

5. Rodent–Ecosystem Relationships: a Review

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Abstract

Because of their ability to use agricultural production and their role in spreading disease in humans, rodents are often viewed as having negative impacts in modified and natural ecosystems. Some species, such as the black rat, have been further implicated in the extinctions of many species of insular land birds, small mammals and invertebrates. In this review, I focus on the interactions of rodents with chemical and structural attributes of the environment, using the concept of ‘ecosystem engineering’ as a framework. I also discuss the direct and indirect impacts of rodents on food resources.

Many rodents alter the structure of their environment by surface tunnelling, construction of leaf or stick nests, arranging pebbles around burrow entrances, or stripping bark from trees. These activities provide living space or resource opportunities for other organisms, and represent examples of simple allogenic engineering. In more complex examples, digging, nest-building and other activities modify the environment more extensively and modulate resource flows to other organisms. Burrowing rodents such as pocket gophers, prairie dogs and mole-rats alter soil structure and microtopography, nutrient cycling and water flows over local or regional areas, and have dramatic effects on the growth and species composition of plant communities. Nest structures that divert resource flows also represent complex allogenic engineering. For example, beaver impoundments affect nutrient cycles and water flow, and consequently the species richness of aquatic invertebrates, fish and riparian vegetation at local and catchment scales. Rodents also engineer local environments biotically by dispersing seeds and the storage organs of geophytes, as well as the spores of hypogeous fungi that form mycorrhizal associations with plants. Some species probably also play a minor role as pollinators. Rodents, finally, have diverse and often pervasive effects on their food resources; there is much evidence of positive and negative effects on growth form, standing crop and the species composition and physical structure of plant communities.

Rodents therefore contribute importantly to ecosystem function, and may have value as indicators of environmental change. Management of rodent pests will need to move away from the broadly destructive current approach of chemical warfare toward ecologically-based solutions that sustainably control only the target species.

Keywords

Ecosystem engineering, environment, rodent, facilitation, predation, nests, burrows

INTRODUCTION

ALTHOUGH SOME 1,800 species of modern rodents have been described (Corbet and Hill 1991), few have been well-studied and the majority remains poorly known. Not surprisingly, most knowledge has been obtained on species that impact on humans by exploiting agricultural production or by spreading diseases (Chitty and Southern 1954; Twigg 1978), or are useful in laboratory research (Barnett 1975). Different species of rodents, especially *Rattus* spp., have been implicated also in the demise of island vertebrate faunas (Atkinson 1985, 1996), and have often been subject to intensive control to achieve conservation objectives. Effective management of rodent pests remains an elusive but important goal in many parts of the world, and for different reasons. As discussed by various authors in this book, solutions may lie more with ecologically-based management than with simple one-factor approaches that have been used previously.

Despite the often negative effects of rodents in natural and modified ecosystems, many species have been shown to contribute to ecosystem function and to have value as indicators of environmental change. For example, microtine rodents are important at times in the cycling of carbon, nitrogen and other elements (Inouye et al. 1987a, Huntly 1991), while beavers cause alteration of hydrological regimes (Naiman et al. 1988). Such species have been termed 'ecosystem engineers' (Jones et al. 1994). Other species may be important as pollinators or vectors of fungal spores (Tory

et al. 1997). Both microtine and sciurid rodents have been used as indicators of industrial pollution (Kostelecka-Myrcha et al. 1981; Lepage and Parker 1988), while some murids have been used to indicate the severity of impact wrought by defoliants used in chemical warfare (Sokolov et al. 1994; Evgenjeva and Fadeeva 1996). Several further species also may be sensitive barometers of climatic change (Frey 1992; Bright and Morris 1996).

The range of interactions of rodents with the environment is not well appreciated, perhaps because the interactions are diverse, often complex, or not apparent in studies carried out in small study areas or for short periods. However, such an appreciation is likely to be important for successful management of rodent pests, and essential if management is to be ecologically-based.

In the present paper, I present a selective review of rodent–ecosystem relationships, focusing on the impacts of rodents on the physical, chemical and biotic environments and the consequences of these impacts for other biota. Little attention is given to competitive relationships among rodents or to rodents as prey, because reviews of these topics are available elsewhere (Sinclair 1989; Brown and Harney 1993; Dickman and Doncaster, submitted for publication). Where possible, studies that demonstrate interactions experimentally have been emphasised, because these are most likely to identify the nature and magnitude of any interactions that occur. The concept of 'ecosystem engineering' is used to provide a framework for much of the review.

ECOSYSTEM ENGINEERING

The term ‘ecosystem engineering’ was introduced by Jones et al. (1994) and refined by Jones et al. (1997). It may be defined as follows: “Physical ecosystem engineers are organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. Physical ecosystem engineering by organisms is the physical modification, maintenance or creation of habitats. The ecological effects of engineering on other species occur because the physical state changes directly or indirectly control resources used by these other species” (Jones et al. 1997, p. 1947).

Engineers were divided into two broad groups by Jones et al. (1994, 1997). *Autogenic* engineers change the environment by their own physical structures; an example would be the shed limbs of trees that modulate microclimate and microhabitat for other organisms on the forest floor. In contrast, *allogenic* engineers change the environment by transforming living or abiotic materials from one state to another by mechanical or other means. An example would be the construction of burrows by one species that could be used by others. Rodents could be expected to be allogenic engineers.

In both their papers, Jones et al. (1994, 1997) drew a distinction between physical ecosystem engineering and other ecological processes such as pollination, dispersal, competitive and trophic interactions, including the utilisation of living or dead tissue by consumers or decomposers. In the present paper, however, I include the former two of these processes under the term ‘biotic engineering’. Justification for this approach is

given in Figure 1; this approach also provides consistency in this review. Trophic interactions do not fit an engineering paradigm, and the effects of rodents on plant and invertebrate prey species are discussed separately below.

ALLOGENIC ENGINEERING

Simple cases: changes in physical state (Figure 1a)

Rodent burrows are obvious and widespread examples of allogenic engineering. Simple burrows are made by most species at some time in their life cycle, and vary in size, orientation, depth and substrate characteristics. Among Australian desert rodents, *Pseudomys hermannsburgensis* and *Notomys alexis* dig deep, vertical burrows in summer to avoid high daily temperatures, but occupy shallow surface burrows in other seasons when temperatures, and daily variations in temperature, are less extreme (C.R. Dickman, personal observation). Other species, such as *Rattus colletti*, barely modify cracks in the soil (Madsen and Shine 1999) or, like *Rattus villosissimus*, may construct complex networks of tunnels under favourable conditions (Predavec and Dickman 1994). The burrows of many species have been described in the literature (e.g. Kemper 1981; Bronner 1992), with overviews provided by Reichman and Smith (1990), Meadows and Meadows (1991) and Hansell (1993).

The major resource created by burrows is living space for other organisms. Other rodents, lizards, snakes and many species of invertebrates make opportunistic use of burrows (Kiviat 1978; Skinner and Smithers 1990). In arid Australia, several species of

dasyurid marsupials make extensive use of abandoned rodent burrows, being unable to dig burrows themselves (Dickman and Read 1992; Dickman 1996). In one study, the burrowing activity itself, in reducing compaction of soil, was shown to have the additional effect of promoting germination of seeds of an iridaceous geophyte (Contreras and Gutiérrez 1991).

Nests provide another example of allogenic engineering. Simple constructs, such as the cup-shaped grass nests of *Micromys minutus*, may take hours or days to build and last for the duration of one breeding season (Harris and Trout 1991); more complex structures of sticks and other detritus, engineered by *Leporillus* spp. and *Neotoma* spp., often last for generations (Copley 1988). Nests are made from a variety of living and non-living materials, and are sometimes decorated with pebbles or other materials (Anstee et al. 1997) for reasons that remain unclear. As with burrows, nests provide living space for other species of vertebrates and invertebrates. Such exploitation is usually opportunistic. However, blind, wingless earwigs of the genus *Hemimerus* are found primarily in the nests of *Cricetomys gambianus*, and may be obligately associated (Knight 1984).

Two, more subtle examples of allogenic engineering may be cited. The first involves shallow scrapes created in surface soil by foraging rodents that provide sites for accumulation of seeds (McNaught 1994, see also below). The second involves bark-stripping of trees by *Sciurus*, *Sundasciurus* and other squirrels (Medway 1983). De-barking facilitates access of fungal pathogens to vascular tissues (Abbott et al. 1977), while dead trees provide nesting,

roosting and shelter sites for several species of birds, bats and other arboreal mammals (Corbet and Harris 1991; MacKinnon et al. 1996). It is likely that rodent-induced damage to plants provides opportunities for exploitation by a broad range of organisms, but few relevant studies have been carried out to confirm this (for a general discussion, see Karban and Myers 1989).

Complex cases: state changes that modulate resource flow (Figure 1b)

Continual and intensive burrowing activity by rodents may provide temporary living space for other organisms, but it also affects nutrient cycling, water flow, soil structure and microtopography. Such effects have been studied in detail in several species of fossorial and terrestrial rodents, especially North American geomyids, or pocket gophers, prairie dogs and Old World mole-rats.

The digging activities of pocket gophers (70–350 g) produce small piles of fresh surface soil that may, over extended periods, accumulate into large mounds termed mima mounds (Inouye et al. 1997). In some habitats, digging activity can cast over 15,000 kg of soil/ha/year onto the surface, and mima mounds of 25–50 m in diameter and 2 m in height may be common (Beuchner 1942; Ross et al. 1968). Some 50–100 mima mounds have been recorded per hectare in some areas, with higher densities occurring usually in disturbed prairie and agricultural landscapes (Mielke 1977). The mounds may consist entirely of topsoil, or soil with gravel and pebbles 50–60 mm diameter; in some locations the presence of soil horizons within mounds suggests a long period of stabilisation (Cox and Gakahu 1986).

Comparisons of soils from mounds and undisturbed inter-mound areas have shown differences in texture, organic content, water-holding capacity and nutrient status (Mielke 1977; Hobbs and Hobbs 1987; Inouye et al. 1987b; Huntly and Inouye 1988). These differences in turn promote heterogeneity in plant species composition and growth responses. In shortgrass prairie, the burrowing activities of *Thomomys bottae* may kill standing vegetation but provide opportunities for establishment of herbaceous perennial dicots (Martinsen et al. 1990). In serpentine grassland, mounds of *T. bottae* are invaded by different species of plants depending on prevailing rainfall

conditions (Hobbs and Mooney 1991); the timing and intensity of soil disturbance may also be important (Moloney et al. 1992). Finally, in tallgrass prairie, the mounds of *Geomys bursarius* have complex effects on both vegetation and fauna. Mounds break the prairie canopy and provide recruitment sites for dicot seedlings, often increasing local plant diversity (Hartnett and Keeler 1995). Mounds also attract some herbivores such as grasshoppers, but may either attract or repel mammalian herbivores such as the meadow vole *Microtus pennsylvanicus* (Whittaker et al. 1991; cf. Klaas et al. 1998). If mounds alter local patterns of herbivory, this is likely to produce further effects on

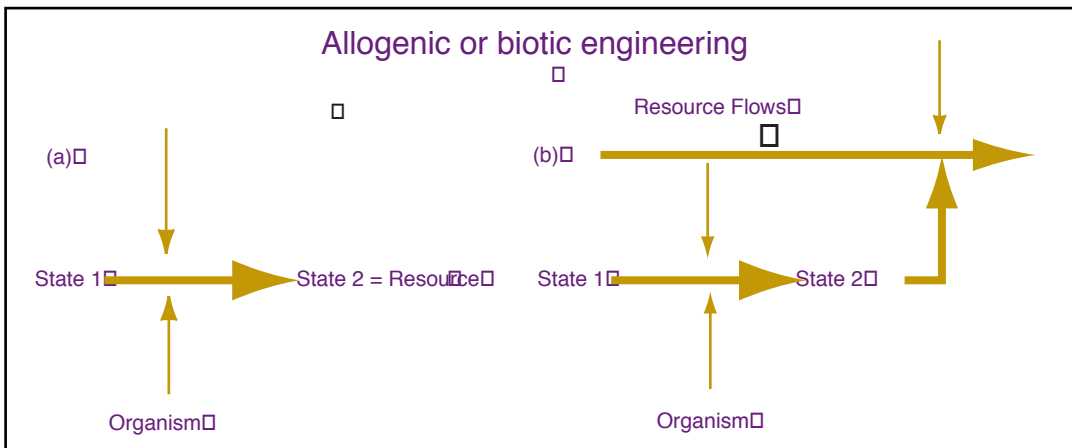


Figure 1. Conceptual models of allogenic and biotic engineering, as applied to rodents (after Jones et al. 1994, 1997).

In the simplest case, (a), living or non-living raw materials are transformed by animal activity from state 1 to state 2. The point of modulation is shown by opposing arrow heads. In allogenic engineering, state 2 is a new engineered resource such as a burrow that usually can be used immediately. In biotic engineering, state 2 is an activated but incipient resource such as a pollinated flower or dispersed seed or spore that may be structurally no different from the state 1 condition.

In the more complex case, (b), the products of state 2 modulate the flow of one or more resources to other species. Such modulation may be rapid if state 2 resources have been engineered allogenicly, but slow if engineering has been biotic and is contingent on growth of plant or fungal tissue. Jones et al. (1994, 1997) discussed additional types of allogenic and autogenic engineering, but these do not appear relevant to rodents. 'Biotic engineering' is used for the first time here.

plant community structure and heterogeneity, perhaps promoting species richness over time (Klaas et al. 1998).

Like their smaller counterparts, prairie dogs (1 kg) also modulate resource flows to other species by digging. Research on the best-studied species, *Cynomys ludovicianus*, shows that colonies develop on deep, productive soils where flooding is unlikely, and range in size from tens to hundreds of hectares (Dahlsted et al. 1981; Hoogland 1994). Up to 300 burrows may occur per hectare, with soil mounds 1–2 m diameter surrounding each burrow entrance (Whicker and Detling 1988). Digging affects soil structure and compaction, increases drainage and, with grazing by prairie dogs, the cycling of nitrogen and other nutrients (Coppock et al. 1983). Although grazing and engineering effects have not been disentangled in studies of *C. ludovicianus*, both probably contribute to extensive patterning of plant communities within prairie dog colonies. In mixed-grass prairie, Coppock et al. (1983) showed that grasses decreased in biomass with colony age whereas forbs and dwarf shrubs increased; nitrogen in graminoid shoots also peaked in long-established colonies. The modified habitats produced by prairie dog excavations favour increased local abundances and diversity of open-plain birds but decreased species richness of small mammals (Agnew et al. 1986). Interestingly, colony sites also contain higher densities of soil nematodes than undisturbed areas (Ingham and Detling 1984), perhaps reflecting greater ease of establishment in loosened soil.

Burrowing and tunnelling activities by fossorial rodents such as mole-rats displace

large volumes of soil and often result in the creation of surface mounds. These surficial structures resemble the mounds of pocket gophers and prairie dogs in size and composition, and have usually similar effects on nutrient status, water flow and organic content (Jarvis and Sale 1971; Cox and Gakahu 1985; Cox et al. 1987). Cox and Gakahu (1985) showed that coverage of forbs and shrubs on mima mounds of *Tachyoryctes splendens* was more than double that on inter-mound plots, whereas coverage of grass and *Acacia* trees was much reduced. These authors also noted a correlation between the activity areas of mole-rats and a fungus-gardening termite—*Odontotermes* sp., and suggested that termites preferentially use the rich organic deposits in mole-rat nest chambers to establish fungus gardens. A wide range of invertebrates has been documented using the nest mounds of the blind mole-rat *Spalax ehrenbergi* (Heth 1991). However, it is not clear here whether mound use represents a simple case of allogenic engineering, or a more complex case where mounds modulate food or other resources that sustain the invertebrate communities. Further examples of fossorial or semi-fossorial rodents modulating resource flow for other species by their burrowing activities occur within the Microtinae, Octodontidae and Heteromyidae (e.g. Chew and Whitford 1992; Contreras and Gutiérrez 1991; Gómez-García et al. 1995; Borghi and Giannoni 1997). A useful review is provided by Huntly and Reichman (1994).

Nest structures that divert resource flow represent a further class of examples of complex allogenic engineering. Beaver dams are the most conspicuous examples of such

structures; similar but less extensive nests are made by muskrats *Ondatra zibethicus* and occasionally by *Myocastor coypus* (Ebenhard 1988).

Beaver dams are constructed of young and mature trees that the animals cut themselves, as well as sediments and other debris. The North American beaver, *Castor canadensis*, builds some 2–16 dams per kilometre of stream, with small dams containing 4–18 m³ and larger dams >100 m³ of wood (Naiman et al. 1986, 1988). The major effect of dams is to alter the stream channel by impounding water, creating patch bodies (sensu Johnston and Naiman 1987) of water, sediment, aerobic soil beneath the pond and anaerobic soil in deeper strata. The surrounding riparian zone is also affected by damming, with stream widths sometimes increased by an order of magnitude from their original condition (Naiman et al. 1988). Because of the changed hydrological regime and the additional effects of beaver herbivory, patch bodies show dramatically different fluxes of carbon, nitrogen and energy compared with unaltered streams. Impoundments usually have relatively low inputs of carbon, but high standing stocks and outputs (Naiman et al. 1986); significant fluxes arise from release of methane (Naiman et al. 1991; Yavitt et al. 1992). Impoundments have been shown further to enhance accumulation of nitrogen in sediment by 9–44 fold compared with undisturbed streams (Francis et al. 1985). The effects of impoundment on pH, dissolved oxygen, fluxes of energy, other nutrients and ions have been much studied for *C. canadensis* in many parts of its range (e.g. Wilde et al. 1950; Hodkinson 1975; Pinay and Naiman 1991; Naiman et al. 1994)

and, to a lesser extent, for the related *Castor fiber* in Europe (Cirimo and Driscoll 1993; Macdonald et al. 1995).

The physical structure of beaver dams, and particularly the effects of dams on resource flows, have important consequences for aquatic and terrestrial animals and riparian vegetation. In the short term (years) impoundments may kill streamside trees and provide nest or roost sites for volant vertebrates following formation of hollows. In the longer term (decades to millenia), impoundments are likely to be colonised by wetland plants and follow successional pathways that may lead to meadows, bogs or wetlands (Figure 2). The relative roles of beaver engineering and other physical processes such as erosion, sedimentation and fire in directing particular pathways remain unclear, but likely differ between regions (Naiman et al. 1988, 1994; Johnston 1995).

Damming produces a shift from lotic (fast flowing) to more lentic (still-water) conditions, especially in higher order streams. Among aquatic invertebrates, this shift favours collector and predator species such as tubificid worms, clams and dragonflies over shredder and scraper species such as blackflies, scraping mayflies and net-spinning caddisflies (McDowell and Naiman 1986). However, lotic taxa may still be represented highly on the dam walls, perhaps because the dam acts as a net that traps drifting lotic fauna (Clifford et al. 1993). Among fishes, lotic taxa give way similarly to still-water specialists in beaver impoundments. Species richness and composition differ in dammed headwater and lower-order streams and vary also with age of the impoundment (Keast and Fox

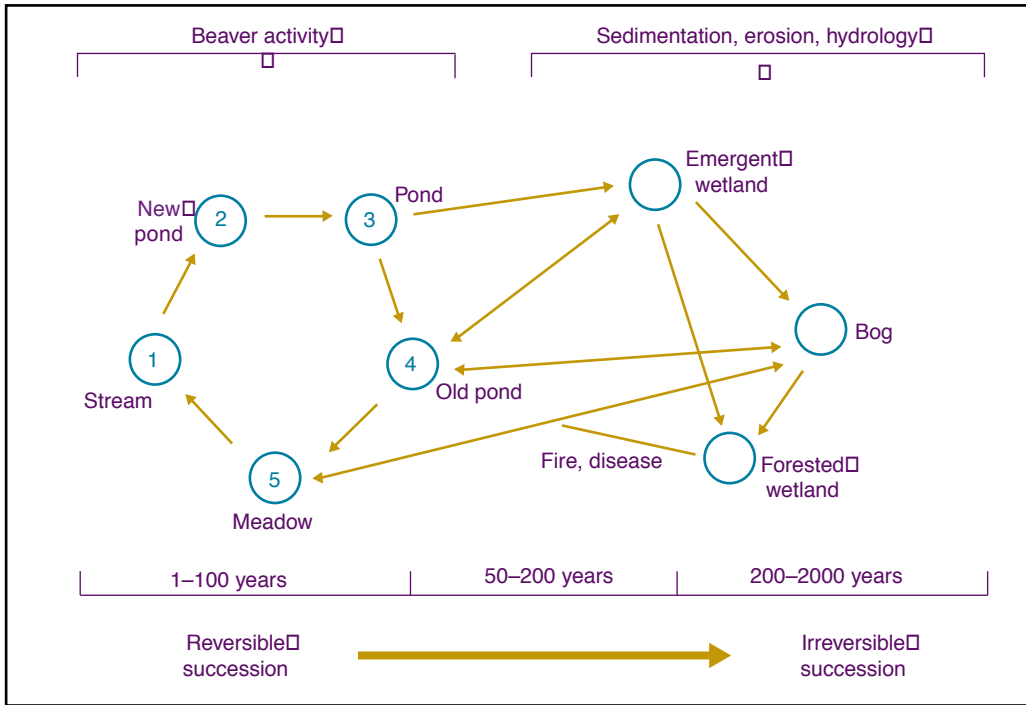


Figure 2. Potential effects of beaver (*Castor canadensis*) on vegetation and landscape patterns, based on work by R.J. Naiman and colleagues in the boreal forests of northern Minnesota (after Naiman et al. 1988).

1990; Hägglund and Sjöberg 1999; Snodgrass and Meffe 1998).

Descriptive and experimental studies have suggested further that beaver ponds act as reproductive source populations for fish whereas adjacent streams act as sinks (Schlosser 1995). If so, beaver dams may be seen as important components of fish metapopulations at catchment or larger spatial scales.

The engineering activities of beavers may, finally, have subtle indirect effects on terrestrial invertebrates. Martinsen et al. (1998) have shown recently that resprout growth from beaver-cut cottonwood trees (*Populus fremontii* and *Populus angustifolia*) is attractive to a specialist leaf beetle,

Chrysomela confluenta. The beetles sequester phenolic glycosides from the cottonwood leaves and use them as a means of predator defense. Martinsen et al. (1998) asserted further that habitat mosaics created by beaver activity increase the diversity of arthropods and perhaps higher vertebrates as well, but provided no evidence in support of this claim.

A final class of examples of complex allogenic engineering is the surface digging activity of rodents that results in accumulation of organic material and diversion of water flow. Gutterman (1982) showed that the diggings of Indian crested porcupines, *Hystrix indica*, accumulate seeds and other organic matter, and provide

microhabitats favourable for the germination and establishment of certain species of plants. Diggings are more suitable for germination in protected than exposed habitats, apparently because they allow runoff of rainfall for longer periods (Gutterman and Herr 1981; see also Yair and Rutin 1981). Steinberger and Whitford (1983) presented similar findings from their work on the surface digging activities of desert heteromyids.

Studies of larger mammals such as brush-tailed bettongs (*Bettongia penicillata*) and grizzly bears (*Ursus arctos horribilis*) indicate that surface digging activity can dramatically decrease soil water repellency and enhance levels of mineral nitrogen (Garkaklis et al. 1998; Tardiff and Stanford 1998). Such effects might be predicted also from the digging activity of larger rodents, but do not appear yet to have been documented.

BIOTIC ENGINEERING

Dispersal of seeds and spores

Although movements of seeds or spores from one place to another constitute biotic engineering as defined here, the phenomenon is ecologically more relevant after growth of the embryonic tissue has become sufficient to modulate resource flow to other organisms. Movement of seeds by rodents is well established. In some species, such as tropical squirrels, seeds are ingested and later excreted elsewhere in the animals' home ranges (Emmons 1992; MacKinnon et al. 1996). In many other species, seeds are collected and cached, or hoarded, for later consumption (Gurnell 1983; Reichman and Price 1993). Seeds often survive caching to

germinate and become established (Vander Wall 1990), but the role of rodents as dispersal agents remains poorly known. In one particularly instructive recent study, Vander Wall (1997) showed that some 80% of piñon pine (*Pinus monophylla*) seeds, placed experimentally on the ground beneath trees, were gathered by rodents. Radioactively labelled seeds were mostly cached, either in scatter-hoards or larders, at distances up to 38.6 m from the source. Over a third of caches occurred beneath shrubs; these appeared to favour establishment, and served as nurse plants for young pines. Vander Wall (1997) demonstrated seed caching by four species of rodents in captivity—*Peromyscus maniculatus*, *Peromyscus truei*, *Perognathus parvus* and *Dipodomys panamintinus*—and inferred that these were the main seed dispersers in his field site too.

Fossorial rodents have also been demonstrated to move the storage organs of geophytic plants, often concentrating them within mounds or burrow systems (Galil 1967; Gómez-García et al. 1995). Sprouting of storage organs at their new locations suggests that rodent-induced dispersal can be effective (Borghgi and Giannoni 1997).

Dispersal of fungal spores by rodents has received relatively little attention. Many species eat the fruiting bodies of fungi (e.g. Maser et al. 1978; Claridge and May 1994; Tory et al. 1997), but it has not always been shown that ingested spores remain viable. However, spores usually remain structurally intact following passage through rodent guts, and Claridge et al. (1992) showed that spores recovered from faeces of another mammal, *Potorous tridactylus*, developed ectomycorrhizae on the roots of two species

of *Eucalyptus*. Importantly, the fungi ingested by many species of rodents are hypogean and form mycorrhizal associations with the roots of trees and other vascular plants, thus potentially assisting plant growth. Future research should seek to clarify the extent to which rodents disperse viable spores, and also quantify their contribution to regeneration and development of forest environments (Reddell et al. 1997; Tory et al. 1997).

Pollination

Bats and primates that visit flowers for food are often effective pollinators, especially in tropical and arid habitats (Fleming and Sosa 1994). The effectiveness of rodents as pollinators, however, is less clear. Many species visit flowers and could transfer pollen that has lodged in the fur (Recher 1981). Examples include arboreal species such as dormice—*Muscardinus avellanarius* (Bright and Morris 1996), tree-rats—*Solomys* spp. (D. Fisher, pers. comm.) and desert rodents in the genus *Pseudomys* (C.R. Dickman, personal observation). Few studies have shown that rodents carry significant loads of pollen between flowers (Lumer 1980; Wiens et al. 1983; Van Tets 1997) and none has yet distinguished the relative importance of rodents as pollinators compared with other taxa (Carthew and Goldingay 1997). As Fleming and Sosa (1994) point out, the genetic effects of even the more conspicuous mammalian pollinators and frugivores on plant populations have been rarely investigated; there is much scope for new research.

TROPHIC IMPACTS OF RODENTS

Rodents take a very broad range of plant and animal foods, so their potential effects on prey species and communities could be pervasive. Some species of rodents specialise in taking only one or two prey taxa (e.g. the heteromyid *Liomys salvini* specialises seasonally on seeds of *Enterolobium cyclocarpum*, a Central American leguminous tree; Janzen 1981), whereas others are broadly omnivorous (e.g. many species of Australian desert rodents; Murray et al. 1999). The direct impacts of rodent predation have a long history of study, especially with respect to effects on crops and other vegetation, but indirect impacts have been recognised increasingly in recent work. This is a vast topic that can only be treated superficially here.

The best estimates of rodent impact on food resources are from agro-ecosystems in different parts of the world (e.g. Buckle and Smith 1994; Singleton and Petch 1994; other chapters in this book). In these simplified environments, rodents can reach extraordinary densities (e.g. >3,000/ha for *Mus domesticus*; Caughley et al. 1998) by eating one or a very few types of food, and cause great damage to crops. Both native and introduced species of rodents can become pests, and achieve higher densities in crop systems than in the natural environment. Very high densities may be achieved transiently by rodents in unmodified environments, often following drought-breaking rains (e.g. 1,200/ha for *R. villosissimus*; Palmer 1886), but impacts on food resources under these conditions have been little-studied (Batzli and Pitelka 1970; Noy-Meir 1988).

In natural or little modified environments, rodents may have local or broad-scale effects on vegetation. Below ground, herbivory often modifies plant community structure, reducing the standing crop but increasing local species richness (Andersen 1987; Huntly and Reichman 1994). Selective foraging on individual plant species may benefit certain life-history stages such as seeds or small bulbs by reducing intraspecific competition (Contreras and Gutiérrez 1991), but can also depress plant biomass and flower production (Reichman and Smith 1991) or even result in local plant extinction (Cantor and Whitham 1989). Above ground, rodent herbivory (including frugivory and granivory) has even more dramatic effects on vegetation. Selective foraging may again deplete favoured species in local areas, and alter trajectories of plant succession (Johnston and Naiman 1990). Generalist foraging has been shown to have pervasive effects on life form, growth, allocation of nutrients and energy stores within plants, as well as on the physical structure and species composition of plant communities (Batzli and Pitelka 1970; Brown et al. 1979; Brown and Heske 1990; Holland et al. 1992; Jefferies et al. 1994; but cf. Gibson et al. 1990). Although this topic is too broad to discuss fully here, the effects and mechanisms by which herbivores affect plant communities have been reviewed by Crawley (1983) and Huntly (1991), and the induction of plant defenses has been reviewed by Karban and Myers (1989). Short-term feedbacks and longer-term coevolution between herbivorous rodents and plants also have been discussed in detail elsewhere (Crawley 1983; Coley and Barone 1996; Pastor et al. 1997).

Perhaps because the impacts of rodents on vegetation are often obvious and economically relevant, the effects of rodents on other food groups have been seldom studied. However, limited experimental evidence suggests that high density populations of omnivorous species may deplete the local richness of epigeal invertebrates (Figure 3). On Boullanger Island, Western Australia, invertebrate species richness increased on average by 3% on plots from which *M. domesticus* had been removed, in contrast to a decrease of 18% on control plots (Figure 3a). Increases occurred primarily in beetle and spider species, which the mice ingested (C.R. Dickman, personal observation). In urban woodland in the United Kingdom, invertebrate species richness increased similarly by 83% on plots from which *Apodemus sylvaticus* had been removed, compared with only a 32% increase on control plots (Figure 3b). Increases occurred in species of beetles, spiders and snails—taxa found commonly in the diet of urban *A. sylvaticus* (C.R. Dickman, personal observation). Primarily insectivorous rodents such as grasshopper mice (*Onychomys* spp.) likely affect individual species and communities of invertebrates at times also, but evidence is lacking.

In circumstances when omnivorous rodents have been introduced to new environments, they have sometimes had dramatic effects on populations of invertebrates and small vertebrates. On Lord Howe Island, for example, an endemic phasid, *Dryococelus australis*, disappeared following establishment of *Rattus rattus*, while numbers of two species of island snails were severely depressed (Smithers et al. 1977).

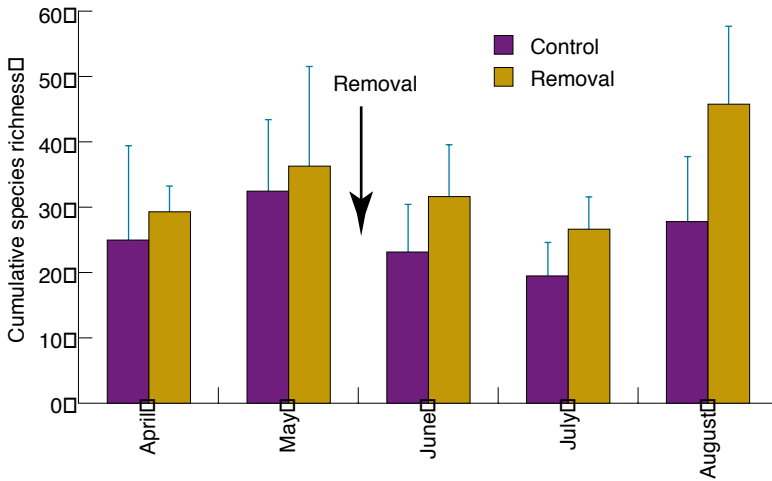
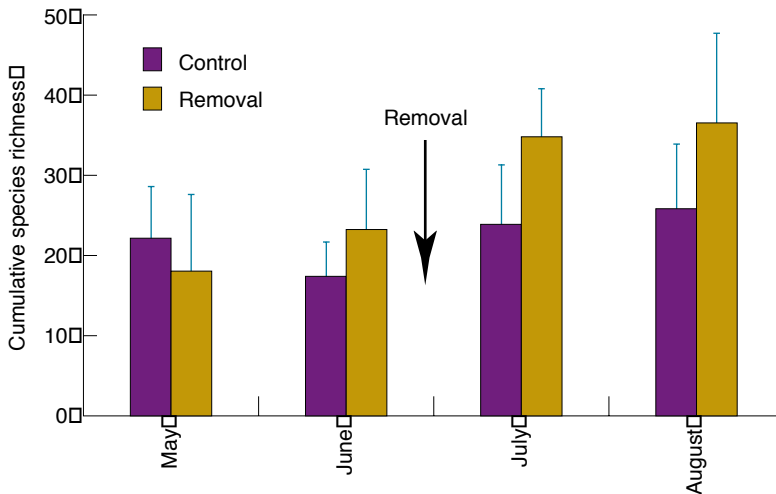


Figure 3.

Effects of rodent removal on species richness of invertebrates.

(a) *Mus domesticus* was removed from trapping plots on Boullanger Island, Western Australia, and invertebrates sampled by pitfall trapping before and after removal in both the removal and control sites ($n = 3$ control, 3 removal plots, means shown \pm standard deviation (SE); mean before/after ratios of species richness differed significantly between control and removal treatments, $P < 0.05$).



(b) *Apodemus sylvaticus* was removed from trapping plots in urban woodland in Oxford, United Kingdom, and invertebrates sampled in the same manner as in (a) ($n = 3$ control, 3 removal plots, means shown \pm SE; mean before/after ratios of species richness differed significantly between control and removal treatments, $P < 0.01$). Methodological details are given in Dickman (1988), Dickman and Doncaster (1989; also unpublished data).

Extinctions and range contractions of many other species of large invertebrates and small vertebrates, including seabirds and flightless birds, have occurred on islands off the coast of New Zealand and throughout the Pacific following introductions of *R. rattus*, *Rattus exulans* and *Rattus norvegicus* (Steadman 1989; King 1990). Although rats appear to have been the only obvious threat introduced to some islands, in many cases their impact is difficult to distinguish from the effects wrought by other introduced species and by habitat change.

It remains equivocal also whether rat impacts were caused by predation, competition, introduction of diseases or other processes, although direct predation has been implicated by most authors (Smithers et al. 1977; King 1990; Atkinson 1996).

Finally, while most research has evaluated the direct trophic impacts of rodents, some recent work indicates that rodent foraging may have far-reaching indirect effects. In Californian grassland, Batzli and Pitelka (1970) showed that forb and grass cover increased in plots that excluded the herbivorous meadow vole, *Microtus californicus*, as compared with cover levels in control plots. An indirect effect of the vole exclusion was a dramatically increased abundance of the pillbug (*Armadillidium vulgare*) within two years; this species was apparently favoured by the denser vegetation or increased food resources that it contained. In analogous experiments, removal of *M. domesticus* from plots on Boullanger Island resulted in a 24% increase in litter depth within just three months, compared with a 16% decrease in litter depth on control plots over the same period (Figure 4).

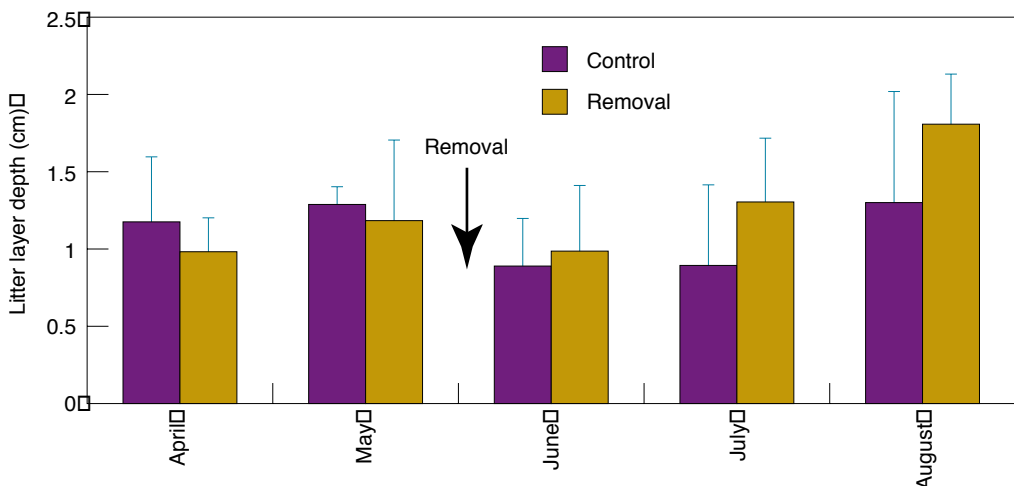


Figure 4. Effects of removal of *Mus domesticus* on depth of the leaf litter layer on Boullanger Island, Western Australia ($n = 3$ control, 3 removal plots, means shown \pm standard deviation; before/after ratios of mean litter depth differed significantly between control and removal treatments, $P < 0.01$). Further details are given in Dickman (1988).

Capture rates of the skinks (*Ctenotus fallens* and *Morethia lineocellata*) increased in the *Mus*-removal plots by up to 35% (C.R. Dickman, personal observation), presumably because of the increased shelter afforded by the deep leaf litter or the more diverse food resources that were available (Figure 3a). Over larger periods, rodent foraging can indirectly facilitate other taxa. In the Chihuahuan Desert, Thompson et al. (1991) demonstrated that the foraging activities and abundance of granivorous birds declined markedly in rodent exclusion plots over a period of 10 years. In the absence of rodents, especially kangaroo rats (*Dipodomys* spp.), litter accumulated and concealed seeds on the soil surface from the view of the visually foraging birds. In control plots by contrast, rodent foraging activities created areas of bare soil and trails, hence exposing seeds and facilitating access by birds. Brown and Heske (1990) considered kangaroo rats in the Chihuahuan Desert to be a keystone guild in recognition of their major direct and indirect effects on biological diversity and biogeochemical processes. More complex webs of direct and indirect effects of rodent foraging are suspected (e.g. Klaas et al. 1998), and will require much ingenuity to study and understand.

CONCLUSIONS

This review shows that rodents interact extensively with their physical, chemical and biotic environments, and that their activities have complex but often beneficial effects on other organisms across a broad range of spatial and temporal scales. This should not be surprising, because of the great species richness, abundance and

ubiquity of rodents in terrestrial environments.

With respect to the management of rodent pests, the review also allows the conclusion to be drawn that we must be more clever and more focused in our approaches to rodent control. In many regions, broad-scale application of poison remains the favoured control method (Buckle and Smith 1994; Singleton and Petch 1994). In the 1993 mouse plague in south-eastern Australia, for example, some 350,000 ha of cropland in South Australia alone were baited with the poison strychnine (Caughley et al. 1994). Such broad-scale campaigns may reduce the numbers of the target pest, but very likely decimate populations of non-target species (Dickman 1993), including those with potentially positive effects on the physical and biotic environment. In the wheat-growing areas of New South Wales, native rodents have been virtually eliminated by introduced species, changes in land use, and perhaps also by agrochemicals that are used to maintain the changes (Dickman 1993). It is clear that management of rodent pests will need to eschew its damaging reliance on chemical warfare and embrace sustainable, ecologically-based solutions. Heartening moves in this direction include fertility control (Chambers et al., Chapter 10), mortality control via predators or parasites that target pest taxa (Buckle and Smith 1994), and physical barrier methods that limit access of pests to crop areas (Singleton et al., Chapter 8).

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