystem processes; e.g. the Iberian lynx, the most endangered cat in the world, needs at least 1 rabbit/ha during autumn and 4.6 during spring to establish breeding territories (Palomares et al., 2001); the endangered black-footed ferret needs between 412 and 1412 prairie dogs to support a female and her young for a year (Stromberg et al., 1983).

According to this review, it seems clear that these small mammals are keystone species where they occur at high enough densities to potentially be perceived as pests. But then, are they keystone species or pests? In general, the term "pest" is undefined and depends on the context of the species and/or groups of species considered (Smith et al., 2006; Olea et al., 2009; Dickman, 2010). For instance, there are abundant data in the literature about the economic and social damage caused by invasive pests (Pimentel, 2002; Vilá et al., 2010), which is particularly evident in the case of alien insect species (Reay-Jones et al., 2008). However, as we have reviewed, in the case of native small mammals damage to crops and economic losses due to competition with livestock have been rarely documented; even in such cases where damages were reported these were not extremely high. Additionally, other studies suggest these species do not damage crops or compete with livestock, and on some occasions benefits attributable to these small mammals have been reported. This analysis suggests that for these species, the term pest usually derives from a social perception rather than a scientific assessment. In central Spain, for example, despite current rabbit abundance being much lower than that several decades ago (Delibes-Mateos et al., 2009), the percentage of municipalities that requested permits to control rabbits has increased from 4% during the 1960s to 70% at present (Ríos et al., 2007), which may be due to a change in the perception of managers toward damage caused by rabbits. This situation is not exceptional for these small mammals, as there is much evidence in the literature for a significant mismatch between the perception of risk and actual degree of risk in many human–wildlife conflicts (Dickman, 2010). In Zanzibar, for example, farmers often perceive that the endangered red colobus (*Procolobus kirkii*) causes detrimental effects upon coconut (*Cocos nucifera*) harvests, although it has been revealed that red colobus coconut consumption was positively correlated with final coconut harvests, probably due to pruning (Siex and Struhsaker, 1999).

In general, land managers and policy makers observe high densities of these small mammals and immediately draw a connection between these animals and the area (e.g. grasslands, crops, etc.) that they perceive as damaged (Smith et al., 2006). The management recommendation is often the widespread control of small mammals, whereas intermediate steps, such as research to determine the accuracy of these assumptions, are bypassed (Smith et al., 2006). An example of this dynamic was recently documented in Castilla y León, northern Spain. There, pressure from farmers led the regional government to officially declare a common vole (*Microtus arvalis*) outbreak as an agricultural plague and to finance three extensive campaigns to poison voles. This administrative action occurred despite the absence of any scientific study of vole damage to crops in Spain, although there had been at least four outbreaks in this area since the 1980s (Olea et al., 2009). On the other hand, and although different authors have interpreted scientific information about the key role of these small mammals in various, and sometimes conflicting, ways (contrast Vermeire et al., 2004, with Miller et al., 2007; or Limbach et al., 2000, with Smith and Foggin, 1999), researchers generally agree that these species contribute significantly to the preservation of native biodiversity in some important ecosystems worldwide. Indeed, as we have documented (Table 1), a great number of scientific papers demonstrate that some of the roles of these species are essential and unique in their ecosystems.

8. Current management of abundant small mammals

In general, policy makers attempt to identify and define significant issues, and ultimately make decisions about them. They are usually influenced by and must answer to a host of stakeholders, including those with economic interests in the issues under consideration (Smith et al., 2006). This seems to be the main reason that eradication programmes of some of these small mammals are still on-going (Forrest and Luchsinger, 2006). The juxtaposition between the desires of stakeholders, primarily with economic interests, and the results of enacted eradication programmes, however, presents several significant paradoxes. For example, the large allocation to control the plateau pika on the newly formed Sanjiangyuan National Nature Reserve (Ma, 2006) has been justified as a means to preserve ecosystem biodiversity (Fan et al., 1999), whereas the poisoning of this keystone species has been shown to severely deplete local biodiversity (detailed above). And the primary economic reason for pika control – to improve grassland health and facilitate livestock husbandry – has not worked; livestock weights are down and the rangeland has been classified as increasingly degraded, all within the same time-frame that the pika control programme has been in force.

The present management of European rabbits and prairie dogs is even more paradoxical, as it is based on two opposing goals: the recovery of their populations in some areas and their continued persecution in others (Figs. 1 and 2). In Spain, governments subsidise the recovery of rabbit populations where they have declined (e.g. in Doñana National Park >19,000 rabbits have been released during the last decade; Cabezas and Moreno, 2007) while, at the same time, they facilitate the persecution of rabbits (e.g. allowing their hunting during the whole year) in areas where they are abundant (Angulo and Villafuerte, 2003). Moreover, it is noteworthy that more than 4 million rabbits are killed by hunters in Spain every year (Delibes-Mateos et al., 2008), while the situation of the world's most endangered felid, the Iberian lynx, which depends on the rabbit for survival, becomes more precarious (Palomares et al., 2011). Reintroduction sites of the black-footed ferret, such as at Conata Basin, depend on having a large population of prairie dogs, and at the same time, prairie dogs are being poisoned in adjacent areas (Hoogland, 2006). Overall, the US government invested $6,200,000 in the prairie dog eradication programme between 1980 and 1984, and during 1991 it spent >$1,500,000 on the captive breeding and reintroduction programme for the black-footed ferret (Miller et al., 1994). These conflicting programmes (expenditures) continue to the present day (Slobodchikoff et al., 2009).

9. Management recommendations

Because their keystone status implies that management for these small mammals will benefit other species and ecosystem processes, it provides an important evaluation criterion for balancing two dominant and opposing management themes: species eradication and conservation (Kotliar et al., 1999; Dickman, 2010). Moreover, conservation of these keystone species, no matter how political the situation, would be far more cost-effective than trying to ensure the viability of each individual species that depends on them (Collins et al., 1984; Slobodchikoff et al., 2009). We agree with Miller et al. (1994) that managing these keystone species could provide an effective change from single-species management to ecosystem management, and with Soulé et al. (2001) that they should be managed at ecologically effective densities in as many places as possible. Thus, the conservation of these species should be promoted under most circumstances. However, the success in achieving biodiversity objectives in the real world is closely linked to the extent to which these objectives can be integrated with the social, economic, and cultural objectives of local people (Woodroffe et al., 2005). Under this perspective, a "win–win" approach, where management responses are designed simultaneously to enhance the well-being of local people and to conserve biodiversity (e.g. Adams et al., 2004) would be ideal for the management of European rabbits, plateau pikas and prairie dogs. In Fig. 2 we present a management model that outlines a means to conserve these important species, while incorporating local, social and economic interests. Nevertheless, in most cases win–win solutions are difficult to realise, and trade-offs and hard choices need to be made (McShane et al., 2011). We make specific recommendations for a wide range of contexts and situations, with the aim of conserving abundant small mammals by integrating the interests of the different stakeholders involved in the conflict. It is important to note that not all the possibilities in the model occur for each species, or for a species in all the areas it inhabits.

First, we recommend that the conservation of these species should be encouraged in areas of high conservation value: areas that are irreplaceable or of particular conservation value (e.g. uncommon and/or noticeable habitat types or landscapes, or species-rich areas harbouring important species from a conservation point of view). It is particularly important to retain keystone species in areas of high conservation value where they maintain high numbers, and hence their effects on biodiversity are still crucially important (B in Fig. 2). This strategy means that the persecution

		Density of keystone small mammals	
		Low density	**High density**
Prioritization of the area	**High conservation value**	**A.** Conservation measures to increase density and improve habitat	**B.** Maintain high density and good habitat
	High commercial value	**C.** Maintain low density	**D1.** Change the prioritization of land use from agriculture to conservation **D2.** Reduce densities of small mammals (population control)

Fig. 2. A proposed scheme for managing populations of keystone small mammals in relation to an area's conservation value. Capital letters indicate potential management goals: (A) increase density of small mammals where density is low in areas of high conservation value; (B) maintain high density and good habitat in areas of high conservation value where density is high; (C) maintain a low density of small mammals where conflict with agriculture is high and these species can no longer play a keystone role in the ecosystem; (D1) change the prioritization of land use from agriculture to conservation in areas with a high density of small mammals, high conflict with agriculture, and high probability that their ecological role can be maintained; (D2) reduce densities of small mammals where conflict with agriculture is high and these species can no longer play a keystone role in the ecosystem.

of abundant small mammals should be avoided in these areas. Constraining European rabbits, plateau pikas or prairie dogs to low numbers in small populations may allow them to persist, but the resulting low densities and scattered distribution will preclude them from performing their ecosystem functions (e.g. Miller et al., 2007). It is also of crucial importance to preserve the natural habitats in which these species occur at high density. Moreover, management efforts (e.g. species protection, habitat restoration) should be conducted to increase the density of these small mammals in areas of high conservation value where they have declined substantially. This intervention would facilitate the conservation of some important natural ecosystems and consequently the preservation of biodiversity (A in Fig. 2).

In areas of high commercial value, where density of these mammals is high, managers ideally should consider changing the prioritization of the area to high conservation value, by purchasing the land or obtaining a conservation easement on it, in order to maintain the ecological role of these keystone species (D1 in Fig. 2). These compensation programmes have been used frequently in other conservation conflicts worldwide. For instance, in the United States the National Wildlife Federation provides incentives to leaseholders who retire their grazing leases to reduce conflicts between livestock and brown bears or wolves (*Canis lupus*) on national forest lands around Yellowstone National Park. This programme increases habitat security for wildlife, financially benefits the rancher, and reduces management headaches for the US Forest Service (Miller et al., 2007). Similar options should be considered for the management of abundant small mammals in areas of high commercial value. In some areas within Spain, damage caused by rabbits is compensated through the payment of the estimated yield loss; e.g. an average of >€72,000 in hunting estates about 6000 ha in size (Villanúa et al., 2005). Alternatively, in some areas within southern Spain it has been suggested that damage caused by rabbits could be reduced through diversionary feeding (Barrio et al., 2010), which involves providing an alternative food source that diverts the individual or population away from its damaging behaviour or lures it away from the problem site (Conover, 2001). Moreover, compensation programmes might pose a lower investment for policy makers than present eradication programmes (Miller et al., 2007; Slobodchikoff et al., 2009).

Ideally, population control may assume a high priority in areas of high commercial value and relatively low conservation concern. The density of these species could either be maintained at a low level (C in Fig. 2) or reduced in those situations where density is currently high (D2 in Fig. 2). It is very important to stress that damage attributed to small mammals is usually a social perception and therefore should be scientifically documented prior to initiating any population control. In fact, a simple perception of damage does not justify the need to control the numbers of small mammals. In any case, damage caused by small mammals, and hence the need to control them, would only occur in localised cases, and not over larger landscapes (Miller et al., 2007). A good example to illustrate this option comes from some intensive agricultural areas in the Iberian Peninsula. In these areas, where biodiversity richness is low (natural vegetation, predators and other ecologically important groups of species are practically absent), European rabbits locally reach high densities and can damage crops (Barrio et al., 2010). In such areas, controlling rabbits would help to minimise their adverse impacts to commercial activities, and therefore reduce conflicts. A slightly different scenario is possible on the Tibetan Plateau, where plateau pikas reach their highest densities in areas that have been severely overgrazed. A temporal variant of Fig. 2 could be enacted, with pikas being controlled (but not eliminated) on such overgrazed areas with simultaneous cessation of grazing. Following meadow recovery, lower stocking rates of livestock should be utilised and pika populations allowed to become restored to natural levels. The resulting regime could therefore maintain sustainable livestock husbandry, pika populations, and wildlife species dependent upon pikas.

We suggest that the control of these species should only be justifiable in localised cases, in areas of low conservation value, and when the damage they cause is scientifically demonstrable. Nevertheless, it is also important to address how these species could be controlled, relying on some of the lessons provided by the literature about the eradication of invasive species. For instance, Zavaleta et al. (2001) stressed that the removal of an invader should be viewed in a whole-ecosystem context. Under this perspective, poisoning would not be a sustainable strategy to control abundant small mammals in their native ranges, because the agents used to poison small mammals can also affect many other species in the ecosystem directly (Brakes and Smith, 2005; Olea et al., 2009), and can pose a risk for human health (Arnon et al., 2001; Olea et al., 2009). Therefore, less aggressive methods should be used, such as the management system employed in some areas of Spain. There, rabbits are captured in intensive agricultural regions, where they cause damage to crops, and are used in translocation programmes aimed to recover this prey species in areas where it has declined over recent decades and predators of conservation concern still exist (Rouco et al., 2008).

Biodiversity-related conflicts are generally embedded in an ecological, economic, and social context. Recent studies have stressed the need to integrate all these aspects into a general framework that can serve to analyze and resolve conflicts (White et al., 2009; Dickman, 2010; McShane et al., 2011). We have presented a conceptual model that integrates the actors implicated in the management of abundant small mammals that, although being keystone species, have been traditionally persecuted as pests in their native areas. Hopefully, such a balanced, holistic view with a variation in management regimes on a large spatial scale will help to preserve biodiversity and to reduce conflicts with commercial interests.

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