Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands

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The world's grassland ecosystems are shaped in part by a key functional group of social, burrowing, herbivorous mammals. Through herbivory and ecosystem engineering they create distinctive and important habitats for many other species, thereby increasing biodiversity and habitat heterogeneity across the landscape. They also help maintain grassland presence and serve as important prey for many predators. However, these burrowing mammals are facing myriad threats, which have caused marked decreases in populations of the best-studied species, as well as cascading declines in dependent species and in grassland habitat. To prevent or mitigate such losses, we recommend that grasslands be managed to promote the compatibility of burrowing mammals with human activities. Here, we highlight the important and often overlooked ecological roles of these burrowing mammals, the threats they face, and future management efforts needed to enhance their populations and grassland ecosystems.

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Grassland ecosystems worldwide are fundamentally shaped by an underappreciated but key functional group of social, semi-fossorial (adapted to burrowing and living underground), herbivorous mammals (hereafter, burrowing mammals). Examples include not only the phylogenetically similar species of prairie dogs of North America (*Cynomys* spp); ground squirrels (Family Sciuridae) of North America, Eurasia, and Africa; and marmots (*Marmota* spp) of North America and Eurasia, but also the more distantly related but functionally similar plains vizcachas (*Lagostomus maximus)*, Patagonian maras (*Dolichotis patagonum*), and degus (*Octodon degus*) of South America; pikas (*Ochotona* spp) of Asia; ice rats (*Otomys sloggetti*) and springhares (*Pedetes capensis*) of Africa; and burrowing bettongs (*Bettongia lesueur*) and southern hairy-nosed wombats (*Lasiorhinus latifrons*) of Australia (Figure 1). Often living in colonies ranging from tens to thousands of individuals, these mammals collectively transform grassland landscapes through their burrowing and feeding activity. By grouping together socially, they also create distinctive habitat patches that serve as areas of concentrated prey for many predators. Their ecosystem engineering and trophic effects help maintain grassland biodiversity and, consequently, they frequently play keystone roles in these ecosystems (Figure 2).

In a nutshell:

- Social, burrowing, herbivorous mammals play important functional roles in grasslands around the world
- These mammals face many threats, including intentional poisoning, exotic diseases and pests, overhunting, habitat loss, and climate change
- Grassland management must include promoting sufficient numbers of burrowing mammals to fulfill their landscape-scale functional roles, so as to maintain the health and biodiversity of grassland systems and the ecosystem services they provide

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Despite their importance to grassland ecosystems, burrowing mammal populations have declined dramatically, primarily as a result of human impacts; indeed, because grasslands provide the world's most important habitat for agricultural and livestock production, burrowing mammals are often in direct conflict with human activities (Smith *et al.* 2006; Miller *et al.* 2007; Delibes-Mateos *et al.* 2011). Human-mediated introductions of exotic species, disease agents, and overhunting are also reducing their populations (Branch *et al.* 2002; Gage and Kosoy 2005; Wingard and Zahler 2006; Rodriguez 2009). The population dynamics and ecological roles of most burrowing mammal species remain poorly understood, however. The patterns discussed here apply to most, but not necessarily all, of the species mentioned. What is known about the few well-studied species suggests that burrowing mammals likely play widespread and important ecological roles, and that their loss can have cascading detrimental effects on the grassland ecosystems on which both humans and wildlife depend.

An important challenge facing grassland managers is maintaining the important functional roles of these burrowing mammals in ways that are compatible with human activities. Here, we present a conceptual model (Figure 2) that illustrates the common but underappreciated roles

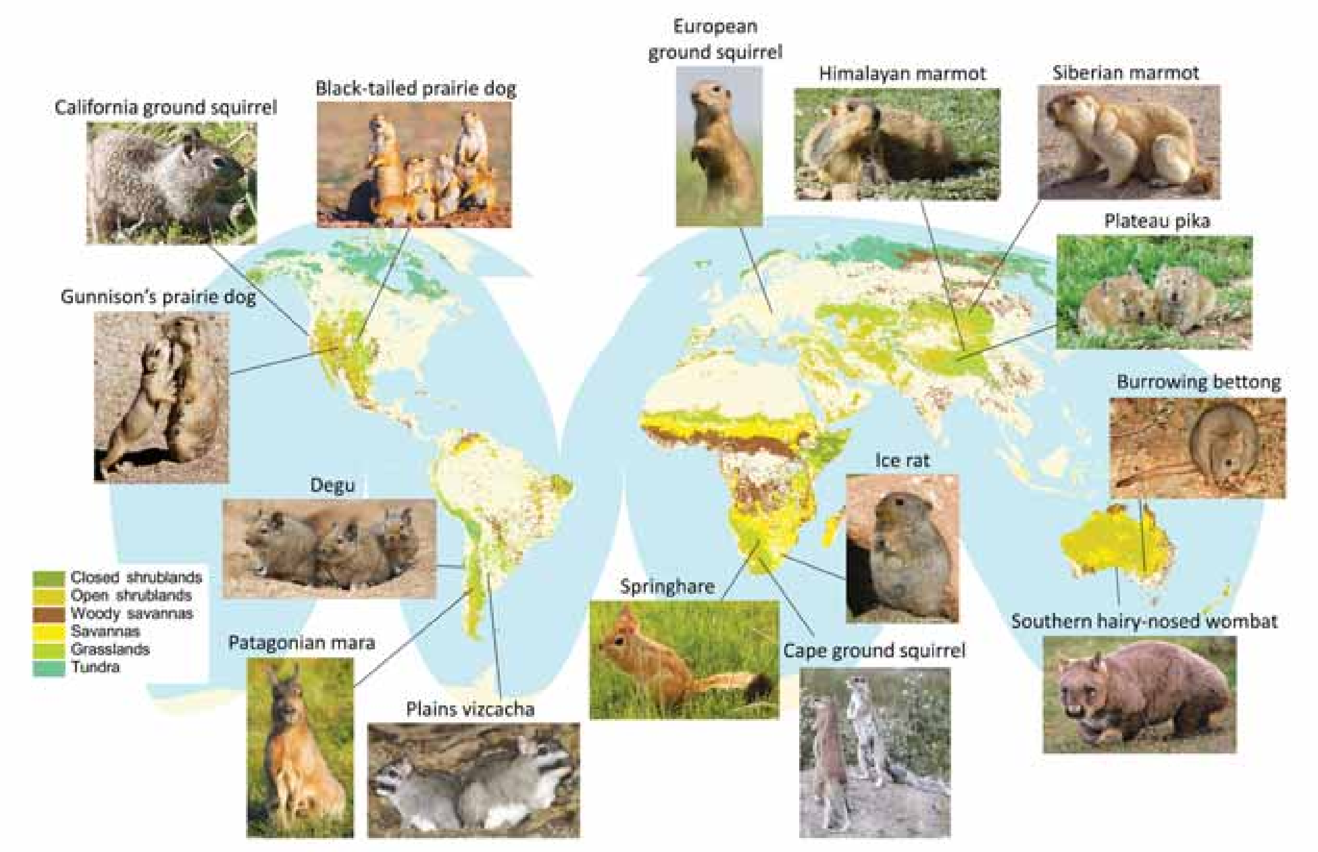

Figure 1. *Examples of social, burrowing, herbivorous mammals from grasslands around the world. North America: California ground squirrels, black-tailed and Gunnison's prairie dogs; Eurasia: European ground squirrels, Himalayan and Siberian marmots, plateau pikas; Australia: burrowing bettongs, southern hairy-nosed wombats; Africa: ice rats, Cape ground squirrels, springhares; South America: degus, Patagonian maras, plains vizcachas. Map from World Resources Institute (White* et al. *2000). (See WebTable 1 for species names and WebPanel 1 for photo credits.)*

that burrowing mammals play in grasslands and highlight the widespread threats facing these species. We also outline future directions required for their conservation and management.

■ Ecological roles of burrowing mammals

Because they tend to cluster in social groups or colonies, burrowing mammals create islands of open grassland habitat that differ from the surrounding landscape and that attract numerous animals (Figure 3). Many burrowing mammals preferentially forage on grasses, thereby facilitating the establishment of forbs; this foraging activity also creates a low mat of grazing-tolerant grasses and forbs within their colonies (Figure 3; Whicker and Detling 1988; Branch *et al.* 1996b; Yoshihara *et al.* 2009). Burrowing mammals also dig underground tunnels, which provide dens and shelter for many animals. This digging activity creates aboveground patches of disturbed soil that can vary in size and type: from open areas surrounding pika burrows (≤ 0.5 m^2); to aboveground soil mounds of 0.5–3 m^2 around prairie dog, marmot, and ground squirrel burrows; to 15–65 m^2 soil mounds created by wombats and bettongs; and to vizcacha mounds that are 300–700 m^2 with up to 100 burrow entrances (Figure 4; Steele and Temple-Smith 1998; Noble *et al.* 2007b; Wesche *et al.* 2007; A Smith and L Branch pers comm). Some burrowing mammals, such as prairie dogs, create numerous small mounds, while others, such as vizcachas and bettongs, construct one large mound that houses the entire colony or family group (Figure 4). Each mound, and often also the colony, provides distinctive habitat that supports plant and animal assemblages that differ from those in the surrounding grassland (Branch *et al.* 2002; Komonen *et al.* 2003; Davidson and Lightfoot 2006). Although their colonies and mounds may be more or less species-rich than adjacent grassland (Lenihan 2007; Noble *et al.* 2007b; Yoshihara *et al.* 2009), these distinctive habitat patches increase overall heterogeneity and biodiversity at multiple scales across the landscape (Figure 5; Whicker and Detling 1988; Davidson *et al.* 2008; Hogan 2010).

Burrowing mammals often move large amounts of soil during burrow construction. For instance, Arctic ground squirrels (*Spermophilus parryii*) and wombats can move as much as 20 metric tons and 1.3–6.0 metric tons, respectively, of soil per hectare (Price 1971; James and Eldridge 2007). The underground systems of burrowing mammals provide an important ecosystem service by facilitating

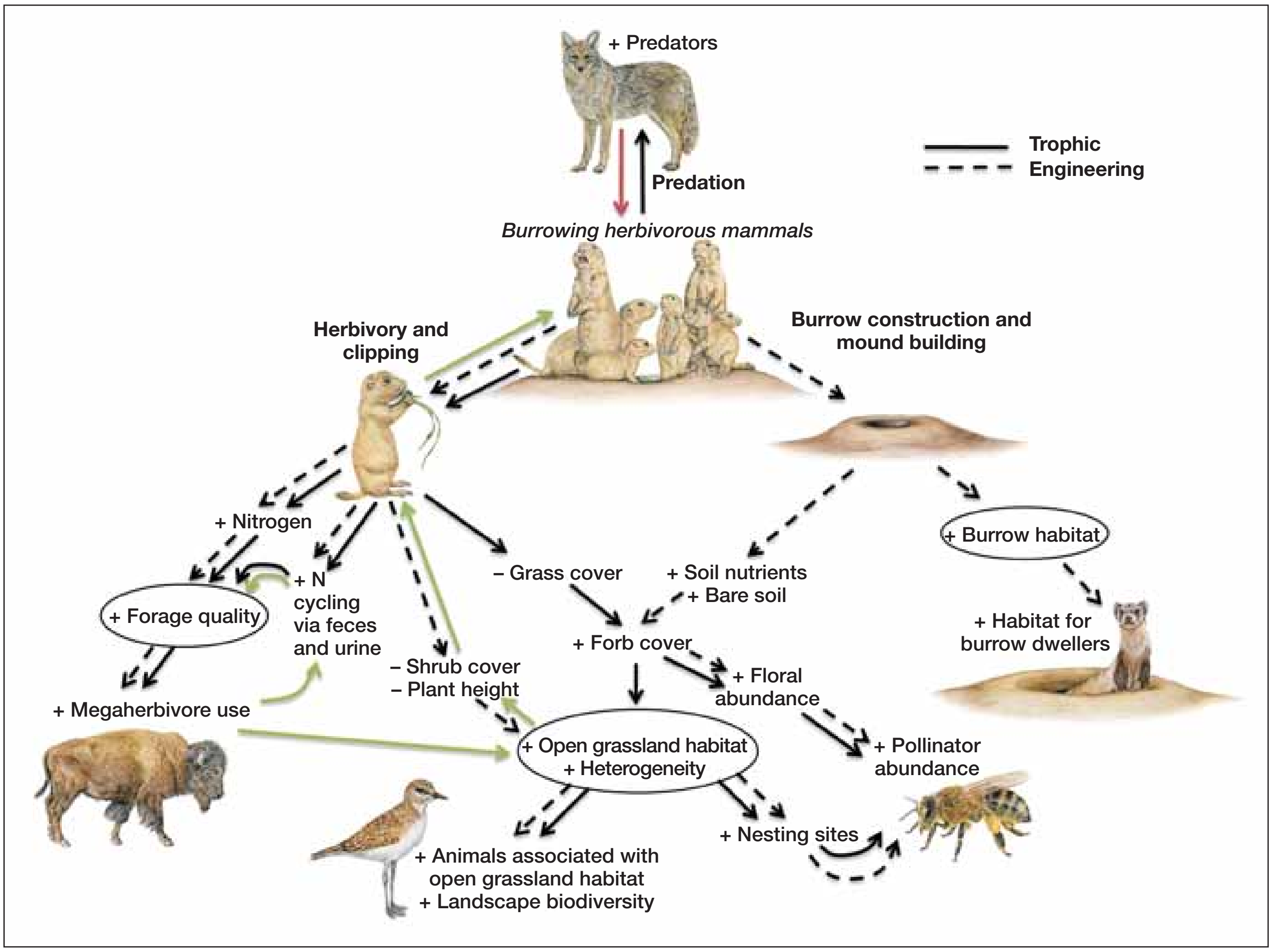

Figure 2. *Conceptual diagram showing the trophic (herbivory, prey) and ecosystem engineering (clipping, burrow construction, and mound building) effects of burrowing mammals on grassland ecosystems, based on the best-studied species: the black-tailed prairie dog in North America. Plus signs indicate an increase; minus signs indicate a decrease. Black arrows depict the effects of burrowing mammals (eg prairie dogs), green arrows depict the impacts of megaherbivores (eg bison), and the red arrow indicates the role of predators. (Drawings provided by SN Davidson.)*

water infiltration (eg Kotliar *et al.* 2006; Hogan 2010). Soil mixing and urine and fecal deposition around mounds can also increase soil organic matter and inorganic nutrients (Noble *et al.* 2007b; Wesche *et al.* 2007; Villarreal *et al.* 2008).

Burrowing mammals help maintain grasslands and open habitat. Species like vizcachas, burrowing bettongs, and prairie dogs prevent invasion and establishment of shrubs through their foraging and clipping (ie pruning) (Weltzin *et al.* 1997; Branch *et al.* 2002; Noble *et al.* 2007a). Shrubland expansion in semi-arid regions of North America and Australia has been attributed, in part, to population reductions of prairie dogs and bettongs, respectively (Weltzin *et al.* 1997; Noble *et al.* 2007a).

Herbivory and burrowing activities can reduce overall plant biomass associated with burrowing mammal colonies, but the higher levels of soil nutrients and greater degree of water infiltration that occurs around their mounds can result in elevated foliar nutrient concentrations and greater plant biomass surrounding their burrows (Retzer 2007; Van Staalduinen and Werger 2007; Hogan 2010). Grazing by burrowing mammals also enhances plant nitrogen uptake, resulting in increased forage quality on their colonies (Whicker and Detling 1988; Wesche *et al.* 2007; Villarreal *et al.* 2008). Increased forage quality apparently attracts megaherbivores, such as bison (*Bison bison*) and cattle (*Bos taurus*), to prairie dog colonies in North America (Whicker and Detling 1988; Davidson *et al.* 2010); grazing and defecation by such megaherbivores further increases forage quality and decreases vegetation height (Whicker and Detling 1988). Consequently, megaherbivores and small burrowing mammals can have mutualistic relationships (Krueger 1986; Davidson *et al.* 2010). Indeed, grazing by megaherbivores facilitates increases in population densities of burrowing mammal species that prefer more open grassland, thereby increasing their overall impact on the ecosystem. This relationship has been observed among native megaherbivores and many burrowing mammals, such as that between bison and prairie dogs, as well as among live-

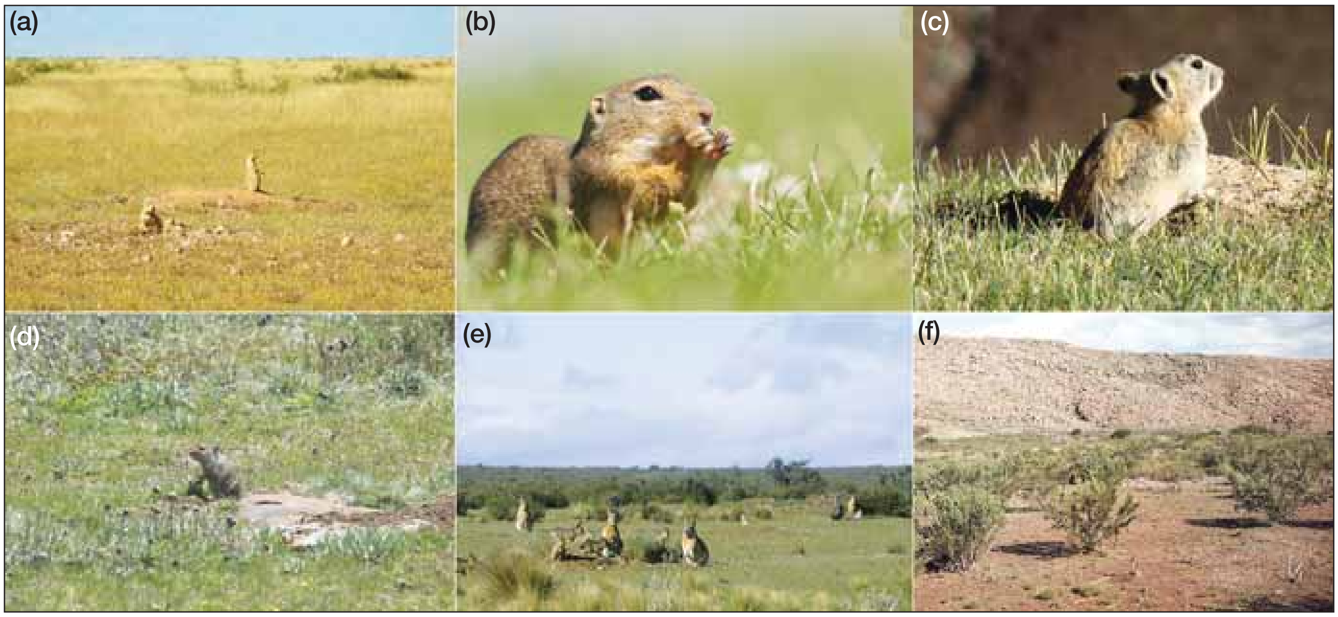

Figure 3. *Photos showing the open habitats that burrowing mammals help create. (a) Black-tailed prairie dogs, (b) European ground squirrel, (c) plateau pika, (d) ice rat, (e) Patagonian maras and their habitat, and (f) grass understory heavily grazed by vizcachas. (See WebPanel 1 for photo credits.)*

stock species and prairie dogs, vizcachas, Patagonian maras, springhares, marmots, pikas, Brandt's voles (*Lasiopodomys brandtii*), and long-tailed ground squirrels (*Urocitellus undulatus*; Jackson 1988; Augustine *et al.* 1995; Ronkin *et al.* 2009). Although burrowing mammals often benefit from grazing by megaherbivores, overgrazing by the latter may result in food limitation and desertification, frequently leading to population declines in burrowing mammals (Komonen *et al.* 2003; Read *et al.* 2008; Rodriguez 2009).

The excavations created by burrowing mammals provide important belowground habitat for many grassland animals. For example, burrows can increase overall arthropod diversity and abundance by two- to threefold (Davidson and Lightfoot 2007; Read *et al.* 2008), and herpetofauna commonly use such burrows to escape from predators and as breeding sites (WebTable 1; Smith and Foggin 1999; Davidson *et al.* 2008; Hogan 2010). These burrows are also important for other rodents, such as spotted ground squirrels (*Xerospermophilus spilosoma*), northern grasshopper mice (*Onychomys leucogaster*), and Bennett's chinchilla rats (*Abrocoma bennettii*), and ground-nesting birds, such as burrowing owls (*Athene cunicularia*), miners (*Geositta cunicularia*), swallows (*Notiochelidon cyanoleuca*), ground jays (*Pseudopodoces humilis*), snowfinchs (*Montifringilla* spp and *Pyrgilauda* spp), and ant-eating chats (*Myrmecocichla formicivora*) (WebTable 1). Several mustelids, herpestids, felids, and canids that prey on burrowing mammals also inhabit their burrows (Branch *et al.* 2002; Waterman and Roth 2007; Murdoch *et al.* 2009).

Aboveground, burrow mounds attract many animals, including unique grasshopper and ground-dwelling arthropod species assemblages, lizards that use mounds for basking, and megaherbivores like bison that wallow in the disturbed soil (Coppock *et al.* 1983; Davidson and Lightfoot 2007; Davidson *et al.* 2008). At the landscape scale, colonies of burrowing mammals attract species that prefer open grassland habitat, such as lesser earless lizards (*Holbrookia maculata*) on prairie dog colonies (Davidson *et al.* 2008), and bird species, such as mountain plovers (*Charadrius montanus*), long-billed curlews (*Numenius americanus*), and burrowing owls (Branch *et al.* 2002; Kotliar *et al.* 2006). Open grassland habitat increases the ability of animals to detect predators. This benefits co-existing burrowing species like Patagonian maras, yellow mongoose (*Cynictis penicillata*), meerkats (*Suricata suricatta*), and spotted ground squirrels that also profit from the sociality of, and predator detection by, the burrowing mammals with which they associate (Waterman and Roth 2007; Villarreal *et al.* 2008; AD Davidson pers observ). The greater abundance of forbs and dwarf shrubs associated with colonies also attracts ungulates like pronghorn (*Antilocapra americana*) (Krueger 1986), and the high floral densities and open soil habitat (used for nesting) on colonies increase the abundance and diversity of insect pollinators (Hardwicke 2006; Yoshihara *et al.* 2010a).

Because their colonies represent high-density, localized patches of reliable prey, burrowing mammals also attract predators (Figure 6; WebTable 1). Indeed, the abundance and richness of carnivorous mammalian and avian fauna is often greater in areas where burrowing mammal colonies are located (eg Lai and Smith 2003; Kotliar *et al.* 2006; Lenihan 2007; Ceballos *et al.* 2010). Raptors, canids, felids, herpestids, mustelids, and some snakes are common predators of many burrowing mammals, and the predator communities that associate with them are similar across different grassland ecosystems (Figure 6). For instance,

Figure 4. *Photos showing the different sizes and types of soil disturbances that burrowing mammals create when building their underground burrows. (a) Plateau pika burrows, (b) black-tailed prairie dog mounds, and (c) a southern hairy-nosed wombat warren. (See WebPanel 1 for photo credits.)*

black-backed jackals (*Canis mesomelas*) and honey badgers (*Mellivora capensis*) are common predators of springhares and Cape ground squirrels (*Xerus inauris)* in Africa, whereas coyotes (*Canis latrans*) and American badgers (*Taxidea taxus*) are important predators of North American prairie dogs (WebTable 1). Small cats also prey on burrowing mammals, including bobcats (*Lynx rufus*) on California ground squirrels (*Otospermophilus beecheyi*) and prairie dogs, Geoffroy's cats (*Leopardus geoffroyi*) on vizcachas, Pallas's cats (*Felis manul*) on pikas and long-tailed ground squirrels, and African wild cats (*Felis silvestris lybica*) on springhares and Cape ground squirrels (WebTable 1). Raptors like giant eagle owls (*Bubo lacteus*) prey on springhares (Skinner and Chimimba 2005), while Daurian pikas (*Ochotona dauurica*) often make up more than 70% of the Eurasian eagle owl's (*Bubo bubo*) diet (Smith and Foggin 1999). Wolves (*Canis lupus*), brown bears (*Ursus arctos*), mountain lions (*Puma concolor*), and snow leopards (*Uncia uncia*) also prey on burrowing mammals (WebTable 1); for example, mountain lions in South America often rely on vizcachas for up to 50–85% of their diets, while on the Tibetan Plateau, plateau pikas (*Ochotona curzoniae*) can represent as much as 50% of Tibetan wolf (*C lupus chanco*) and 78% of brown bear diets (Branch *et al.* 1996a; Smith and Foggin 1999; Xu *et al.* 2006).

Ecosystem engineers and keystone species

Species considered to be ecosystem engineers physically create, maintain, and modify their environment (Jones *et al.* 1994), whereas those that have irreplaceable ecological impacts that are large relative to their abundance are referred to as keystone species (Power *et al.* 1996). Because of the large, transformative effects that burrowing mammals have on grassland ecosystems, they are often considered ecosystem engineers, keystone species, or both (Samjaa *et al.* 2000; Branch *et al.* 2002; Lai and Smith 2003; Kotliar *et al.* 2006). Although the relative importance of burrowing mammal impacts may vary across species, space, and time, these animals play unique and non-substitutable keystone roles (Davidson and Lightfoot 2006). Moreover, although population densities of burrowing mammals can be quite high within their colonies, they are not necessarily abundant across the greater landscape. Consequently, because they create unique patches of important grassland habitat, increase biodiversity across the landscape, and are needed in large numbers to support associated species, the ecological roles of burrowing mammals must be examined from a landscape perspective (Figures 2, 5, and 6; WebTable 1).

■ Conservation status and current threats

The conservation status of burrowing mammals varies greatly across species, but populations of most species are heavily and negatively impacted by humans (WebTable 1). Some, like Siberian marmots (*Marmota sibirica*), are listed as "Endangered" on the International Union for Conservation of Nature (IUCN) Red List, whereas others, such as the Patagonian mara and European ground squirrel (*Spermophilus citellus*), are listed as "Near Threatened" and "Vulnerable", respectively, and are declining at a rate of 30% or more per decade. Despite being nearly eradicated on Australia's mainland, burrowing bettongs are considered "Near Threatened" because their populations are now stable or improving. Many others are listed in the category of "Least Concern" by the IUCN, but several of those species – such as prairie dogs, bobak marmots (*Marmota bobak*), southern hairy-nosed wombats, and vizcachas – have also experienced dramatic population declines across much of their former ranges. Some species considered of "Least Concern", such as ice rats and degus, are thought to be common and have stable populations, but others, including several species of pikas, are in decline because of extensive, ongoing poisoning campaigns. For many other species of burrowing mammals, population trends are poorly known. Below, we describe the primary threats impacting burrowing mammals around the world.

Habitat loss

Grasslands cover 41% of the world's land surface and are the primary environments used for growing crops and grazing livestock (White *et al.* 2000). Widespread conversion of grassland to cropland and extensive overgrazing and desertification have resulted in 20–80% declines in

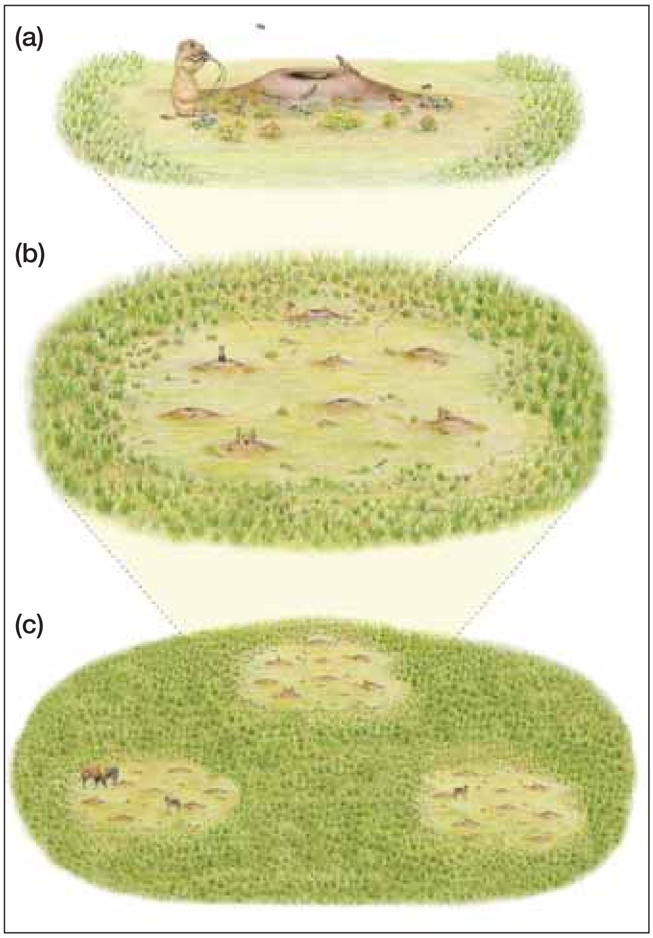

Figure 5. *Diagram illustrating the distinctive islands of habitat that burrowing mammals create across multiple spatial scales with their (a) mounds, (b) individual colonies, and (c) colony complexes. These features enhance habitat heterogeneity and, consequently, increase biodiversity across grassland landscapes. This illustration is based on black-tailed prairie dogs in the Great Plains grasslands of North America. (Drawing provided by SN Davidson.)*

grassland area across all continents (White *et al.* 2000), leading to substantial reductions in the amount of suitable habitat for burrowing mammals and consequent population declines in many species (eg Hoogland 2006; Noble *et al.* 2007b; Ceballos *et al.* 2010).

Conflicts with livestock

Heavy reliance on grasslands for livestock production has resulted in major conflicts between the livestock industry and burrowing mammals (Miller *et al.* 2007; Delibes-Mateos *et al.* 2011). A common threat facing burrowing mammals in many parts of the world is widespread persecution because of their perceived competition with livestock; for instance, the extensive poisoning and shooting of prairie dogs in North America during the past century is largely responsible for the 98% decline in their populations (Hoogland 2006). Poisoning is also prevalent throughout Asia (eg pikas and Brandt's voles), South America (eg vizcachas), and Africa (eg ice rats) (Branch *et al.* 2002; Bagchi *et al.* 2006; Mokotjomela *et al.* 2009). Governments spend millions of dollars each year "controlling" burrowing mammal populations to benefit the livestock industry, despite research repeatedly demonstrating that such campaigns are not cost effective and result in the indiscriminant poisoning of other types of wildlife (Hoogland 2006; Wesche *et al.* 2007; Delibes-Mateos *et al.* 2011). In fact, burrowing mammals, particularly at low to moderate densities, can have beneficial effects by increasing forage quality and productivity (Whicker and Detling 1988; Smith and Foggin 1999; Noble *et al.* 2007b). Livestock weight gains are minimally affected when burrowing mammal colonies cover less than 30% of the landscape (Derner *et al.* 2006), and livestock mass has been shown to decline over the same period that burrowing mammals are poisoned (Smith and Foggin 1999). Still, burrowing mammals are often blamed for grassland degradation, despite having co-existed with free-ranging, native megaherbivores for millions of years. Many grasslands are simply overstocked with livestock (Smith and Foggin 1999; Bagchi *et al.* 2006; Mokotjomela *et al.* 2009); for example, Ceballos *et al.* (2010) described a grassland in Mexico that could sustainably support 200 head of cattle but was being grazed by 2000 cattle. Concomitant with this excessive livestock grazing was the collapse of one of the largest remaining black-tailed prairie dog (*Cynomys ludovicianus*) colonies (Ceballos *et al.* 2010). However, where they co-exist, the effects of livestock on grasslands are not independent of burrowing mammals. Indeed, relationships between livestock and burrowing mammals can be mutualistic, and their combined effects on the grassland ecosystem can be synergistic (Davidson *et al.* 2010). Burrowing mammals also tend to have more intensive localized effects due to their sedentary, colonial behavior, whereas megaherbivores have more diffuse impacts across larger spatial scales (Davidson *et al.* 2010; Yoshihara *et al.* 2010b).

Overexploitation

Many burrowing mammal species are overhunted, often for their pelts. Siberian marmots of the Mongolian steppe, for example, once numbered around 40 million individuals; overhunting reduced their populations to 20 million by 1990, and fewer than 5 million remained by 2002 – a 70% decline in little over a decade (Wingard and Zahler 2006; IUCN 2011). Plains vizcachas, Patagonian maras, European ground squirrels, long-tailed ground squirrels, gray marmots (*Marmota baibacina*), Siberian marmots, bobak marmots, Himalayan marmots (*Marmota himalayana*), and Arctic ground squirrels, among others, are similarly threatened by overexploitation (WebTable 1).

Introduced species and disease

Exotic species also pose major threats to many burrowing mammals. Plague, a disease caused by the bacterium *Yersinia pestis*, is native to rodents in Asia but has been introduced

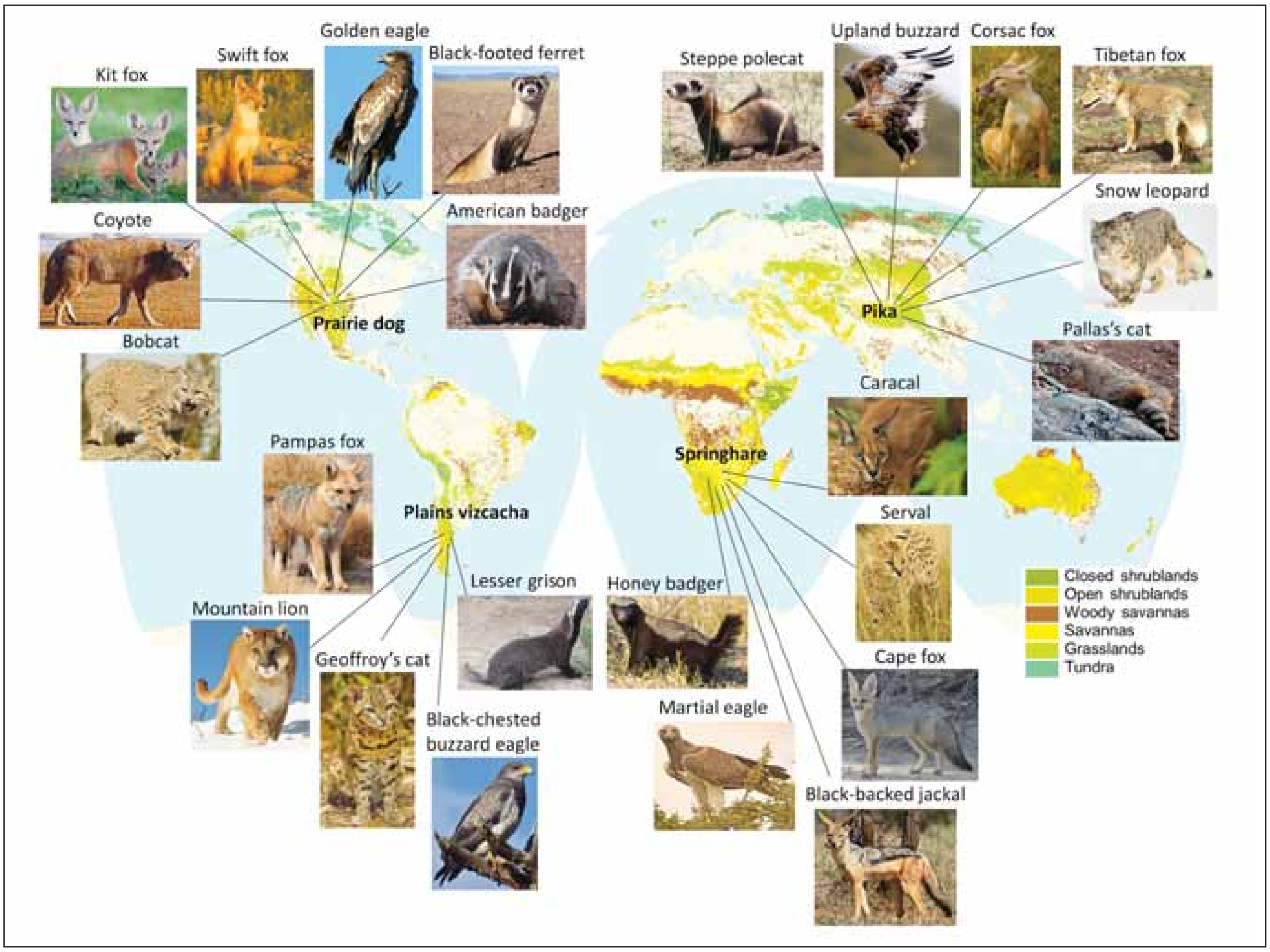

Figure 6. *Broadly similar predator communities associated with burrowing mammals around the world. Examples of predators associated with prairie dogs of North America, pikas of Eurasia, springhares of Africa, and plains vizcachas of South America are shown. Map from World Resources Institute (White* et al. *2000). (See WebTable 1 for predator species names and predator communities associated with these and other burrowing mammal species. See WebPanel 1 for photo credits.)*

to Africa and the Americas (Gage and Kosoy 2005). Since its introduction to these parts of the world, this exotic pathogen has been devastating populations of some species, such as prairie dogs in North America, that lack immunity (Gage and Kosoy 2005, but see Rocke *et al.* 2012). Even in its native range, plague can cause massive, episodic die-offs in Siberian marmots, exacerbating declines of this already endangered species (Wingard and Zahler 2006). Sarcoptic mange (*Sarcoptes scabiei*) is an emerging disease threatening the highly fragmented populations of southern hairy-nosed wombats in Australia (IUCN 2011). Overgrazing by introduced European rabbits (*Oryctolagus cuniculus*) and domestic livestock, as well as predation by introduced predators, are also important threats to Australia's bettongs and wombats (Noble *et al.* 2007b; IUCN 2011).

Climate change

The impacts of climate change on burrowing mammals are only beginning to be detected. For instance, prairie dog populations have declined dramatically in parts of the southern distribution of their North American range after periods of drought, which are projected to increase considerably in this region over the coming decades (Ceballos *et al.* 2010). Plague epizootics correlate positively with precipitation (Gage and Kosoy 2005), so a changing climate may lead to shifts in areas impacted by plague. Recently, plague has expanded eastward in the US, possibly due to a changing climate, occurring recently and for the first time in the Conata Basin of South Dakota, where the largest remaining complex of black-tailed prairie dog colonies in the US occurs. This has caused large die-offs in prairie dogs and endangered black-footed ferrets (*Mustela nigripes*) (USFWS 2009).

Ecological consequences of burrowing mammal declines

Consistent with the loss of keystone species (Power *et al.* 1996), the impacts of burrowing mammal declines can cascade throughout ecosystems (WebTable 1). Not only can their loss facilitate woody plant invasion (Weltzin *et* *al.* 1997; Noble *et al.* 2007a; Ceballos *et al.* 2010), but animals that rely on their colonies for nesting habitat are also negatively affected, such as mountain plovers that have declined with the loss of prairie dogs, burrowing owls that have declined with losses of both prairie dogs and vizcachas, and ground-nesting birds that have declined following pika poisoning (Branch *et al.* 2002; Lai and Smith 2003; Kotliar *et al.* 2006). Predators dependent on burrowing mammals for prey have also shown dramatic declines. Black-footed ferrets, for example, rely on prairie dogs for about 90% of their diet; largely because of the extensive decline in prairie dogs, black-footed ferrets have become one of the most endangered mammals in North America (Kotliar *et al.* 2006). Interestingly, the US Fish and Wildlife Service's multi-million-dollar breeding program to recover black-footed ferret populations is running out of suitable reintroduction habitat because ferrets require extensive prairie dog colony complexes to support them, but such complexes are now extremely rare as a result of habitat fragmentation, introduced plague, and government-funded extermination programs. Similarly, European ground squirrel populations have experienced major declines, which may be causing an associated decline in one of their predators, the steppe polecat (*Mustela eversmanii*) (IUCN 2011). Ferruginous hawks (*Buteo regalis*), which are highly reliant on Gunnison's prairie dogs (*Cynomys gunnisoni*) for prey during their winter migration, are now threatened, mainly because of the fall in prairie dog populations (Cartron *et al.* 2004). Comparably, where plateau pikas have been poisoned in the Tibetan Plateau, bird species abundance and richness have declined considerably, reflecting declines in species that nest in pika burrows or prey on pikas. In fact, many predators that rely on plateau pikas as key prey – including upland buzzards (*Buteo hemilasius*), saker falcons (*Falco cherrug*), brown bears, Pallas's cats, Tibetan foxes (*Vulpes ferrilata*), and steppe polecats – have nearly disappeared from areas where pikas have been poisoned (Lai and Smith 2003; Delibes-Mateos *et al.* 2011).

Research, policy, and management implications

Burrowing mammals play important functional roles in grasslands and a variety of other ecosystems around the world (Kelt 2011). However, their requirements and impacts vary by species, which have been shaped by their evolutionary histories and extrinsic environmental conditions, such as climate, soils, vegetation, and associated animal species. The distinctive impacts that each burrowing mammal species has play out across broad landscapes, where they facilitate associated species and perform key ecosystem functions. However, because many burrowing mammal populations have undergone severe numerical reductions, their key ecological roles have been greatly diminished throughout much of their geographic range. To support the ecosystems associated with burrowing mammals, we recommend that conservation and management efforts include maintaining or re-establishing these populations and their functional roles at the landscape scale.

Research needs

Because most species of burrowing mammals remain poorly studied, considerable additional research is necessary to understand their impacts, conserve their populations, and preserve or restore their ecological roles. Among the most critical research needs are to:

(1) Quantify and understand their roles in maintaining biodiversity, and identify those species with which they are strongly associated. We also need to better understand their population trends and conservation needs, because declines in burrowing mammals are likely to have cascading effects throughout the ecosystems in which they occur.
(2) Determine under what conditions their interactions with associated species can be positive, neutral, or negative, and how this translates into overall grassland health. This includes quantifying the ecosystem services they provide and their potential economic value.
(3) Study the relationships between burrowing mammals and livestock to determine how they can co-exist, from ecological, economic, and social perspectives.
(4) Determine sustainable harvest rates for those species threatened by overhunting.
(5) Develop the capability to predict and help prevent disease outbreaks, such as plague and mange, possibly through the use of vaccines like those being developed to protect critical populations of North American prairie dogs from plague.

Policy and management implications

As the demand for food production continues to grow over the next decades, conflicts between burrowing mammals and people are bound to increase. Although we have cited evidence that these animals have positive impacts on their environment, and that eradication programs are typically costly and ineffective, burrowing mammals remain highly misunderstood and heavily persecuted. The traditional assumption that they compete and have other net negative interactions with livestock needs to be re-evaluated. Results of recent research should be used to educate managers and the public on their diverse ecological roles and positive impacts. Such efforts could help change public attitudes, correct misconceptions, and reverse government policies that continue to fuel eradication programs (Smith and Foggin 1999; Miller *et al.* 2007; Delibes-Mateos *et al.* 2011). In areas where their populations must be controlled, managers may be able to reduce burrowing mammal populations by simply reducing livestock grazing and allowing grass to grow tall (Smith *et al.* 2006; Davidson *et al.* 2010). Overall, however, grassland management must be more holistic, managing not only for livestock production but also for preserving burrowing mammal populations that are essential for maintaining healthy grasslands over the long term.

Finally, conservation plans are needed to reverse the declines in burrowing mammal populations and associated species. Reintroductions are currently an important component of such conservation efforts but are expensive, intensive, and small in scale. Consequently, managers should focus on maintaining and increasing existing populations wherever possible, including the creation of protected areas, engagement of local communities, and provision of economic incentives whereby landowners receive financial compensation for supporting burrowing mammals and the ecosystem services they provide (Hoogland 2006). Bolstering populations is also important to mitigate against future losses of these species as a result of disease and climate change. Without such actions, there is serious concern as to how species threatened by multiple, compounding human impacts today will be able to withstand a rapidly changing environment.

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